The Social Structure and Behaviour of Western Lowland Gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo

Richard J. Parnell

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Declaration

I declare that the work undertaken and reported throughout this thesis is my own and has not been submitted in consideration of any other degree or award. I acknowledge the contribution of three research assistants who aided in the collection of some of the data.

R.J. Parnell

Abstract

Most of what we know of the socioecology and behaviour of gorillas comes from studies of mountain gorillas (*Gorilla beringei beringei*), despite their representing less than 1% of all gorillas in the wild. Western lowland gorillas (*Gorilla gorilla gorilla*) have received far less research effort, and difficulties in habituation have led previous studies to rely heavily on indirect trail evidence. This has prevented any in-depth comparison of social structure and behaviour between species. The discovery of swampy clearings frequented by western lowland gorillas in northern Congo has offered the first opportunity to obtain accurate demographic and behavioural data. This thesis reports on 6273 hours of observer presence at Mbeli Bai, which yielded 1681 hours of direct gorilla observation. Most data come from a population of 13 groups and 7 solitary silverbacks. Group size ranged from 2 to 16 (mean = 8.4, SD 4.3) which does not differ significantly from data published on most other populations. Female natal and secondary transfer were recorded, and male emigration from the natal group appeared universal (no multi-silverback groups were recorded). No evidence of sub-grouping or a fission-fusion grouping pattern was found. During intra-group interactions, no evidence was recorded of female philopatry, and silverbacks herded and intimidated females (especially new immigrants) to prevent emigration. Inter-unit interactions took place on only 42% of shared bai-use occasions, and levels of silverback agonism were much lower than in mountain gorillas, with peaceful mingling of groups recorded. Display behaviour was common, and two previously unrecorded agonistic displays (the splash display and the crest display) are described. No contact aggression between silverbacks was observed but evidence of wounding sustained in the forest suggests that the bai environment may inhibit such aggression. High visibility and the ease of silverback 'policing' are thought to create an unusually tolerant social dynamic, and as such, frequencies of certain social behaviours should probably be viewed as site-specific. The thesis offers the fullest account of western gorilla social structure and behaviour to date. Long-term monitoring of life history variables, if continued, will provide an unparalleled opportunity to understand the effects of habitat and food availability and more stochastic influences on western gorilla social structure, fitness, and survival.

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Publications and Presentations

Results from Chapter 4 have been published as:

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Data from Chapter 4 were also presented as:

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Results from Chapter 4 are also included in the following article:

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Results from Chapter 6 were presented at the Western Lowland Gorilla Conference, Max Plank Institute, Leipzig, May 2002, as:

Parnell, R.J. (2002). *Inter-Unit Interaction in Western Lowland Gorillas at Mbeli Bai, Congo.* A manuscript based on this is under review for a forthcoming book featuring papers from the conference.

Results from Appendix 7 have been published as:

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Data on gorilla food processing and handedness collected for, but not included in, this thesis are published in:

Parnell,R.J. (2001). Hand Preference for Food Processing in Wild Western Lowland Gorillas (*Gorilla gorilla gorilla*). *Journal of Comparative Psychology*, 115 (4): 365-375.

Popular articles describing results from the thesis include:

Parnell, R.J. (1999). Gorilla Exposé. *Natural History*, 108: 38-43.

Contents

Chapter 1

Introduction

From the earliest reports of the Carthaginian Hanno who explored the west coast of Africa around 2500 years ago to the work of Dian Fossey and other contemporary ape researchers, the similarities between gorillas and ourselves have made them a source of seemingly endless fascination. However, both scientific and public perception of the gorilla has changed dramatically both as new information from the field has come to light, and with shifts in our attitudes towards wildlife and other cultural mores. Hanno shows little of the dualism to come when describing his encounters with 'wild men' and '..women with hairy bodies..'. By the mid-nineteenth century, however, our fascination with apes was tinged with horror, with the gorilla seen as a bestial, savage shadow of humankind. Paul Du Chaillu (1861) encapsulates this in what is an otherwise relatively accurate description of a silverback western lowland gorilla encountered in the wild, "..and now truly he reminded me of nothing but some hellish dream-creature – a being of that hideous order, half man, half beast, which we find pictured by old artists in some representations of the infernal regions."; a perspective later amplified to mythical proportions in the 1933 film production "King Kong".

Over the course of the last century, however, western society's perception of many animals has been tempered and shaped by cultural influences such as the anthropomorphism of Walt Disney, and more latterly, the popularised fieldwork of primatologists such as Jane Goodall and Dian Fossey. The startling findings of these and other researchers have found an eager popular audience, many of whom have been happy to elevate nonhuman apes, and gorillas in particular, to a new mythical status; not one of horror and savagery, but that of the 'gentle giant'. The veneration of gorillas as new-age ambassadors for the planet now borders on the absurd, with, for instance, one recent televised documentary on western gorillas, suggesting that "maybe we ought to hope that we are more like these sensitive creatures rather than less; perhaps then there would be more hope for us". Somewhere between these two extremes lies the true nature of the gorilla, and the purpose of this thesis.

Taxonomy and distribution

Gorillas were first described to science by Savage and Wyman (1847) under the name *Troglodytes gorilla.* The genus was subsequently changed to *Gorilla* by Saint-Hillaire (1851). These were the apes now known as western lowland gorillas (*Gorilla gorilla gorilla*). In 1903, Matschie first described gorillas (shot a year earlier by Captain Oscar von Beringe) from the slopes of the Virunga Volcanoes, naming them *Gorilla beringei.* Matschie was a prolific taxonomist and, in addition to several other gorilla sub-species, described *Gorilla diehli* from Cameroon, and in 1914 proposed a new species, *Gorilla graueri*, from what is now eastern Democratic Republic of Congo (D.R. Congo).

Several subsequent systems have been proposed, but the most widely accepted taxonomy of recent years has been that of Groves (1967, 1970) which in its final form described one genus and three sub-species. This system, based on a multivariate analysis of the morphological characteristics of skulls, recognised the following sub-species: *Gorilla gorilla gorilla* (western lowland gorilla), *Gorilla gorilla graueri* (eastern lowland, or 'Grauer's' gorilla), and *Gorilla gorilla beringei* (mountain gorilla). However more recent genetic and morphological analyses (e.g., Ruvolo et al.,1994; Garner & Ryder, 1996; Stumpf et al., 1998) have prompted the proposal that the genus be reorganised into two species, with four sub-species. While still in a transition phase, this nomenclature has been largely accepted by most gorilla researchers and is used throughout this thesis. Under the proposed system, western gorillas and eastern gorillas become separate species (*Gorilla gorilla* and *Gorilla beringei*). Within western gorillas, two sub-species are recognised; these consist of the majority of western gorillas, ranging in Cameroon, Congo, Gabon, Central African Republic (C.A.R.), Cabinda and Equatorial Guinea, known as western lowland gorillas (*Gorilla gorilla gorilla*), and the Cross River gorilla (*Gorilla gorilla diehli*), which survives in eight or nine tiny and isolated sub-populations in the Nigeria-Cameroon border region. Within western lowland gorillas, recent genetic analysis points to three distinct subgroups: the gorillas of Northern Congo and C.A.R., those from

Equatorial Guinea, and gorillas in Gabon and south central Congo (Clifford et al., 2002). Eastern gorilla populations, which are separated from those in the west by approximately 750km, comprise the eastern lowland gorilla (Grauer's gorilla – *Gorilla beringei graueri*) which ranges in the Itombwe Mountains, Mt. Tshiaberimu, Kahuzi-Biega, and a few other areas of the eastern D.R. Congo lowlands, and the mountain gorilla (*Gorilla beringei beringei*) with two small populations centred around the Virunga Volcanoes. Within *G. b. beringei*, the debate as to whether the northern population or 'Bwindi gorillas' should be classed as a sub-species separate from the Virunga population to the south is as yet unresolved (e.g., Sarmiento et al., 1996).

The historical factors influencing the current distribution of gorilla populations remains unknown. Groves (1971) proposed that gorillas originated in montane habitats prior to expanding west into lowland forest. His reasoning was based on ecological and morphological observations (gorillas are at higher densities in montane habitats than lowland ones, indicating that they are better adapted to these areas; gorilla morphology is congruent with a species adapted primarily to a montane habitat; greater morphological variation in eastern gorillas suggests that they have been isolated from one another for a longer time and are thus more likely to represent the original stock for later dispersal westwards). However, Fay (1997) rejects each of these factors as evidence for an east-west dispersal and in some cases cites more recent data contradicting them. Fay proposes a western lowland origin for the gorilla, citing the importance of lowland refugia (e.g., Colwyn et al., 1991; Maley, 1996) during dryer climatic periods, in creating the greater genetic diversity of western gorillas. Gorillas have undergone many periods of climate and subsequent habitat change in what is believed to be the 2.5 million years since the divergence of the subspecies. Current gorilla distribution is likely to be linked to recent changes in forest distribution due to climate change, human disturbance, and restrictions to dispersal by large rivers (Fay, 1997).

Current status of the gorilla

In 1984, Tutin and Fernandez published the results of a three year country-wide census of western lowland gorillas in Gabon. To the surprise of many researchers, the population of gorillas in Gabon was estimated to be approximately 35,000. Previous estimates, based primarily on the mistaken belief that gorillas were limited in their distribution by the availability of secondary vegetation, had predicted that as few as 9,000 western gorillas survived in the wild (Gartlan unpubl. report; Harcourt, pers. comm.; cited in Tutin & Fernandez, 1984). Such findings exemplify the dangers of predicting the density and abundance of a species without an adequate knowledge of its ecology. Although subsequent censuses have been conducted within the western gorilla's range, the scale of these operations, variation in methods, and a lack of quality control with regard to observer bias probably means that the current estimates of 100,000 gorillas (e.g., Harcourt, 1995) approach reality, but lack precision. IUCN rates western lowland gorillas as 'endangered' (Hilton-Taylor, 2000). The current status of the Cross River gorilla is better known, given that only a few isolated sub-populations remain. Current estimates give between 190 and 250 individuals (e.g., McFarland, 2002; Oates, pers. comm.) and the sub-species is IUCN listed as 'critically endangered'. Grauer's gorilla is IUCN listed as endangered, and a figure of 17,000 individuals has been suggested (Hall et al., 1998). However, these figures refer to estimates prior to the widespread killing of gorillas in the Kahuzi-Biega National Park beginning in 1999. Numbers may now be as low as 3000 (Yamagiwa, pers.comm.). The two critically endangered populations of mountain gorillas consist of approximately 360 'Virunga' gorillas (Kalpers et al., *in press*) and approximately 300 'Bwindi' gorillas (McNeilage et al., 2001).

Threats and conservation

The campaign to conserve the mountain gorilla has been among the most widely publicised of any conservation program. Census results in the early 1970's indicated a dramatic decline in gorilla numbers (Harcourt & Groom, 1972) and prompted efforts to identify the causes. Among those identified were poaching, habitat loss and disturbances caused by war and incursion by cattle herders. In response, anti-poaching efforts were stepped up, and critically, a broad-based campaign was initiated (The Mountain Gorilla Project) which began an education program among local people and encouraged the development of gorilla tourism. Tourism in particular gave a monetary value to the protection of the gorillas, becoming the third highest source of revenue for Rwanda (Tutin & Veder, 2001). As a testament to the success of these programs (and the dedication of Park staff), gorilla numbers have risen since the 1970's, and even years of catastrophic civil war resulted in relatively few gorilla deaths. However, civil unrest remains a potent threat to mountain gorillas, as does the menace of human-borne disease resulting from increased human presence within the gorillas' range.

As mentioned earlier, eastern lowland gorilla numbers are believed to have been decimated in the Kahuzi-Biega National Park in D.R. Congo. The hunting pressure behind this was generated by large scale incursions into the Park by illegal miners, extracting the precious mineral Coltan (Yamagiwa, pers. comm.). Over half of all gorillas in the better protected highland sector of the Park have been killed, including most members of four habituated tourist and research groups. The situation in the lawless, and much larger lowland sector is thought to be even worse, and it is predicted that the eastern lowland gorilla may now be in critical danger of extinction (Yamagiwa & Kahekwa, 2001).

The small isolated populations of Cross River gorillas clearly face many of the same threats as mountain gorillas, and are extremely vulnerable to disease, hunting and habitat loss. Only with the recent re-classification of these populations as a separate sub-species has greater world attention been paid to their vulnerability. Current conservation efforts centre around establishing goodwill among local people, creating more effective protected areas and minimising human disturbance (e.g., Oates, 2000).

Western lowland gorillas, being the most numerous and widespread of the gorillas, face a consequently wide range of threats. Chief among these is illegal hunting for bushmeat. All gorillas are protected by international wildlife laws, but range countries frequently lack the resources, and in some cases, the political will to effectively enforce them. The proliferation of commercial logging activities across the range of western gorillas has provided an ideal conduit for vast quantities of bushmeat to reach its main market in the larger towns and cities. The creation of new roads into previously isolated forest regions, the introduction of sometimes thousands of people (forestry workers) into formerly uninhabited areas, and the steady flow of logging trucks leaving the forest for the larger population centres all contribute to a lethal cocktail for gorillas and other forest wildlife. Efforts are now being made to check the bushmeat trade, both voluntarily by some logging companies, and also through improved law enforcement at a national level, but the trade in bushmeat continues at wholly unsustainable levels. Another major threat to western gorillas is disease. Although international conservation efforts inevitably focus on attainable goals such as the control of the bushmeat trade, natural threats may also have catastrophic effects on gorilla abundance. For instance, it is now believed that the virus Ebola may have killed many thousands of gorillas in the north-east of Gabon. Sixty-nine gorilla deaths have been confirmed as attributable to Ebola (Abernethy, pers. comm.) but it is estimated that up to 80% of all gorillas in the Minkebé region of Gabon may have succumbed to the disease since 1996. Little can be done to protect gorillas from such occurrences, but their presence reinforces the need for adequate protection from threats of human origin. Fundamentals to achieving this are first and foremost, adequate law enforcement, both within and outside of protected areas. Secondly, and as an aid to conservation management, a long-term monitoring program is essential if population trends are to be adequately measured.

The history of gorilla study

Each of the main data chapters in this thesis begins with a review of the literature on the subject matter in question. However, in order to place the current study within a general contextual framework, it may be helpful to briefly review the development of gorilla study in the second half of the twentieth century.

The first real landmark study on wild gorillas was undertaken by George Schaller between 1959 and 1960. This was a broad-based study of all aspects of the natural history of the mountain gorilla (Schaller, 1963) and the first to realise the potential of habituation. Many of the methods used by Schaller have become routine, and many of his findings have been upheld by later and more detailed studies. The name Dian Fossey, more than any other, is synonymous with the study and conservation of mountain gorillas. Fossey created the Karisoke research site in the Rwandan sector of the Virunga volcanoes in 1967, and spent most of her life there before being killed in 1984. The findings of Fossey and Harcourt (e.g., Harcourt, 1978, 1979a, 1979b; Fossey, 1974, 1983; Fossey & Harcourt, 1977; Harcourt et al., 1976, 1980) dominated gorilla research in the seventies and early eighties, providing the basic blueprint of gorilla social organisation, based on largely single male groups, male and female dispersal, male competition for females, stable family groups, and weak bonds between females. In the eighties, research broadened and more longitudinal results became increasingly important, highlighting considerable variation in life-histories, group types and social dynamics (e.g., Fossey, 1983; Yamagiwa,1987a; Watts, 1989). The influence of ecological variables on social structure also became a focus of research effort during this period (e.g., Watts, 1984, 1985, 1990b). In the nineties, interactions within and between groups were studied further (e.g., Watts, 1992; Sicotte, 1993, 1995) and variation in the role and life-histories of males within gorilla society were explored (e.g., Robbins, 1995, 1999; Watts, 2000).

This cursory review of research at Karisoke (*see* Stewart et al., 2001, for a fuller review) brings the reader to the period between the mid-nineties and the present, during which time, due to the security situation in the region, research has been largely confined to the monitoring of key groups and the recording of major demographic events such as births, deaths and emigrations. Were normal research an option, the naïve student might well ask what topics remain to be studied on the Virunga mountain gorilla. In the late seventies and early eighties, the student of western gorillas would be more likely faced with the problem of where to start. Despite representing over 90% of all gorillas, in 1980, three years prior to the publication of 'Gorillas in the Mist', virtually nothing was known about the western lowland gorilla. Earlier reports (e.g., Jones & Sabater Pi, 1971; Sabater Pi, 1977) offered insights into diet and group size, but were based on somewhat disturbed populations, and were contextually set during a period when western gorillas were largely thought to be restricted to secondary forest-types.

The census work of Tutin and Fernandez (1983) helped to alter this perception, and clearly provided a more legitimate estimate of numbers and distribution, but it was not until the establishment of the Station d'Etudes des Gorilles et Chimpanzés (S.E.G.C.) in the Lopé Reserve in 1984 that long-term records of feeding, ranging, and nesting behaviour began to accumulate. Throughout the eighties and early nineties, research at Lopé highlighted the diversity and variation in western gorilla diet. In particular, research focused on the considerable importance of fruit in the diet and its influence on ranging and seasonal patterns of habitat use (e.g., Rogers et al., 1988, 1990; Williamson et al., 1990; Tutin & Fernandez, 1993a; Tutin, 1996). Much to the regret of the researchers, however, gorillas at Lopé proved resistant to efforts at habituating them to the levels achieved in the Virungas (Tutin and Fernandez, 1991), and only one group became relatively tolerant of observer presence. As such, little data on social behaviour were forthcoming and the inherent errors present in nest-site data (Tutin et al., 1995) meant that social structure could only be loosely described for the population.

Following the pattern of Lopé, several other ecology-based studies have been initiated (e.g., Ndoki - Nishihara, 1994, 1995; Bai Hokou - Remis, 1994; Goldsmith, 1996b; Ndakan - Fay, 1997; Mondika - Doran & McNeilage, 1998) which have all to a greater or less degree addressed questions regarding social organisation and structure, dietary patterns, and ranging. While secondary trail evidence and nest-counts can be used as tools in this endeavour, they are open to error, both in terms of data collection and interpretation, and the social findings of such studies should be viewed with some caution. More recently, some gorilla groups have begun to respond well to habituation (e.g., Bermejo, 1997; Cipolleta, 2001). While these studies and others like them should provide invaluable information regarding intra-group behaviour, the extremely labour-intensive task of habituation is likely to place firm limits on the numbers of groups that can be studied, thus preventing them from addressing questions relating to intra-population variability in social structure and behaviour, and severely limiting the study of inter-group interaction.

Thus, by the early nineties, a relatively complete picture of mountain gorilla socio-ecology was available, and a broad consensus had been reached regarding food availability and diet in western lowland gorillas. Both behavioural and ecological studies had been undertaken on eastern lowland gorillas (e.g. Casimir, 1975; Goodall, 1977; Yamagiwa, 1983) which permitted some degree of comparison with mountain gorilla socio-ecology, but, as eastern lowland gorillas inhabit a range ecologically somewhat overlapping that of the mountain gorilla and the western gorilla, few conclusions could be drawn.

Unquestionably the missing link to a more complete understanding of the effects of habitat type on social organisation and behaviour in gorillas was reliable demographic and behavioural data on highly frugivorous western populations. Mountain gorillas have year round access to abundant high quality herb foods (e.g., Schaller, 1963; Fossey & Harcourt, 1977; Watts, 1984), and it is proposed that intra-group relationships reflect this through a low level of scramble and contest competition between individuals, the lack of strong female dominance hierarchies, and other factors (Harcourt, 1979a; Watts, 1985, 1994a, 1994b, 1996). Western lowland gorillas, by contrast, have been shown generally to occupy ranges with reduced herb densities. This, plus the utilisation of patchy and potentially monopolisable fruit resources, predicts that females in particular may face greater costs from feeding competition which in turn may have significant effects on day-range length, group-spread and cohesion, inter- and intra-group interactions, and pivotally, transfer decisions (*see* Doran & McNeilage, 2001, for review). For some time, it seemed that traditional methods of study would not be adequate to the task of providing data allowing hypotheses regarding the effects of food availability and competition on social structure to be tested.

However, in the early nineties, the discovery of open, swampy clearings frequented by gorillas in the forests of northern Congo permitted clear and prolonged observation of whole western lowland gorilla groups for the first time (Olejniczak, 1994, 1997; Fay, 1997; Magliocca et al., 1999). Full-time data collection began at Mbeli Bai, Nouabalé-Ndoki National Park, in 1995, and continues to the present. While other bai studies have been initiated since the start of the Mbeli study (e.g., Langoué Bai, Gabon; Maya Nord Bai, Lokoué Bai, and Guga Bai, Congo), Mbeli remains the longest running and most detailed study undertaken.

Aims of the current study

The primary aims of this study are as follows:

1. To describe the group size, composition and number of gorilla social units (groups and solitary males) visiting the clearing.
2. To record the type and frequency of demographic changes within those units.

3. To describe the social interactions of gorillas using the clearing, both within groups, and between units.

It is hoped that data on these topics will not only provide the largest and most accurate description of a western lowland gorilla population to date, but will permit a preliminary exploration into the question of whether the social organisation of the species differs significantly from that of the mountain gorilla. Predictions on what differences may be likely, based on past and current models of socioecology (e.g., Wrangham, 1980; Sterck et al., 1997) are introduced under each new chapter heading. Differences in social organisation are likely to impact considerably upon the nature of all adult interactions, and thus interaction data will also be used to examine for possible differences between the western lowland and mountain gorillas.

While recognising the potential of bais for facilitating the accurate description of social organisation, it is important to recognise that these areas may, in themselves, have an impact upon the social lives of the gorillas using them. This may in some cases prove to be a confounding variable in the interpretation of interaction data, but should nevertheless offer additional clues to the motives and imperatives of the gorillas. The phenomenon of bai-use is new to gorilla research and remains largely unrecorded. As well as being likely to provoke the exhibition of new behaviours specific to the habitat, the exceptional observation conditions at bais should allow more common behaviours to be recorded and described with greater accuracy and insight. Within the realm of display behaviour in particular, important physiological adaptations that may be inconspicuous to observers in the forest, may become more evident when viewed in the open, well-lit setting of a bai.

Summary of chapters

Chapter 2 introduces the Nouabalé-Ndoki National Park and the Mbeli Bai study site, describing the vegetation, climate, and other bai-users. The general methodology of the study is described, including notes on age-classing of gorillas, recording methods and statistical analyses.

Chapter 3 develops some of these themes with particular reference to patterns of bai utilisation in gorillas. Daily influences on bai-use such as climate, insect pests, encounters with other species and food intake are explored. Seasonal influences including climate and fruit availability are examined, and visit frequency is explored as a possible indicator of ranging profiles for the groups using the bai.

Chapter 4 describes the social structure of all units using the bai during the study period. Group size and composition are presented and compared with data from other western lowland, eastern lowland, and mountain gorilla sites, as is the ratio of solitary males per population. Time-line charts present the demographic changes occurring in the Mbeli groups during the study and issues relating to group stability and group type are raised. The duration of the study precludes a detailed analysis of reproductive success, but such data as are available are presented. Finally the chapter presents data and discusses male and female dispersal patterns in the Mbeli population.

Chapter 5 presents an analysis of dyadic adult interactions within groups. Few data are available for this subject, and as such, the chapter focuses on the presence or absence of various behaviours that may be considered 'indicators' of the status of the social system in operation. Of particular significance are interactions between adult females and between adult females and silverbacks.

Chapter 6 draws on a larger data set to explore inter-unit interactions at Mbeli. This is a three-level analysis that looks first at the overall behaviour of units with regard to their frequency of bai-sharing, and the nature of their interactions with other units. Secondly, the behaviour of silverbacks in particular is examined as an indicator of the underlying levels of tolerance and agonism between units. Thirdly, the individual dyadic interactions of all age/sex-classes are examined. The chapter then considers the degree to which interactions observed in the bai can be thought of as representative of those taking place in the forest.

Chapter 7 brings together the main findings of the previous chapters in a more homogenous consideration of gorilla behaviour at Mbeli and its implications for a fuller understanding of gorilla socio-ecology in *Gorilla gorilla* and *Gorilla beringei*.

Appendices include some areas of detail pertaining to the main content of the chapters but inappropriate for inclusion in the main text. Also included is an extended section (Appendix 7) describing some of the behavioural elements employed by gorillas during social interactions. Space restrictions prevent this from being an exhaustive investigation. Instead, the first half of the section details one previously undescribed display form, the 'splash display', in terms of both form and function. The second section is divided into an analysis of staring behaviour, and offers an alternative explanation for a behaviour previously described as gaze aversion. Finally, some observations are offered in regard to the physiology and pelage of the silverback in the context of display and thermo-regulation. While largely speculative, this latter section suggests avenues for future research.

Chapter 2

The Study Site and General Methodology

Location

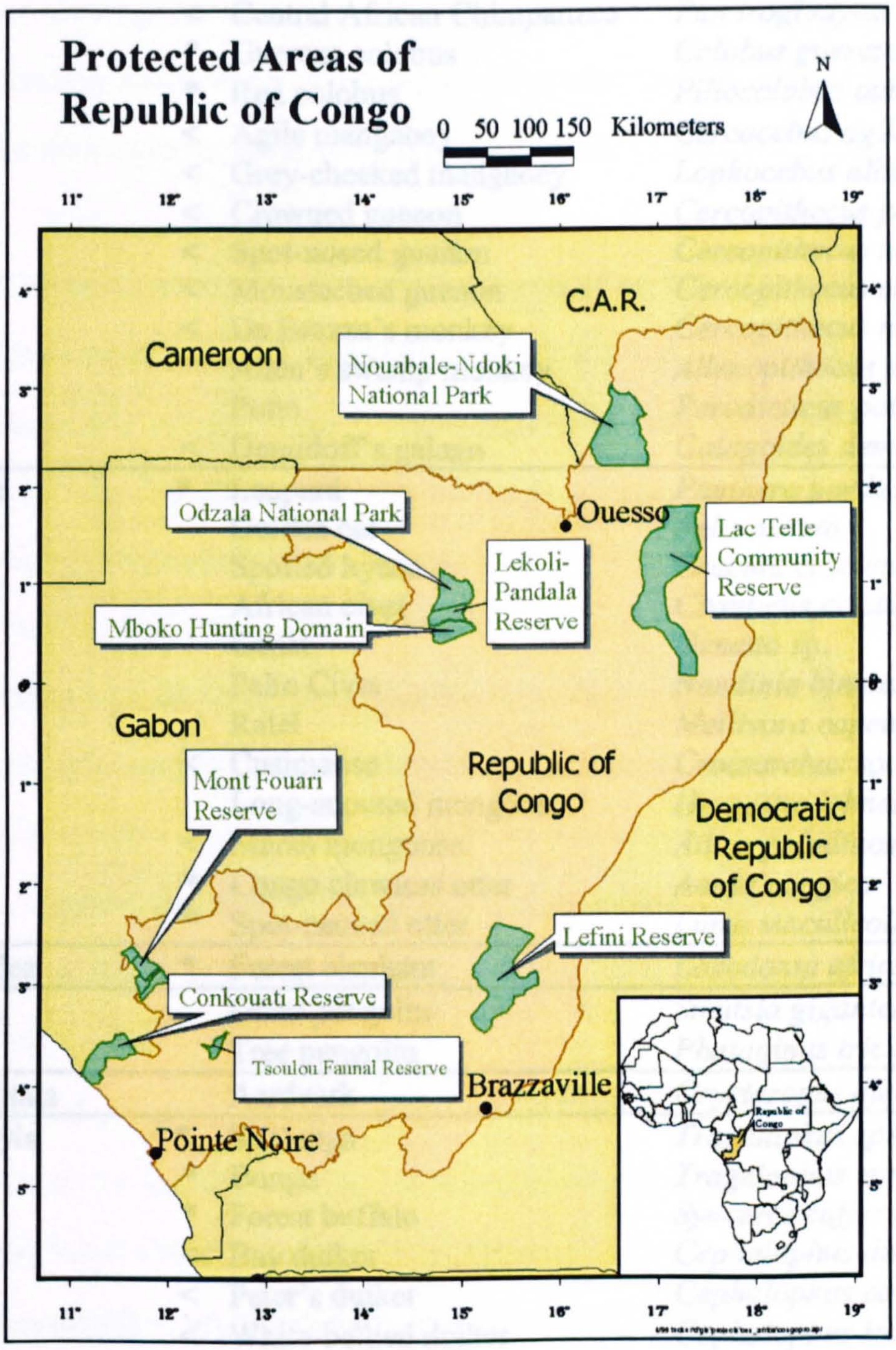
The Republic of Congo is bordered to the north by the Central African Republic and Cameroon, with Gabon and 169km of Atlantic coastline to the West, and the vast mass of the Democratic Republic of Congo (formerly Zaire) surrounding its southern and eastern flanks. Approximately two-thirds (222,300 km^2) of the country's total land-mass of 341,500 km^2 is forested, although almost 30% of this is swamp forest, and thus mostly unavailable for timber extraction. The remainder of the land-mass is primarily savanna (www.cia.gov/cia/publications/factbook/geoscf.html; Hecketsweiler, 1990).

Congo was colonised by the French, but gained its independence in 1960. The human population is low at approximately two and three quarter million, roughly 70% of which live in Brazzaville (the capital), the town of Pointe Noire, or along the railway linking the two. The principal export is oil, which forms the mainstay of the economy. This is followed by timber, and in particular, the extraction of the African mahogany species Sapelli (*Entandrophragma cylindricum*) and Sipo (*E. utile*). There is little large-scale agriculture, though manioc, peanuts, sugar, coffee and cocoa are all produced. In rural Congo those not employed in forestry are mostly small plantation farmers, subsisting on a diet of manioc (cassava), fish and bushmeat. Increasing numbers are, however, involved in the commercial exploitation of wildlife (bushmeat and river fish), serving large urban markets for these products. The trade in bushmeat, and its deleterious effect on many endangered species, has been facilitated by the logging industry. Logging artificially raises rural populations to potentially unsustainable levels (some companies permit or even encourage the hunting of wildlife to provide protein for its workforce), but its most damaging influence is in the opening of previously remote areas to hunters. Logging roads give easy access to the forest, and logging vehicles are frequently used to transport bushmeat for sale in the larger towns and cities. The trade in bushmeat has now been identified as the most serious threat to African forest wildlife, outstripping the direct effects of habitat destruction or alteration through logging alone.

In response to such threats, an area of 386,592 ha in the extreme north of the country gained protected status as the Nouabalé-Ndoki National Park (2° 32'N – 2° 30'N, 16° 10E – 16° 35E) on the 31st Dec 1993. Figure 2.1 shows the position of Nouabalé-Ndoki National Park (NNNP), and also the other protected areas in Congo. The park is managed by the Wildlife Conservation Society (WCS), an arm of the New York Zoological Society, and is contiguous with Dzanga National Park and Ndoki National Park in Central African Republic, and the Lac Lobéké National Park of south-western Cameroon. These areas form a Tri-National Conservation Area of enormous importance to the maintenance of biodiversity in the central African forest.

The Nouabalé-Ndoki National Park contains some of the most pristine forest in Congo, has little recent history of human exploitation, and an extremely low human habitation density of <1/km^2 (Hecketsweiler, 1990). The park supports a rich and diverse fauna including four large mammal species on CITES Appendix I, and 19 species of mammal on Appendix II (Ruggiero and Eves, 1998). In addition, at least 273 bird species have been identified in and around the park (F. Dowsett-LeMaire, unpubl. data). Table 2.1 lists the larger mammals confirmed as extant in the park (NNNP records).

Figure 2.1 The location of the NNNP and other protected areas within Congo



Map courtesy of F. Maisels.

Table 2.1 Larger mammals confirmed as present in the Ndoki Forest

Order		Common name	Scientific name
Primates	*	Western lowland gorilla	*Gorilla gorilla gorilla*
	<	Central African Chimpanzee	*Pan troglodytes troglodytes*
	*	Guereza colobus	*Colobus guereza*
	*	Red colobus	*Piliocolobus oustaleti*
	<	Agile mangabey	*Cercocebus agilis*
	<	Grey-cheeked mangabey	*Lophocebus albigena*
	<	Crowned guenon	*Cercopithecus pogonias*
	<	Spot-nosed guenon	*Cercopithecus nicitians*
	<	Moustached guenon	*Cercopithecus cephus*
	<	De Brazza's monkey	*Cercopithecus neglectus*
		Allen's swamp monkey	*Allenopithecus nigroviridis*
		Potto	*Perodicticus potto*
	<	Demidoff's galago	*Galagoides demidoff*
Carnivora	*	Leopard	*Panthera pardus*
		Golden cat	*Felis aurata*
		Spotted hyena	*Crocuta crocuta*
		African civet	*Civettictis civetta*
		Genet	*Genetta* sp.
		Palm Civet	*Nandinia binotata*
		Ratel	*Mellivora capensis*
	<	Cusimanse	*Crossarchus* sp.
		Long-snouted mongoose	*Herpestes ichneumon*
	<	Marsh mongoose	*Atilax paludinosus*
	*	Congo clawless otter	*Aonyx congica*
	*	Spot-necked otter	*Lutra maculicollis*
Proboscidea	*	Forest elephant	*Loxodonta africana cyclotis*
Pholidota		Giant pangolin	*Smutsia gigantea*
		Tree pangolin	*Phataginus tricuspis*
Tubulidentata		Aardvark	*Orycteropus afer*
Artiodactyla	*	Sitatunga	*Tragelaphus spekei*
	*	Bongo	*Tragelaphus eurceros*
	*	Forest buffalo	*Syncerus caffer nanus*
	<	Bay duiker	*Cephalophus dorsalis*
	<	Peter's duiker	*Cephalophus callipygus*
	<	White-bellied duiker	*Cephalophus leucogaster*
	<	Yellow-backed duiker	*Cephalophus sylvicultor*
	<	Black-fronted duiker	*Cephalophus nigrifrons*
	<	Blue duiker	*Cephalophus monticola*
	<	Water chevrotain	*Hymenoschus aquaticus*
		Hippopotamus	*Hippopotamus amphibius*
	*	Giant forest hog	*Hylochoerus meinertzhageni*
	*	Red river hog	*Potamochoerus porcus*

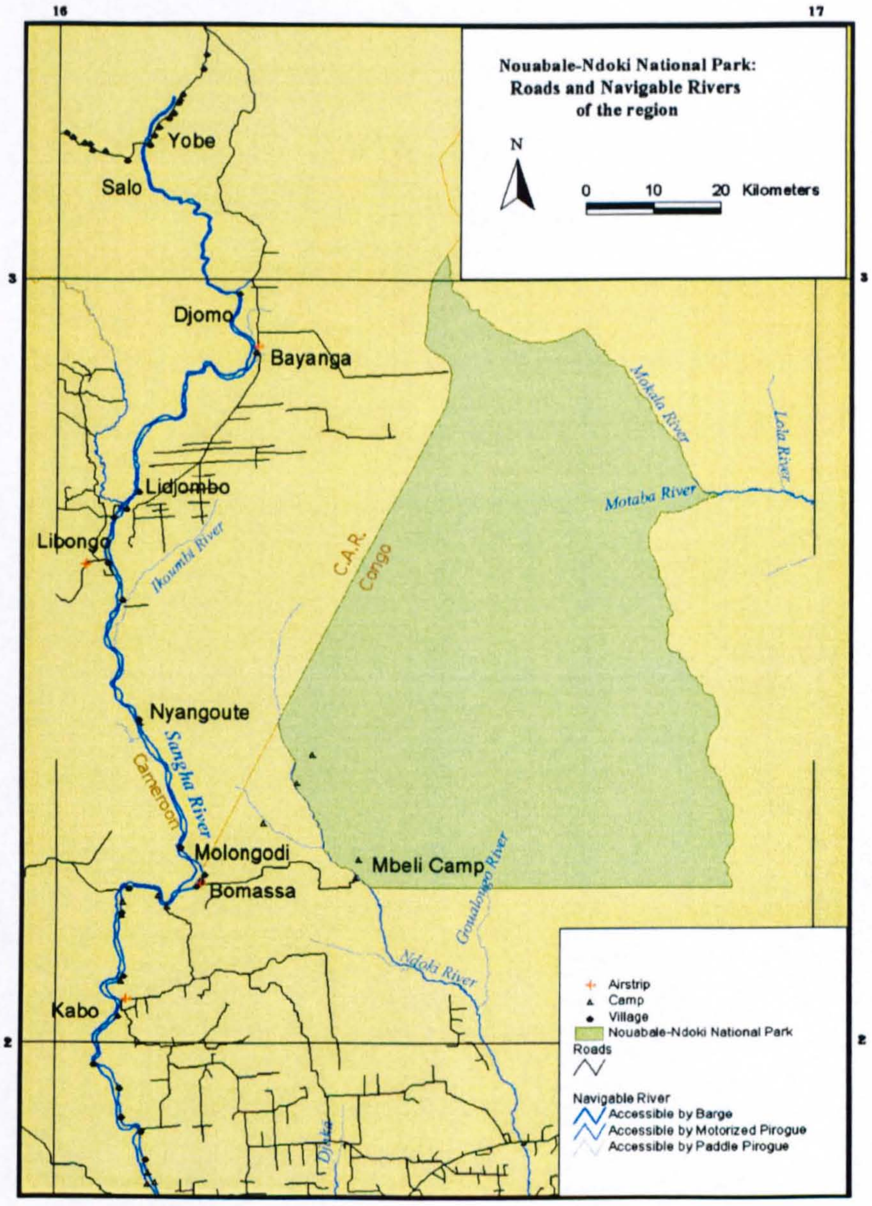
* Observed in Mbeli Bai. < Observed or known to have used bai edge (including canopy).
Nomenclature taken from Kingdon 1997.

The vegetation of the Park is characterised primarily by Sterculiaceae-Ulmaceae moist, semi-deciduous lowland forest, Raphia (*Raphia* spp.) and *Guibourtia demeusei* swamp forest, open clearings dominated by sedge and grass, and mono-dominant *Gilbertiodendron dewevrei* forest-types bordering water-courses and at other locations within otherwise mixed-species forest (Letouzey 1968; Moutsamboté et al. 1994; Fay 1997).

Of the open, treeless clearings characteristic of the Ndoki forest, local inhabitants recognise three main types: 'Yangas' are generally dry and lack the presence of a river or stream; 'Endambas' are permanently water-logged meadows, found on, or adjacent to water-courses, the saturated soils of which support a frequently abundant growth of aquatic and semi-aquatic vegetation; 'Bais' are also found on or adjacent to water-courses, but are generally dryer and of a more sandy nature, lacking the saturated soils of the endambas. Each type may offer diverse and/or abundant vegetation sought by a range of mammals including elephants and gorillas. However, bais (alternately called 'salines' or 'salt licks') are generally sought by elephants for the high mineral content of their soils (sodium, potassium, calcium, magnesium, manganese and phosphorus), either in solution in seep holes, or in soil form (Weir 1972; Ruggiero and Fay 1994; Klaus et al. 1998; Blake 2001; Turkalo and Fay 2001).

Figure 2.2 shows the position of the Mbeli Bai research camp within the N.N.N.P. The map shows the location of roads and navigable rivers in the area. The road approaching Mbeli Camp from the Park Headquarters at Bomassa, is an old logging road, now only accessible to project vehicles and widely used by wildlife (pers. obs.).

Figure 2.2 Location of Mbeli Camp within the Nouabalé- Ndoki National Park, showing road and river access in the area



Map courtesy of F. Maisels.

Mbeli Bai

The clearing known as Mbeli Bai, on the headwaters of the narrow and winding Mbeli River might more accurately be thought of as an 'endamba', due to its permanently flooded, deep and muddy soil, and the dense mats of aquatic vegetation it sustains. However for the remainder of this thesis, it will retain its local name and will be referred to as a 'bai'. The Mbeli River, a tributary of the Ndoki River, is bordered for most of its length by swamp forest which is flooded during rainy seasons, but dries somewhat during periods of reduced rainfall. The flooded forest is in turn bordered for most of its length by a narrow strip of mono-dominant *Gilbertiodendron* forest, before finally grading into mixed-species forest.

The open clearing known as Mbeli Bai is located at a point high on the river where the main course divides into two smaller streams. At present, the bai comprises 12.9 hectares of treeless water meadow (Plate 2.1) along the east-west flowing axis of the main artery of the river.

Plate 2.1 Aerial photograph of Mbeli from the East North East (1993)

● Location of the observation platform for the gorilla study.
Image courtesy of M. Nichols.

Bai formation and vegetation history

The origin of bais is not yet known, though most researchers believe that elephant activity is likely to have been important in the formation and maintenance of many such clearings. Geophagy by elephants and other mammals has been reported extensively (e.g., Weir, 1969; Oates, 1978; Ruggiero and Fay, 1994; White et al., 1993), and has been linked to requirements for mineral supplements in areas where forage may be deficient, to the self-treatment of gastrointestinal conditions such as settling the digestive tract during diarrhoea, and in the absorption of toxins and dietary tannins (*see* Klaus et al., 1998 for review). Elephants in tropical forests are known to dig cliffs and caves in mineral-rich soils. Such excavations frequently undermine the roots of trees, causing them to fall (Klaus et al., 1998; pers. obs.). Large treefalls frequently damage or push over several other trees, and such events in turn attract more elephant activity as animals briefly exploit the suddenly available browse and bark. Subsequent excavation gradually enlarges on the original opening. At Lopé, saline licks in river bends are typically used for several months or even years before being temporarily abandoned, and may eventually expand into substantial clearings (pers. obs.). Whether or not bais were originally created in a similar manner remains subject to speculation. The mineral content of soils and water at Mbeli has been examined (Elkan, unpubl. data), but further testing is required.

Blake (pers. comm.) conducted interviews with a local bantu man who guided hunters to Mbeli Bai in his youth, and who described the clearing as essentially dry and sandy, with a stream running through the centre. This description contrasts strongly with the current appearance of the bai, sounding more akin to dry 'elephant bais' such as Dzanga Bai to the north of Mbeli in the Central African Republic, where elephants come in huge numbers to ingest nutrients from well established sink holes in the sandy, denuded substrate. The guide, if reliable, was describing the bai less than 40 years ago, suggesting that radical changes have taken place in the interim period. One hypothesis that may explain this apparent shift in bai type is that frequent elephant visits are necessary to maintain efficient drainage of sandy, riverine bais. Elephant activity represses the establishment of vegetation which is otherwise likely to slow the progress of any water-course. It is possible that in the recent past, hunting pressure or natural shifts in ranging has reduced the number and frequency of elephant visits to Mbeli, with the resulting plant re-colonisation of the bai slowing the river and trapping sediments to form loose and waterlogged muddy soils above the sand. The aerial photo of Mbeli in Plate 2.2 shows the narrowing of the clearing at the eastern, downstream end. Although this area is still largely waterlogged, the stream is now diverted back into the forest two-thirds of the way down the bai. Although measurements have not yet been taken, it appears that flooded-forest vegetation at this end of the bai is re-colonising (note incursion of shrubs and bushes, and the general narrowing of the bai to the left of Plate 2.2). By contrast, the much wider western (upstream) end contains more standing water than any other area of the bai, and relatively large flooded areas in which there appears to be extensive mortality of mature trees. This effect is possibly caused or intensified by flooding resulting from the slowing of the main channel of the stream. While this remains an unexamined hypothesis, there is clear evidence of change in the nature of the water-course even in the brief duration of the study. The photograph taken of the clearing in 1993 (Plate 2.1) shows the river running through the centre of the bai in a clearly defined channel. Plate 2.2, however, taken at the end of 1999, shows many sections of the channel to be choked with aquatic vegetation.

Plate 2.2 Overhead aerial view of Mbeli Bai (1999)

Photographed for the author by B. Curran.

One effect of this habitat alteration appears to be a shift in the prevalence of otter species using the bai, from *Lutra muculicollis* (the spot-necked otter) at the start of the study (Fay, pers. comm.) to *Aonyx congica* (the congo clawless otter) by the start of the current study period (pers. obs.). The spot-necked otter is primarily a fish hunter that requires open water to chase and capture its prey. By contrast, the diet of the congo clawless otter appears to be dominated by worms, which it catches by reaching into the numerous mud-banks bordering the slow-moving backwaters of the bai (*see 'Other species'* section of this chapter). If Mbeli Bai in its current form is a recent phenomenon, then the clearing types 'bai' and 'endamba' may in fact be merely points in a potentially cyclical evolution of clearings, dependent at least in part, upon the frequency of elephant bai-use.

Current vegetation

To avoid disturbance to the gorillas and subsequent shifts in bai-use patterns, no attempt was made to undertake an extensive vegetation survey in the bai during the study period. However, Blake and Moutsambouté (unpubl. data) conducted a limited vegetation survey prior to this study which contributes to the list of plant species given below. With the exception of a small area of *terra firma* at the western end, the entire clearing is now comprised stream and water-logged soils with an average depth of 1m, below which lies a firmer, sandy substrate. Aquatic and semi-aquatic vegetation dominated by species of Hydrocharitaceae, Cyperaceae and Gramineae families form a floating surface to the bai. Humans have difficulty walking across the bai without breaking through the plant matrix and sinking to the sand layer beneath, and the task is quite impossible for heavier mammals such as forest buffalo and elephant. Blake and Moutsambouté listed 60 species of plant (including bai-edge shrubs) though the identification of many species requires confirmation. Table 2.2 lists the plant species so far confirmed as present in the bai, with those species observed to be eaten by gorillas indicated. Data were not collected on the relative importance of these plant foods to gorillas, though Olejniczak (in prep.) gives *Hydrocharis chevalieri* as the primary choice of gorillas feeding at Mbeli, followed by *Rynchospora corymbosa.*

Table 2.2 Confirmed plant species and gorilla foods at Mbeli Bai

Family	Genus and species	Eaten by gorillas
Hydrocharitaceae	*Hydrocharis chevalieri*	Yes
Cyperaceae	*Rynchospora corymbosa*	Yes
	Fimbristylis sp.	Yes
	Fuirena sp.	Yes
	Oxycaryum cubense	Yes
	Eliocharis sp.	No
	Kyllinga sp.	Uk
	Pycreus lanceolata	Uk
Onagraceae	*Ludwigia* sp.	Yes
Eriocaulaceae	*Eriocaulon* sp.	Uk
Balsaminaceae	*Impatiens irvingii*	No
Thelypteridaceae	*Cyclosorus* sp.	No
Gramineae	*Leersia hexandra*	No
	Echinochloa sp.	No

Uk = Not yet confirmed as a gorilla food.

Gorilla food plant characteristics at Mbeli, processing styles, and laterality of hand use for feeding are described in Parnell (2001). *H. chevalieri* grows primarily on the edge of the more open water-courses, and appears to be the first species to re-colonise open water following disturbance by large mammals. As such, its abundance and distribution within the bai may be limited by the activity of elephants, buffalo and gorillas. Each month, a set of 12 still photographic images was taken of the bai, encompassing the entire area and detailing smaller feeding areas (*see* Plates 2.3 and 2.4 for examples). It is hoped that this resource may eventually provide data on vegetation changes over time by employing GIS software to measure percentage cover of different species and open water. Such analysis has not been possible within the confines of the present study, but the plates clearly show the presence of newly opened channels in some months due to elephant and buffalo activity, and the subsequent 'greening over' of these areas, during periods when such activity was minimal or absent. The images should be viewed in columns from left to right.

Plate 2.3 Monthly bai-photos showing effects of large mammal passage and feeding

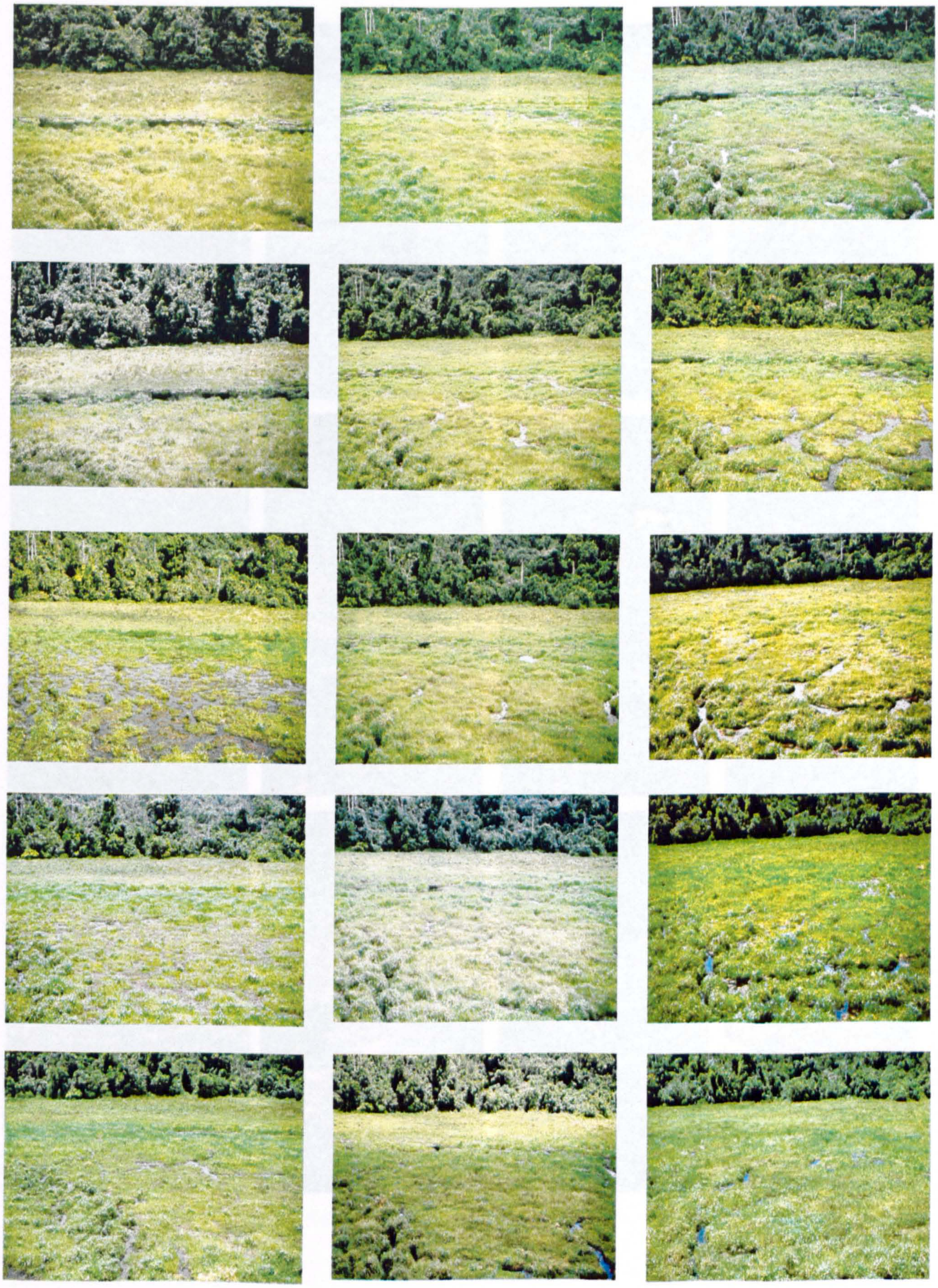
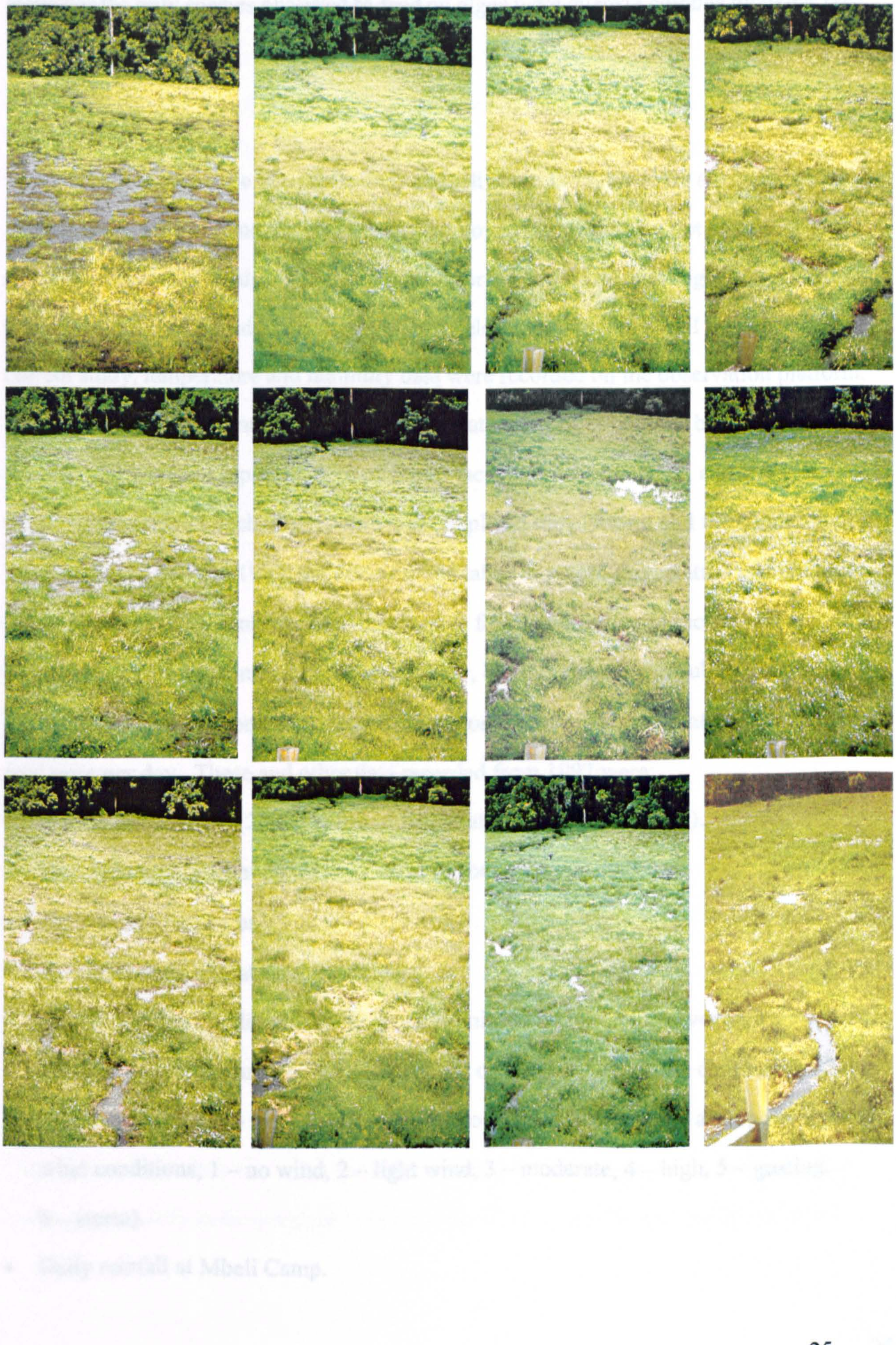


Plate 2.4 Another view of monthly changes in bai soil/plant matrix



Growing in abundance in the slower-moving channels of the clearing is an algae of the family *Spirogyra*. There are no records of toxicity for *Spirogyra* and it is likely to provide an excellent source of vitamin and mineral-rich forage (B. Whitton, pers. comm.). However the only species observed to feed on algae were guereza colobus monkeys (*see 'Other species'*).

Climate

Meteorological data have been collected at Mbeli since 1995, however alteration in the measurement protocol and the instruments employed has meant that not all records are directly comparable. This highlights the need for a rigorous meteorological monitoring protocol to be established at the outset of any field-based project. Until the start of the current study, temperature and humidity data were recorded on the observation platform. While convenient, this method was flawed in that changing conditions beneath the roof of the platform were not representative of any in the natural environment, and were also sensitive to variables such as the number of people on the platform and the condition of the wooden floor. Early in 1997, the decision was taken to record temperature and humidity levels at one bai site; 15m back into the flooded forest at the edge of the bai and at breast height. Readings were initially take on the hour, but this system was subsequently replaced by a remote monitoring device that recorded the same information but could be read once per day. These and other data recorded from 1997 were:

- Hourly temperature (24hrs) at breast height at the bai edge (shaded).
- Hourly humidity from 08.00 to 17.00 at the bai edge (shaded).
- Daily rainfall at the bai.
- Relative height of water-table at the bai.
- Hourly weather conditions (using an eight point scale for cloud-cover and precipitation; 1 – sunny, 2 – hazy, 3 – partly clouded, 4 – complete cloud cover, 5 – light rain/drizzle, 6 – steady rain, 7 – downpour, 8 – fog/mist), and a six point scale for wind conditions; 1 – no wind, 2 – light wind, 3 – moderate, 4 – high, 5 – gusting, 6 – storm).
- Daily rainfall at Mbeli Camp.

- 24 hour minimum and maximum temperature in the forest near Mbeli Camp.

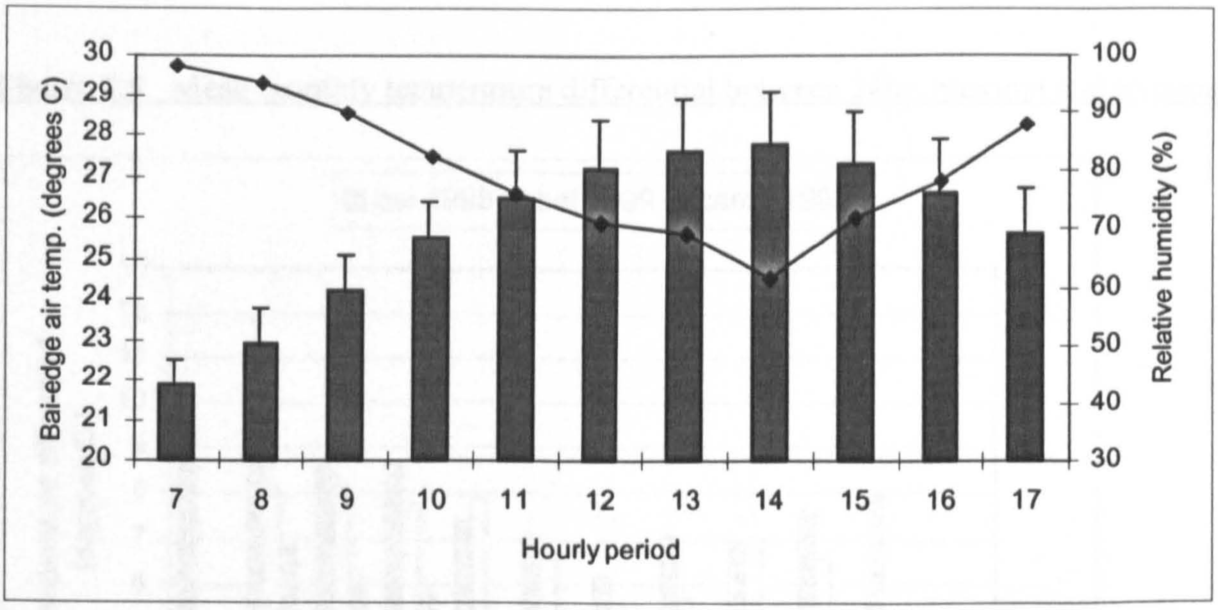
Relative height of water table was measured to monitor any seasonal changes. This was done primarily to examine variables influencing bai-use by otters. A wooden beam was driven into the sandy bed of a stream channel at the edge of the bai, and braced to a nearby tree to prevent movement. A metal scale gradated in centimetres was attached and a reading taken on arrival at and departure from the bai each day. In 1998, a rain-gauge was installed at the centre of Mbeli Camp. This was due to concerns that the gauge at the bai (mounted on a beam that protruded out towards the bai from the observation platform) might be inaccurate due to a rain-shadow effect from the platform and the canopy of the tree about which it was built. The following year a min/max. thermometer was installed in forest near the camp to examine differences between *terra firma* and flooded forest temperature. At the bai, hourly conditions (cloud cover and precipitation type) were scored subjectively as a potential correlate with bai-use by mammals, and wind conditions as a potential variable in elephant visit frequency (fear of human scent being a possible obstacle to bai-entry).

Temperature

Figure 2.3 shows the mean hourly daytime temperature for the study period, measured at the bai-edge weather-station. Also shown are mean average humidity levels taken from 1998. The coolest and most humid period was the early morning with a mean temperature at 07:00hrs. of 21.9°C and relative humidity of 98%: the warmest and driest time of day was at approximately 14:00hrs. with a mean temperature of 27.8°C and humidity of 61.6%.

Figure 2.4 gives the mean of monthly 24 hour minimum and maximum temperature readings at the bai for 1997-1999 (no SD is given for maximum temperature in January as only one value was available). Minimum temperature varied little over the year except in January, when the effects of the main dry season caused a noticeable temperature drop. Maximum temperature was more variable, showing the same depression in January but also a gradual drop in temperature in the middle of the year with the lowest maximum temperature recorded in August. For the whole period, 24hr. monthly minima ranged from 18.6 to 22.7°C. and maxima from 27.0 to 30.6°C.

Figure 2.3 Hourly daytime temperature (mean of monthly averages 1997-1999 ± SD) in bai-edge forest, with mean monthly humidity levels for 1998



Columns = Bai-edge temperature (degrees Celsius), Solid line = Relative humidity.
N = 28 records per hourly period (No records between August and November 1997).

Figure 2.4 Mean monthly 24 hour minimum and maximum temperatures at the bai ± SD (1997 to 1999)

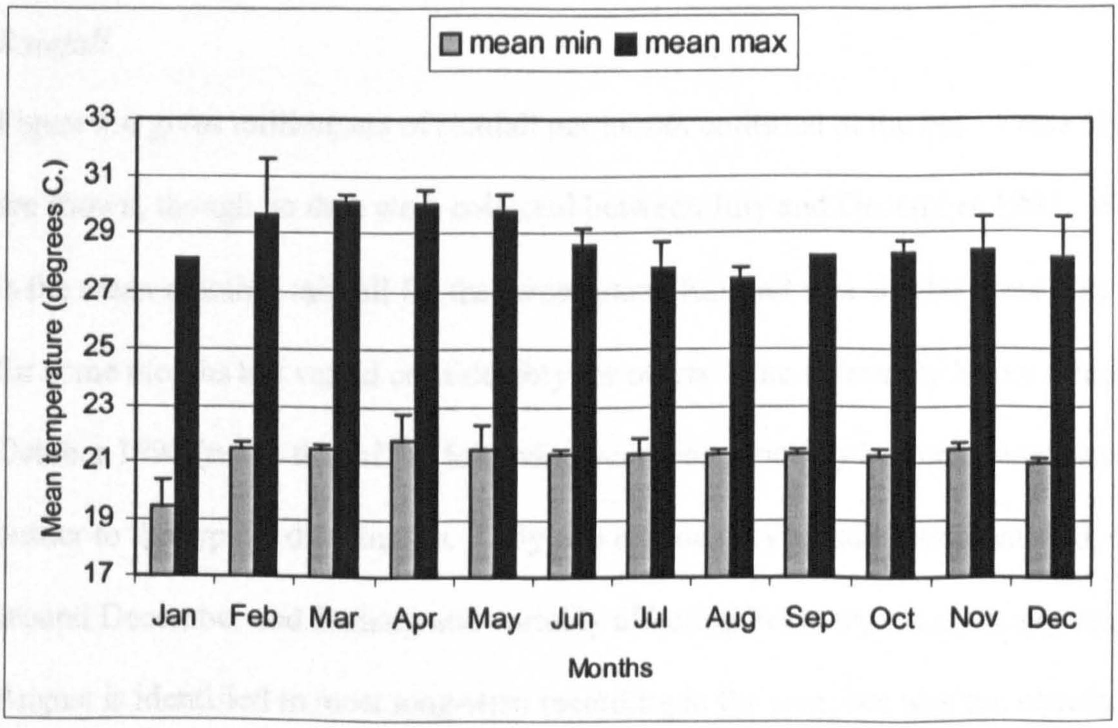
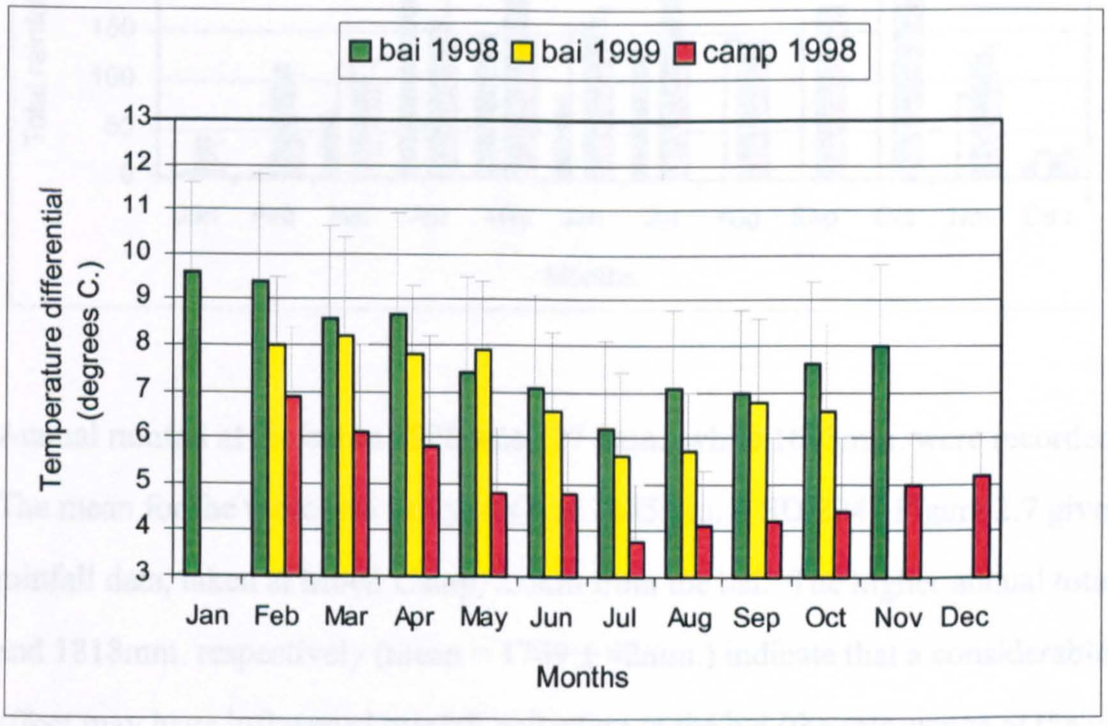


Figure 2.5 shows the mean monthly temperature differential between 24hr. maxima and minima at the bai (1998 and 1999), and from Mbeli Camp (1998). Clearly indicated is a uniform low differential in July and the greatest range in maximum and minimum temperatures coinciding with the main dry season at the start of the year (maxima occurring during the day and minima towards the end of the night).

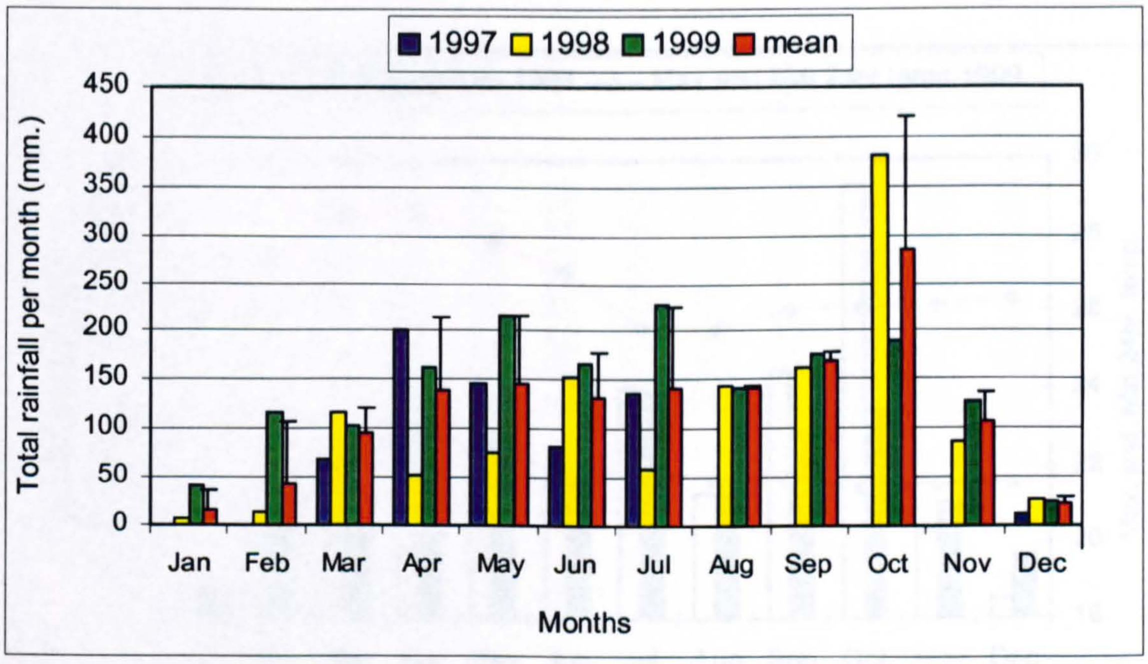
Figure 2.5 Mean monthly temperature differential between 24hr. maxima and minima



Rainfall

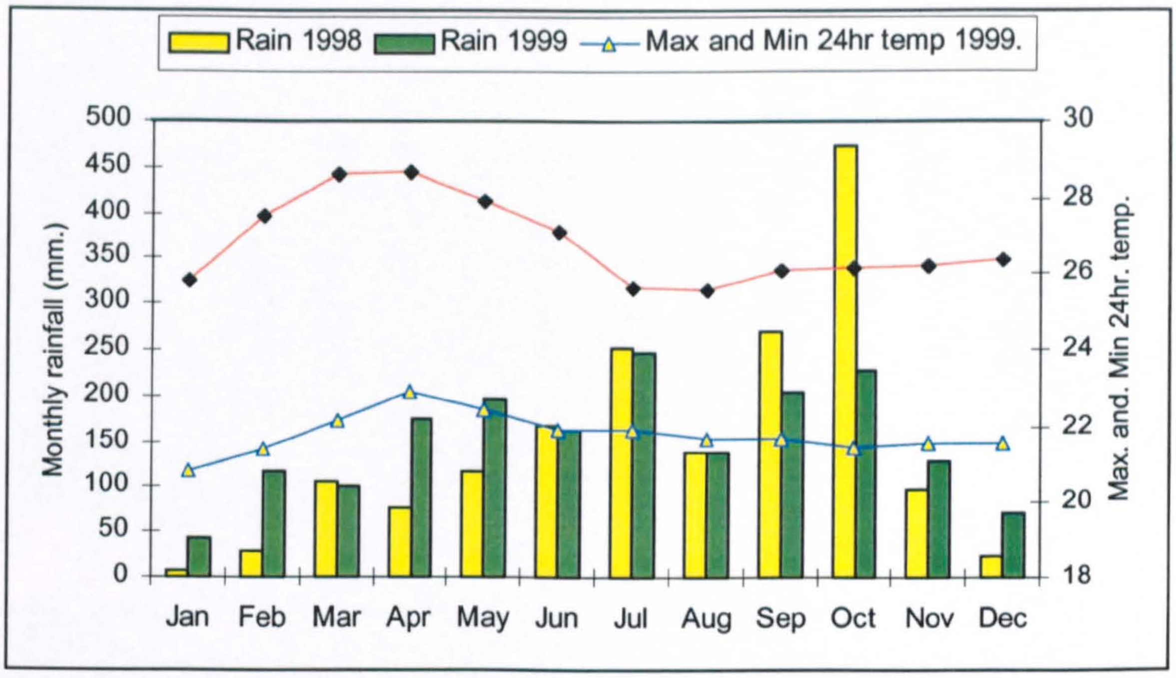
Figure 2.6 gives millimeters of rainfall per month collected at the bai. Years 1997 to 1999 are shown, though no data were collected between July and December 1997. Also plotted is the mean monthly rainfall for the three years. Rainfall was similar across the three years for some months but varied considerably for others. The extremely heavy rainfall of October 1998 (twice that of the following year) can probably be considered unusual and an outlier to the typical distribution. Only one obvious dry season was identified, centered around December and January and variably affecting February. A short dry season in August is identified in most long-term recording in the area, but was not clearly identified during this study. No rain fell during January and February of 1997.

Figure 2.6 Monthly rainfall (mm.) at the bai for 1997, 1998, 1999, and mean monthly rainfall.



Annual rainfall at the bai in 1998 was 1277mm., while 1693mm. were recorded in 1999. The mean for the these two full years was 1485mm. ± SD 294. Figure 2.7 gives two years rainfall data, taken at Mbeli Camp, 2.6km from the bai. The higher annual totals of 1760 and 1818mm. respectively (mean = 1789 ± 42mm.) indicate that a considerable rainshadow effect may have influenced rainfall collection at the bai (the rain-gauge at the camp was in a more open location). These data show a clearer drop in rainfall in August, but are otherwise similar to the bai data in their unambiguous indication of a single major dry season in January and February. Also shown in Figure 2.7 are values for 24hr. mean maxima and minima temperatures in the forest by Mbeli Camp. The chart shows the lowest night-time temperatures coinciding with the dry season, followed by an increase in both maximum and minimum temperature as the rains return. The hottest months of the year are shown to be April and May, however after this period, the temperatures fall again, apparently independently of rainfall.

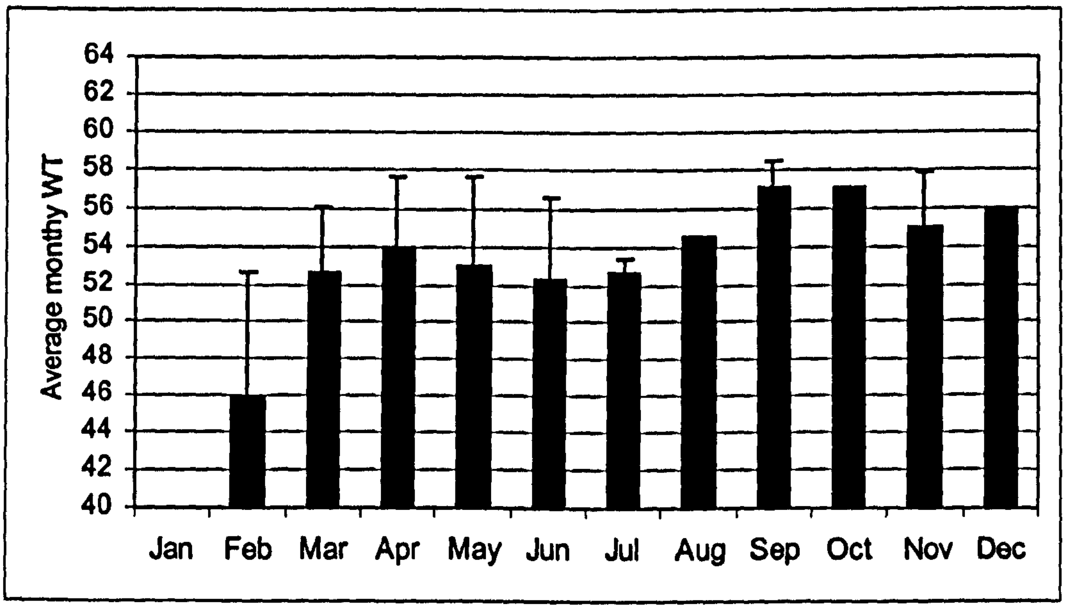
Figure 2.7 Monthly rainfall and 24hr. Min/Max temperatures at Mbeli Camp (1998 and 1999).



Maxima are represented by the red line,and minima, the blue.

Figure 2.8 shows the average monthly value for relative water-table (WT) at the bai. Readings were taken twice a day (am & pm) and the average used to generate monthly means. The mean of these was then calculated from all available data. A low reading from February 1997 reduced the overall mean for that month, though as the SD implies, readings from the other two years were considerably higher. Values for January are not given as data from 1997 are not available. Overall, very little variation in WT was observed across the year. This is slightly puzzling as the water level of the Mbeli River was observed to drop dramatically during each dry season. More data on WT fluctuations are required (especially *vis-à-vis* dry versus wet season) before any conclusions can be drawn regarding this variable.

Figure 2.8 Monthly relative water-table readings from Mbeli Bai, 1997 to 1999



Error bars show standard deviation.

Other species

Bais elsewhere have been shown to be an important resource for other large mammals (e.g., Magliocca, 2000). As part of an ongoing monitoring program within the NNNP, data were recorded at Mbeli on the bai-use habits of several of these. A brief summary of other species activity and visit frequency during the study period is given below.

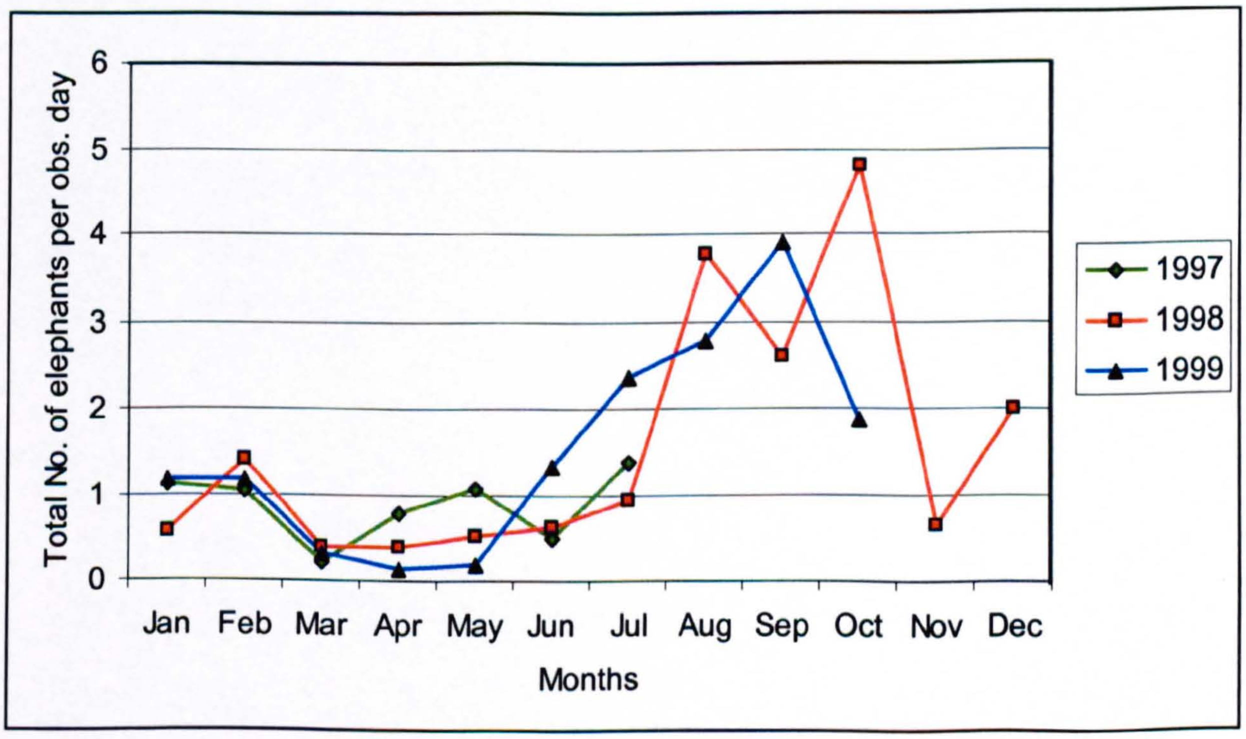
Elephant

All elephants using Mbeli and the surrounding forest are forest elephants (*Loxodonta africana cyclotis*), which are considerably smaller than the savanna sub-species and typically have less curved, downward pointing tusks. As mentioned earlier, it is highly likely that elephants were instrumental in the creation of bais such as Mbeli, with their presence or absence possibly shaping the geo-botanic profile. Elephant trails are seen throughout the bai, but during daylight hours when researchers are present they confine their activities to the streams at the furthest eastern perimiter of the clearing. Vegetation is consumed, but the primary activity is the extraction of mineral soils. Although not yet physially located by researchers, it appears that the stream-bed, particularly in Zone 9 (*see* photo on pg. 104), has several deeper sink-holes within it. Elephants can be observed pushing their trunks down through the stream-bed, while standing in a metre of water, and blowing air and water through them to excavate the sink-hole. Frequently kneeling to gain greater depth, and with their heads almost completely submerged, the elephants suck water-logged sandy soil into the their trunks, then, on regaining their feet, squirt the solution into their mouths.

By the end of the current study period, a total of 125 elephants had been recognised visiting Mbeli (53 adult males, 49 adult females, and 23 immatures). Identification was made by the noting tusk conformation, tail condition, and especially notches, holes and tears in the ears, which were often numerous.

Figure 2.9 shows the total number of elephants seen per month, divided by the number of observation days per month (i.e., elephants per observation day) for the three study years. While not all data points are available, the chart begins to show a dramatic pattern characterised by a period of extremely low visitation in March, April, and May, followed by a general increase in visiting numbers before beginning to fall off again from September/October onwards. The mean duration of elephant, or elephant group visits to the bai (diurnal visits only) for 1998 was 49 minutes (SD 38mins).

Figure 2.9 Elephant visitation rate at Mbeli Bai (as number of elephants seen per month divided by number of observation days)

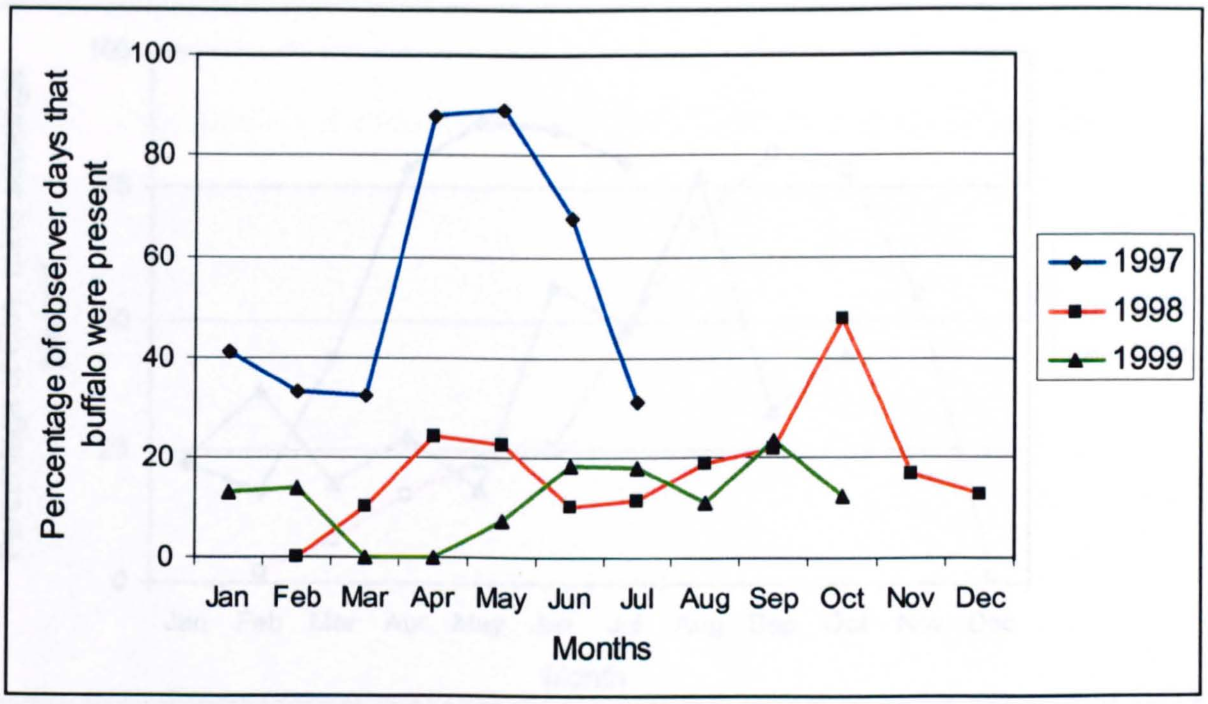


One remarkable observation at Mbeli concerned the self-treatment of a serious wound by a bull elephant in 1997. The individual, already known to the study, appeared on 22 January 1997 with a massive wound: a round area of approximately 60cm diameter just in front of his right hip had been completely skinned, exposing the fat below, with a 6cm wide gash running vertically from top to bottom of the area. The presence of several other apparent puncture wounds and the nature of the main lesion suggested that the injuries were caused by the tusks of another elephant. Between then and July 1997, he visited the clearing 33 times. On every visit, he was observed to irrigate the wound by spraying water from his trunk directly into it. Scan sampling showed that in the first 2 months, this was his primary activity while at the bai, and even a year later, after the wound had apparently healed completely, he was still seen from time to time, spraying water on the old scars.

Buffalo

Within the duration of the study period, little pattern could be discerned in the seasonal usage of the bai by buffalo (Figure 2.10). The bai appeared to feature in the core territory of only one group, which on average, contained nine members (2 adult males, 3 adult females, 1 sub-adult male, 1 sub-adult female, 1 juvenile female and 1 infant male). Although on occasion, members were missing from the group and numbers and composition also fluctuated slightly due to the emigration of offspring and the birth of new calves, the group maintained essentially the same composition throughout the study. The small size of the Mbeli buffalo group is testimony to the likelihood that forest buffalo are probably at the limit of their range in such habitat types, being largely limited to areas with relatively extensive grazing.

Figure 2.10 Days of buffalo presence at Mbeli as a percentage of observer days

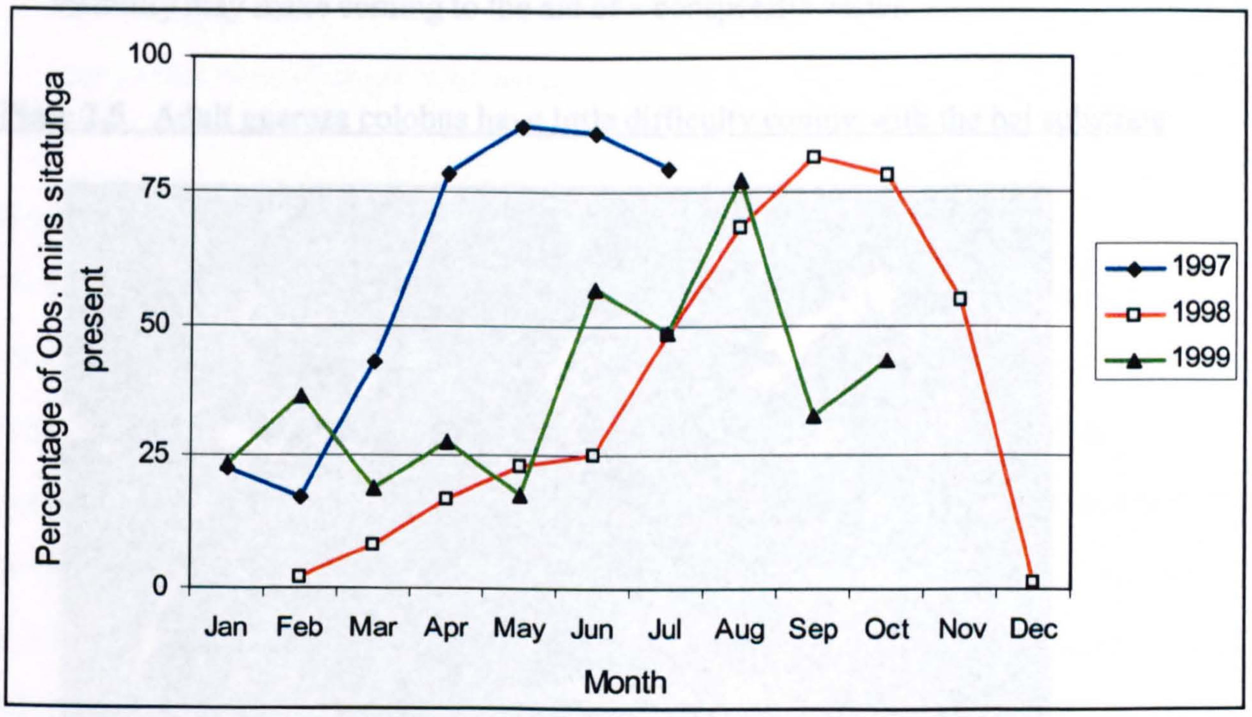


Sitatunga

Sitatunga were the only other species of ungulate that could be considered as truly 'resident' at Mbeli. These antelope are equiped with elongated hoof cleaves in a special adaptation for locomotion over swampy ground: the long hooves spread widely when weight is applied, preventing the leg from sinking in mud or breaking through surface vegetation. On the few occasions when *terra firma* dwelling red duikers (*Cephalophus* spp.) entered the bai, their legs sank immediately and they encountered serious difficulty trying to extricate themselves from the bai. During the three year period, 18 sitatunga were identified.

Figure 2.11, though incomplete, suggests a gradual increase in diurnal use of the bai towards the middle of the year, with a peak in August and September, before falling off again towards the main dry season. Data from 1997 show a similar curve, though with a much sharper increase early in the year and an earlier apparent peak. In 1998, the sitatunga population at Mbeli comprised seven adult females, all of whom bred and raised offspring at the bai (some of whom remained to produce offspring of their own at Mbeli). Four adult males were present, plus two sub-adult males.

Figure 2.11 Sitatunga presence at Mbeli as a percentage of total observation minutes



Other species

Data on bai-use patterns and behaviour were also taken on the following species:

a) Forest guenons; these monkeys did not enter the bai but used the surrounding trees and forest edge shrubs.

b) Chimpanzees; these were only ever recorded in the immediate vicinity of the bai when fruit feeding in the canopies of *Nauclea vanderguchtii*. They never entered the clearing itself.

c) Guereza colobus monkeys; this was the only other primate species other than gorillas that entered the bai. Colobus were fairly common visitors, jumping into the clearing from low edge shrubs, then leaping and wading out into suitable feeding areas (Plate 2.5). The main food item consumed was the algae *Spirogyra* sp., which they scooped up in the fingers of one hand and fed into the mouth. The monkeys were very vigilant during their time in the clearing, frequently standing bipedally to scan. However, no predator attacks on them have been witnessed during the study. This is puzzling as the bai habitat would slow any attmepts to dash for cover. One possibility is that the chances of being mobbed (for a crowned hawk eagle) may be higher in the bai, where individuals typically feed close to one another, and the flat terrain and excellent visibility may make coming to the aid of a conspecific easier.

Plate 2.5 Adult guereza colobus have little difficulty coping with the bai substrate

d) Red river hogs; these forest bushpigs confined their periodic use of the bai to the *terra firma* and shallow stream channels at the eastern edge of the bai, where they appeared to forage with their snouts underwater. White (1995) described red river hogs foraging in elephant dung for seeds and insects, and at Maya Bai, Magliocca (2000) reports that this species spent 33% of its time in the bai searching for seeds from elephant dung. Most such foraging was for seeds that had already been washed from the dung matrix and lay in streams. Although unconfirmed, it is probable that this was also the primary feeding behaviour of red river hogs at Mbeli.

e) Giant forest hogs; these pigs were always seen in discrete family units, mostly crossing the *terra firma* at the eastern edge of the clearing.

f) Leopard; leopards were seen crossing the *terra firma* on several occasions, but were only once seen in the flooded area, when an adult male made a half-hearted attempt to approach a male sitatunga. The antelope was well aware of the cat, barking in alarm, but not bothering to flee despite being only 35m away at one point.

g) Congo clawless otter; as mentioned earlier, these became the most frequetly seen of the two otter species at Mbeli, overtaking the spot-necked otter as stretches of open stream became clogged with vegetation. Difficulty was experienced in individually identifying congo clawless otters, but data were collected on their rate of feeding on the worms that were their prefered bai food.

General Methodology

Pilot studies at Mbeli were conducted by Blake in 1993 (Fay, 1997), and Olejniczak in 1994, prior to the establishment of a permanent research presence in February 1995. The initial, and still current, aims of the study were to monitor animal use of the bai, particularly with regard to gorilla frequency of use, social organisation and behaviour. With so little known of western lowland gorilla socioecology, and acknowledging the difficulties experienced elsewhere in habituating gorillas in the forest, the decision was taken to initially limit research at Mbeli to passive observation at the bai. Attempting to habituate and eventually follow one or more carefully selected groups into the forest is still a possible avenue for future research. However at the time of the present study, it was thought preferable to concentrate on obtaining as full a description of gorilla social structure and behaviour as was possible without using any invasive techniques, such as approaching groups at ground level in the bai, attempting to contact gorillas in the surrounding forest, or intesive nest-site searches in the area. Of particular concern was the risk that overt human presence in the surrounding forest might alarm some groups, thus disturbing their natural bai-use patterns.

As a result, a small observation platform was built (Plate 2.6) around three tree trunks, 8m above the surface of the marsh, at the mid-point along the southern edge (*see* Plate 2.1 for location). No attempt was made to camouflage the platform, and although some caution was evident in visiting groups at the start of the project (Olejniczak, pers. comm.), the gorillas seemed to very swiftly accept the platform as part of the landscape.

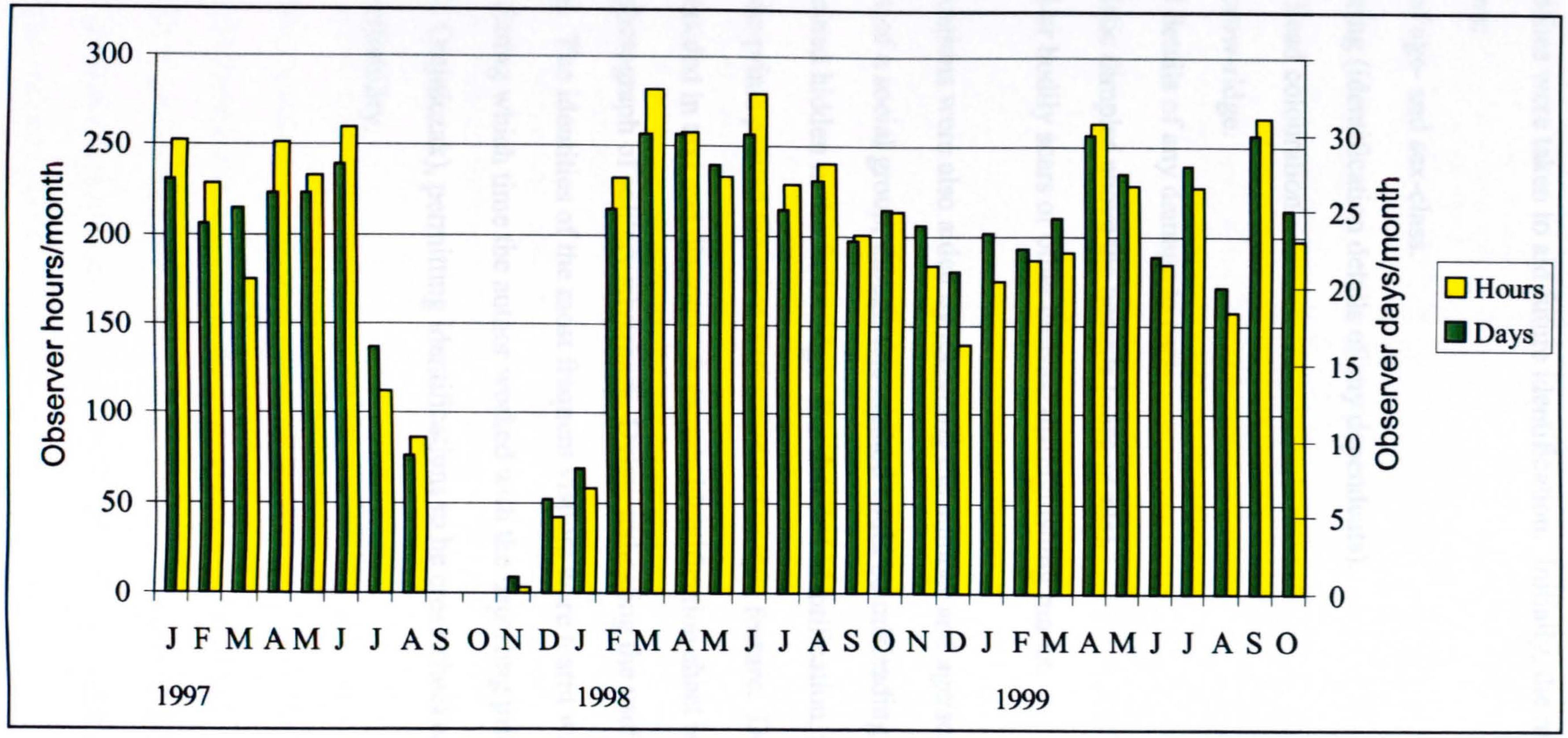
Plate 2.6 The observation platform at Mbeli Bai as viewed from the forest

The platform is accessed by a path from Mbeli Camp. By remaining in *terra firma* forest until the final 50 meters before the platform, it is possible to approach without alerting any gorillas already in the bai. Solitary silverback Vince was occasionally encountered on the path, and generally reacted calmly, often remaining to feed within 10m of an observer. Groups were much more rarely encountered, and generally retreated swiftly. By only using the path at the beginning and end of each day, the chances of meeting gorillas, and thus potentially scaring them from the area, was minimised.

Observer presence

Figure 2.12 gives the number of both hours and days per month of observer presence at the bai. In total, 6273 hours (737 days) of presence were logged between January 1997 and October 1999.

Figure 2.12 Number of observer days and hours per month at the bai during the study period



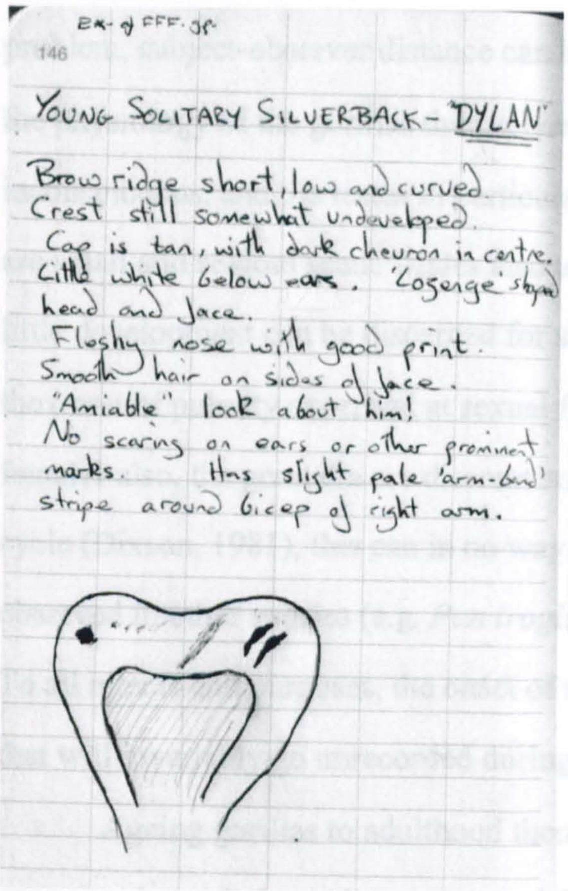
Identification of gorillas

Gorilla observations were made using Leica 10 x 42 binoculars, and Bausch and Lomb 15-45 x 60 and Meade 96x telescopes mounted on tripods. Video records were taken using a Canon XL1 digital camcorder. Whenever an unknown group or individual entered the bai, notes and sketches were taken to aid future identification. Initially, the main areas of focus were as follows:

- Estimate of age- and sex-class.
- Any offspring (identification details of any dependents).
- Body and head colouration.
- Shape of brow-ridge.
- Shape and details of any damage to ears.
- Characteristic dimples above the nostrils (nose-prints).
- Any facial or bodily scars or other unusual distinguishing marks.

Initial identifications were also aided by recording the number and age/sex-class of the other members of a social group, though this method could be misleading when certain members remained hidden in the forest edge. For detailed identification, particularly of immatures, nose-prints proved the most distinctive and unique feature. Details of all the above were recorded in text and diagram. A sample identification sheet is shown in Plate 2.7, next to a photograph of solitary silverback, Dylan, indicating the usefulness of nose-print recording. The identities of the most frequent visitors were learnt within the first three months, during which time the author worked with the departing principal investigator (C. Olejniczak), permitting identifications to be cross-checked and verified for inter-observer reliability.

Plate 2.7 Sample of field identification notes, and the gorilla described (young solitary silverback Dylan)



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YOUNG SOLITARY SILVERBACK – 'DYLAN'

Brow ridge short, low and curved.
Crest still somewhat undeveloped.
Cap is tan, with dark chevron in centre.
Little white below ears. 'Lozenge' shaped
head and face.
Fleshy nose with good print.
Smooth hair on sides of face.
"Amiable" look about him!
No scaring on ears or other prominent
marks. Has slight pale 'arm-band'
stripe around bicep of right arm.

Age classification of gorillas

Few areas of animal study can achieve precision without first establishing the age of the animal(s) involved. Primatologists must know an animal's age before learning anything of detail regarding its physiology, diet, ranging, and social-life. Likewise, the study of groups of animals lacks precision without a reasonable grasp of the age-classes making up a given group or community.

Sadly, unless an individual or group of individuals is studied throughout its entire life, assessing the age of fully adult animals is extremely difficult. Without the opportunity for close physical examination (e.g. of teeth), it is seldom possible to do more than place adults into three classes: those newly turned adult, geriatric animals, and those fitting into the amorphous class in which animals spend the great majority of their lives; an age-class that can be loosely termed 'prime adulthood'.

Ageing gorillas in the wild can be a particularly frustrating endeavour. Observations made in the forest are frequently hampered by poor light, and the animals themselves are frequently concealed. In bai conditions, while lighting is no longer a problem, subject-observer distance can be. These difficulties are greatly compounded by the physiology of the gorillas themselves. The genitalia of male gorillas are extremely inconspicuous, and the testes in particular, which may in other species offer a guide to age, are small and seldom seen. Males also undergo a protracted adolescence during which little development can be discerned for some years. It is not possible to accurately judge the onset of puberty or arrival at sexual fertility in males in the context of bai study. In females also, the genitalia are discreet and although slight labial swelling occurs in mid-cycle (Dixson, 1981), this can in no way be compared to the massive sexual swellings observed in other species (e.g. *Pan troglodytes*, *Cercocebus atys* and *Mandrillus sphinx*). To all intents and purposes, the onset of menarche and fertility in female gorillas are events that will invariably go unrecorded during bai studies.

Ageing gorillas to adulthood then becomes a question of making judgements based on somewhat nebulous phenomena and features such as pelage and body size, and the variable timing of developmental stages gauged through the observation of behaviour (especially weaning). Given that exact ageing is not possible for animals whose date of birth is not known, many studies resort to the use of broad age-groups or classes into which individuals can be placed. Unsurprisingly, such poorly defined methods do not lend themselves well to inter-population and species comparison, especially given the number of alternative age classification systems described (e.g., Schaller, 1963; Harcourt et al., 1980; Weber & Vedder, 1983; Watts & Pusey, 1993; Magliocca et al., 1999). The most detailed of these (Watts & Pusey, 1993) may serve as the best model for other studies, although in referring to the well-studied Virunga Karisoke population, it reflects a level of detailed observation beyond the reach of most other sites. Furthermore, it may be unsafe to assume that the age at which certain developmental markers are reached is identical in different populations, sub-species or species.

At the start of the current study, precise ages were known only for young infants. Age-classes of all other immatures were estimated following a variant of the Harcourt et al.

(1980) system, described by Watts (1990a). This was selected because its broad age-classes appeared to match the developmental stages observed at Mbeli. Under this system, gorillas are 'infants' between birth and 3 years, 'juveniles' between 3 and 6 years, and 'sub-adults' between 6 and 8 years. Females are considered adult from 8 years whereas males between 8 and 12 years are 'blackbacks'. Males are 'young silverbacks' between 12 and 15 years, and 'silverbacks' from 15 years. At Mbeli, young immatures were considered 'juvenile' when weaned. Males nearing full body-size but lacking full colouration and complete sagittal crest development were considered 'young silverbacks'. Males between adult female body size and the young silverback stage were considered as 'blackbacks', and females were considered 'adult' on reaching full adult body-size. The movement from juvenile to sub-adult age-class was the least well-defined transition, and was estimated from body-size and the cessation of juvenile behavioural traits including play and proximity maintenance with the mother.

Clearly, this system of classifying individuals based on subtle developmental characteristics will incur a degree of error, and ages derived from its use should be viewed with caution. However, it may be the only compromise available until such time as the age of all immatures is known from birth.

Table 2.3 Summary of age-class system employed at Mbeli

Age/sex-class	Corresponding age-range (years)
Infant (inf)	Birth to 3
Juvenile (juv)	3 to 6
Sub-adult (s.ad)	6 to 8
Adult female (af)	8+
Blackback male (bb)	8 to 12
Young silverback* (ysb)	12 to 15
Silverback (sb)	15+

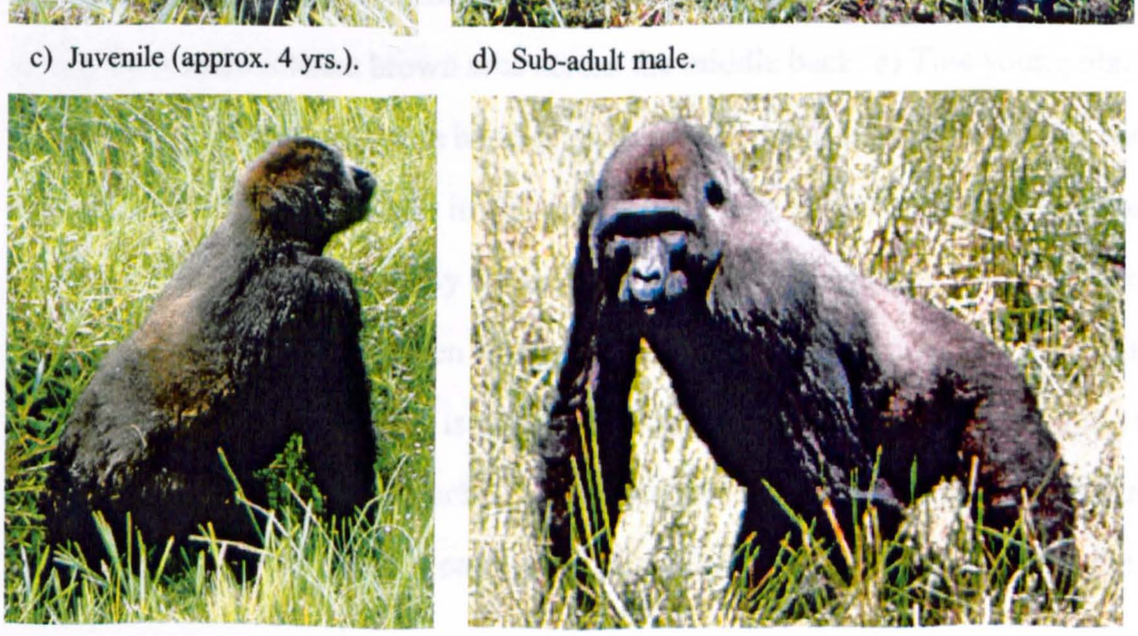
*All solitary males over approximately 12 years were classed as solitary silverbacks.
The abbreviations used for the age-classes throughout the thesis are shown in parentheses.

Plate 2.8 shows examples of Mbeli gorillas in the age-classes described and some variation within classes [all individuals from juvenile upwards are male]: a) New-born infants are dark with sparse hair cover: b) At three years, the body is well covered in fairly even length hair with a noticeably chestnut colour: c) In the juvenile, more red pigmentation may be visible on the top of the head:

Plate 2.8 Age/sex-classes in the Mbeli population

a) Adult female with new-born infant. b) Adult female with 3 yr. old infant.

c) Juvenile (approx. 4 yrs.). d) Sub-adult male.



e) Blackback male (8 yrs.) f) Blackback male (approx 12 yrs.).

g) From left to right: af, sub-adult female, af, juv, af w/inf, sb, juv, af, af

h) Adult female Martha, herded by silverback Basil.

d) Few characteristics distinguishing the sexes are noticeable until the sub-adult stage, when in males, the hair on the arms and shoulders becomes longer and darker; greater colour contrast may be visible between the red of the top of the head and the rest of the body, though the skull-cap is still rounded; some paling of the dorsal hair may be visible, as may be a more intense brown area across the middle back: e) This young blackback male demonstrates not only the band of red pigmented hair across the middle back, but also the first indication that the hair in this area is becoming shorter than elsewhere on the back, rump, arms and shoulders: f) By the time the blackback becomes a young silverback, considerable changes have taken place; the male is now larger than the average adult female; elongation of the skull is taking place and the sagittal crest is beginning to show; the hair on the rump retains much of the appearance of a younger male or adult female, but the middle back is now lightly covered in short, pale hairs; the longer hair of the upper back is silvering and the arms and shoulders are well covered in long, dense black hair: g and h) These two plates show fully matured silverbacks with (g) adult females, sub-adult females, and juveniles, and (h) a single adult female. Sexual dimorphism between the sexes is extreme in adulthood: both images show the female having developed no secondary sexual characteristics, retaining the basic 'juvenile' body proportions and hair length and colour. By striking contrast, the silverback displays specialisation of the muscular and skeletal system, pigmentation and hair type. These remarkable features are discussed further in Chapter 7.

The Mbeli Bai gorilla population

Full details of the gorillas studied at Mbeli are provided in the anaysis of group size and structure in Chapter 4. Table 2.4 however gives the name, age and sex-class of all the best known individuals recorded during the study period. Most age-classes given are those of the individuals at the start of the study in January 1997, though the age-class given for individuals appearing in the population after this time (both through birth and through immigration) is that estimated on the first occasion they were described. Individuals in italics died or were suspected of having died during the study period. One rare group (EME group) is not listed here as, although the composition of the group was known, individuals were less easily recognised and only a few of the 16 members had been individually described and named. The values after each group or solitary male show the number of independent visits made to the clearing by that group or individual.

Throughout the thesis, the term '*group*' refers to any collection of individuals that spend most or all of their time in close association. In order to recognise solitary males as independent social entities, the collective term '*unit*' is used to mean any independent group or solitary individual at large in the population (*sensu* Yamagiwa, 1987b). Units are identified either by their full name (e.g., Mosobomo's group), or by a three letter uppercase abbreviation (MOS). On charts where space is limited, this abbreviation is given in lowercase (mos). No formal criterion was established at the outset to determine at what point a group could be considered an independent entity, but with one exception, all groups thus described are known to have remained stable for at least 24 months.

Table 2.4 Mbeli individuals listed by unit, with starting age/sex-class and number of independent visits to the clearing per unit during the study period.

OB1	**33**	**DUK**	**35**	**SNO**	**51**	**NOO**	**76**
Obi-wan	sb	Duke	sb	Caravaggio	sb	Basil	sb
Sylvia	af	Ella	af	Kd	af	Taragon	bb
Sapwood	inf	Dizzie	juv	Kotzebue	inf	*Noodle*	*af*
Leah	saf	Butch	af	Caroline	af	Dill	juv
Misty	af	Sundance	juv	Kendal	inf	Bayleaf	bb
Elvis	inf	Satchmo	inf	Caroline inf 2	inf	Parsley	sam
Cindy	af	Bessie	af	Salmonberry	af	Cumin	saf
Spalding	inf	Courtney	sad	Spoonface	inf	Coriander	juv
Simone	af	Coltrane	juv	Drift	af		
Skywalker	juv	Bessie inf 2	inf	*Drift inf 1*	inf		
Sunbeam	inf	Bird	bb	Drift inf 2	inf		
Chewy	inf						
Sylvia inf 2	*inf*						
Simone inf 2	*inf*						
DWA	**22**	**MAX**	**2**	**TSB**	**88**	**CLI**	**94**
Dwayne	sb	Max	sb	Solomon	sb	Clive	sb
Buttercup	af	Ffaf	af	Redstripe	bb	Winona	af
Buttercup inf	inf	Ffaf inf	inf	Misha	saf	Wendy	inf
Primrose	af	Beetle	af	Isaak	sam	Jewel	af
Primrose inf	inf	Beetle off 1	inf	Salaam	sam	Peter	inf
Daisy	af	Nsaf	af	Bogplant	juv	Jodie	af
Daisy inf	inf	Nsaf off 1	inf	Moses	juv	Lyle	inf
Blossom	af	Mia	af	Moss	inf		
Bean	inf	AF4	af				
Pansy	af	AF4 inf	inf	**BON**	**48**		
Pansy inf	*inf*	Af6	af	*Bones*	*sb*		
Bluebell	af	Af7	af	Martha	af		
Bluebell inf	inf			Muffin	inf		
Petunia	af			Gretsky	bb		
Peapod	inf			Sahadouche	sam		
Lucy	saf						
Lobelia	saf						
***SSBs**		**MOS**	**51**	**TRA**	**74**	**FFF**	**9**
Frank	76	Mosombo	sb	Travis	sb	Dylan	ysb
Bear	66	Homer	bb	Stockwell	bb	Margo	af
George	51	(joined by		Holly	saf	Iook	inf
Vince	23	Margo & Iook)		Paris	juv	Dougal	sam
Geronimo	9						
Sulatalu	4						

*SSBs = Solitary silverbacks
Values following unit names are the number of visits made to the clearing by that unit during the study period.

Recording methods

Where necessary, these are detailed at the beginning of each chapter. In general, all occurances recording was used when measuring social behaviour, due to its rare and unpredictable nature. Focal and scan sampling techniques (Martin and Bateson, 1993) were only used in the collection of food processing data (Parnell, 2001). Most behavioural observations were described into a Dictatphone as they took place, and were transcribed on the same day. Same-day transcription of events also took place whenever video records were taken.

A disadvantage of not using scan sampling techniques when measuring behaviour is the difficulty encountered when in expressing rates of behaviour as frequencies. Without the standard reference of 'total number of scans' against which to compare observed frequencies, the time spent in a particular behaviour against the total observation time is a potential measure. However, it was often impossible to accurately measure and utilise the duration of behaviour due to, a) its frequently fleeting and unpredictible nature, and, b) the difficulty of calculating the time spent in the bai by particular individuals. Group members seldom entered or exited the bai at exactly the same time, and individuals frequently exited briefly, only to return again a short time later. As a result, the duration of visits was only measured from the entrance of the first group member of a unit to the departure of the last member. Thus the primary unit of measure against which occurrences of behaviour are measured must, by default, become 'the visit'. Inevitably, variation in visit duration will have some degree of influence on the rate of occurrence of some behaviours, but this is only likely to be of any importance at the extremes of visit duration, such as for a unit spending five minutes or five hours in the bai. In general, variation in visit duration was low between units, and although differences in duration were significant (*see* Chapter 3), only three of the 16 units tested were responsible for this result (two solitary males and one group had significantly shorter average durations than three groups). Given this, and the extremely rare nature of social behaviour, the use of visits as comparable units within which to measure frequencies of social behaviour was considered safe and practical alternative to behaviour sampling.

Statistical analysis

Due to a wide range of requirements, statistical methods are described where necessary in each chapter. In the majority of cases, non-parametric tests are employed, normality of distributions having been tested using probability plots and skew and kurtosis values from exploratory statistics. In cases were doubt remained regarding normality, the more conservative approach of using non-parametric statistics was employed, and in rare cases, both medians and means are given in order to allow for comparisons with other studies. All tests are two-tailed and the significant probability threshold set at 0.05.

Independence of data points is discussed in the Methods for each chapter, where relevent. Wherever possible, average values for behaviour from each individual are expressed, and these used towards generating a final, testable sample. However, in some instances, low sample sizes prohibited this, and I was left with no option but to count all instances of a behaviour as data points. Where practical, the number of individuals pooled in the creation of such values is given as a guide to the degree of independence present. Although this is far from being an ideal situation, it should be borne in mind that the level of independence gained through the ability to identify individual gorillas is a rare commodity in gorilla research, and many other reports are unable to take any account of the contribution made to the data by particular individuals.

Chapter 3

Gorillas in the Bai Environment

Introduction

This chapter builds on the summary of the bai environment given in the previous section, with the principal aim of exploring the ways in which gorillas interact with this unusual habitat type. Relatively exhaustive descriptions of the physical nature of gorilla life are provided for mountain gorillas in the books of Schaller (1963) and Fossey (1983). The hurdle of habituation is such that little is known regarding the daily demands of the forest environment on western lowland gorillas. The study of faecal remains and secondary trail evidence provides data on diet, and tracking and the location of nest sites can be used to examine ranging habits. However, without close observation it is difficult to learn how environmental variables other than food availability impact upon gorillas.

Bais represent a minority habitat-type for gorillas, but one in which observation of interactions with the environment are can be easily recorded. Some such interactions may be common also to the forest habitat, and others will be site specific. In both cases, the dearth of records of this nature make these observations of interest, and provide a firmer foundation upon which to view and appreciate other more specific subject areas such as feeding, ranging, and social interactions. Only one other bai study has thus far been undertaken (Magliocca, 2000), and although some resulting data have been presented on bai-use patterns (both daily and seasonal) and the potential for competition between different bai-using species, data were collected from a brief period only, and a shorter study period meant that few data could be considered with regard to inter-unit variation.

By way of introduction, this chapter begins by establishing some perspective on the importance of Mbeli Bai as a site, with respect to the time budgets of the gorillas that visit it. This is important in that it says a lot about what the study *cannot* tell us, a factor that can be easily neglected when analysing more detailed aspects of a data-set. The chapter continues by examining factors affecting bai-use patterns and behaviour exhibited in bais on the basis of daily influences. The timing of bai visits is considered in the light of climatic variables given in Chapter 2. This is followed by a examination of gorilla reactions to the meteorological variables that may be encountered during a given visit. A more detailed section given in the appendices considers a possible link between weather conditions and the incidence of yawning behaviour in gorillas. Other daily conditions receiving comment include interactions and behaviour towards other bai users, including elephants and sitatunga. Finally within the exploration of daily influences, the duration of gorilla visits is examined and reasons for differences suggested.

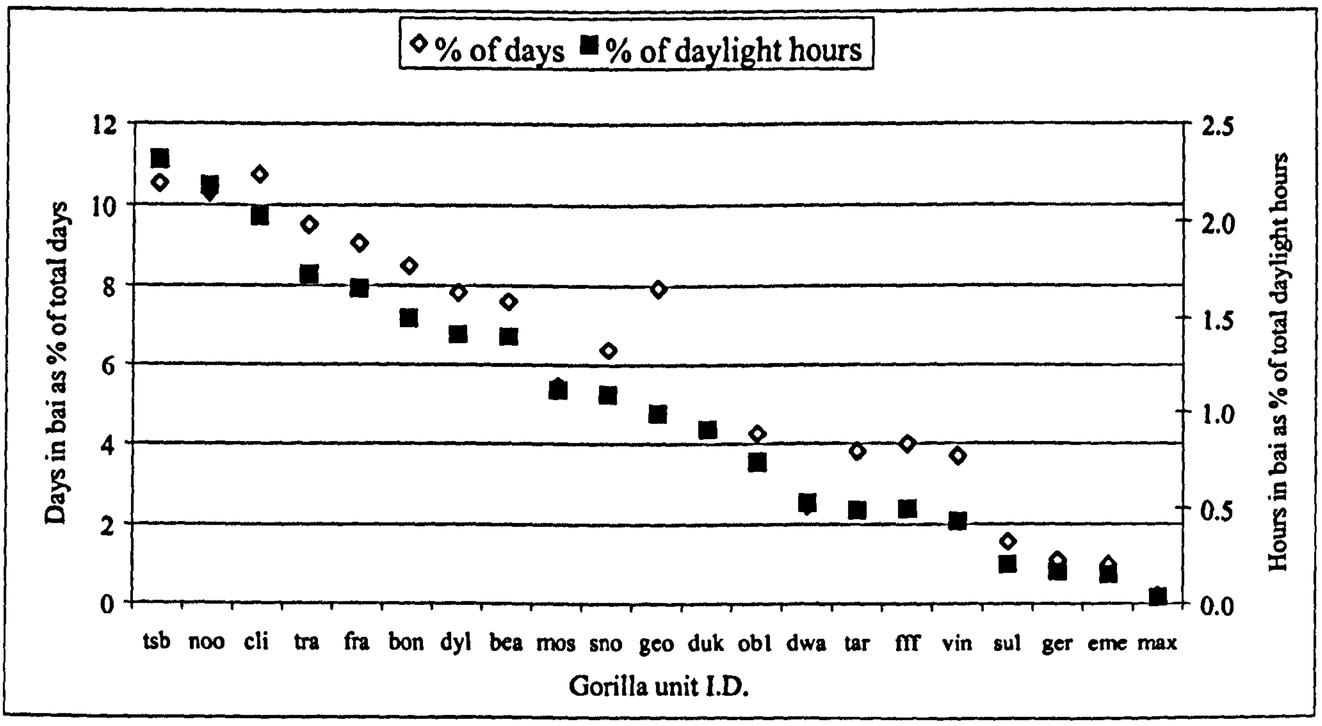
The chapter then considers the degree to which gorilla visitation rate is influenced by seasonal effects, including direct effects of climate, and proximal influences such as fruit availability and the seasonal incidence of insect pests. The chapter concludes with a short consideration of how details of social unit variation in bai-use patterns can be used to provide clues to the ranging patterns of gorillas in the region of Mbeli.

Gorilla use of Mbeli Bai in perspective

Before embarking on more a detailed description of bai-use, it is important to first view gorilla use of Mbeli Bai in perspective. Despite offering unparalleled visibility, there are severe limitations in the extent to which generalisations can be made about gorilla behaviour elsewhere. Primarily, as gorilla whereabouts outside of the bai are completely unknown, it is impossible to gauge how much of a given unit's time is spent in bais, compared with time spent in other habitat types, and thus, how unusual or site-specific such behaviour as is observed, might be. There are approximately 5 other swampy bais within 15km straight-line distance of Mbeli that might possibly offer similar feeding conditions for the Mbeli gorillas, however, survey work is required to assess their suitability for gorillas, and to monitor whether any Mbeli visitors also use these clearings.

Figure 3.1 shows two measures of gorilla presence at Mbeli. The left-hand y-axis shows the number of days on which each gorilla unit visited the bai as a percentage of the total number of days of the study period (excluding the months observers were absent in 1997). The right-hand y- axis shows the number of hours each unit spent in the bai as a percentage of the total number of daylight hours of the study period.

Figure 3.1 Gorilla presence at Mbeli as a percentage of total time available



The number of days on which units visited the bai ranged from 2 (MAX) to 96 (CLI), while the number of daylight hours ranged from 3 (MAX) to 228 (TSB). The range of scores for days in the bai proportional to all available days in the study period was 0.2% to 11%, with a mean value of 6% (SD 3.4). Meanwhile, hours spent in the bai as a percentage of total hours ranged from 0.04% to 2.3%, with a mean score of 1% (SD 0.7). Therefore, on average, 99% of the daylight hours available to the units visiting Mbeli are *not* spent at the bai.

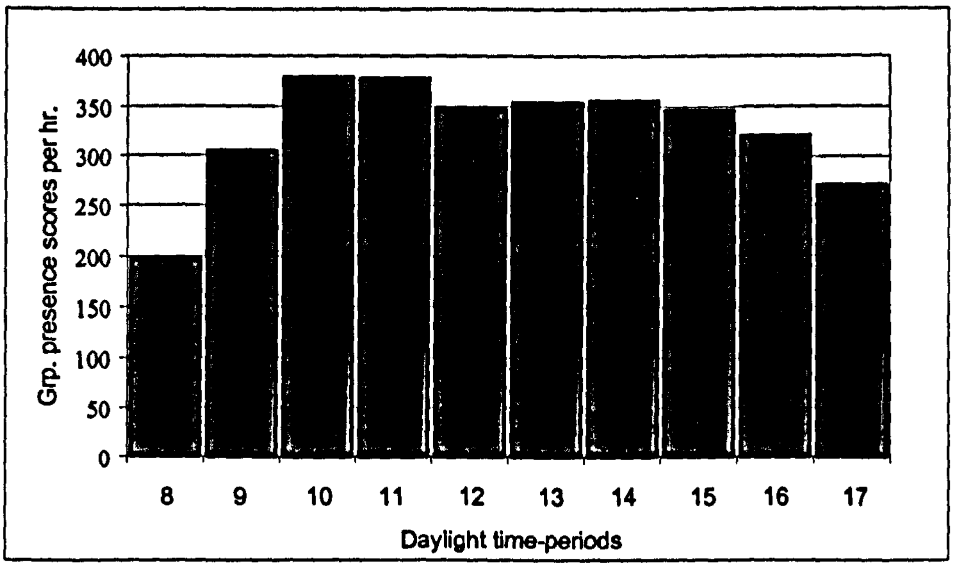
Daily influences on bai-use

Effects on timing of visits

For each day of the study period, each social unit visiting the bai was scored for the hourly periods covered by their visit. For instance, if a group entered the bai between 08:31 and 09:30, a count of one was given for the hour period '9'; if they left the clearing at 11:40, counts of one were also given to hourly periods '10', '11', and '12'.). Figure 3.2 shows a histogram of frequencies of hourly presence for visiting units during the study period. A total of 3255 hourly presence scores were obtained. N.B. There is very little variation in sunrise and sunset times over the year (sunrise 05:38-06:09. sunset 17:40-18-11:

http://mach.usno.navy.mil/cgi-bin/aa_rstablew.pl). Measurements start at 08.00 as records for presence earlier than this are much less frequent.

Figure 3.2 Hourly presence of all visiting social units at Mbeli Bai



The number of hourly periods in which units were present differed significantly ($\chi^2 = 85.8$, df = 9, $P < 0.001$). Figure 3.3 plots the frequency of arrivals and departures for each hourly period throughout the day, using 450 data points from 1998. Understandably, departures are few and far between in the first hours of the morning; they then plateau either side of mid-day before rising very sharply at the end of the day. This sharp rise is in part due to the pooling of all departures between 16:30 and the departure of the observer, but also probably reflects the requirement of gorillas to locate a suitable nest-site during daylight hours.

Arrivals are highest at the very start of the day, before dropping to a low plateau between 10:30 and 13:30, after which they then rise slightly until 16:30, after which they decline swiftly in line with the departure effect described above. Figure 3.4 plots the hourly temperature in the bai-edge (3 yr. mean) alongside the hourly arrival frequency for units (expressed as a percentage of all arrivals in 1998 (N = 450).

Figure 3.3 Frequency of arrivals/departures per hourly period (1998)

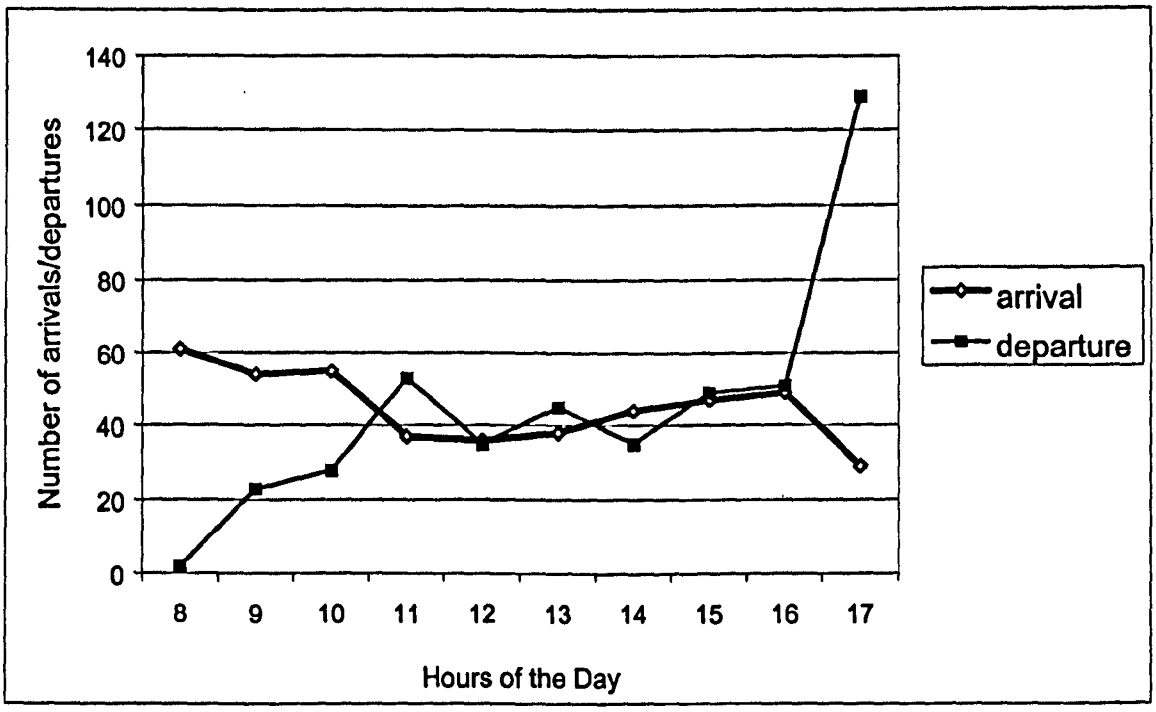
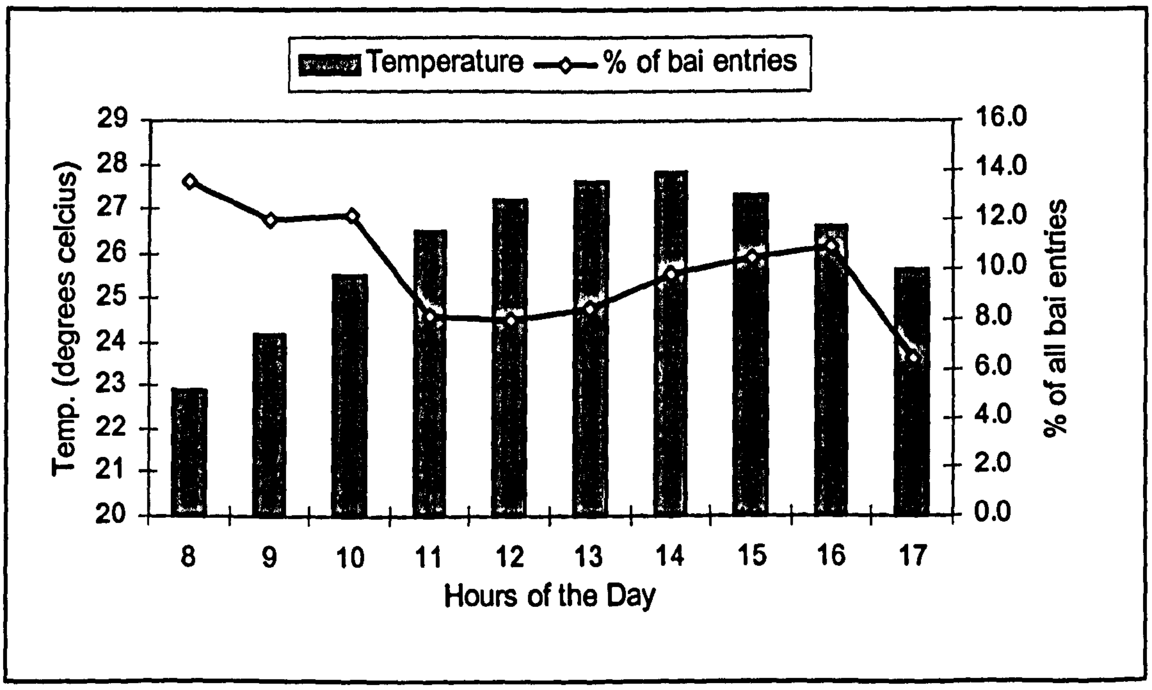


Figure 3.4 Hourly temperature and gorilla arrival times



These variables do not correlate significantly ($r = -0.609$, N = 10, $P = 0.62$), although the chart does suggest the presence of an inverse relationship. However, while temperature may have some effect on the timing of entries, other factors are likely to have a more profound influence. In particular, the time of a unit's arrival at the bai and its temporal feeding habits may be implicated. For instance, a group travelling towards the bai and arriving nearby towards the end of the afternoon may prefer to nest in *terra firma* forest and remain relatively dry for the night rather than submerging in the bai immediately prior to nesting. The following morning however, the bai is likely to be the first major feeding site of the day. Groups following such a pattern are likely to be in the clearing well before 11:00hrs. Conversely, groups not in the immediate vicinity of the bai first thing in the morning may be forced to use an alternative site for their first major feed of the day, after or during which, they may travel in the direction of the clearing. This may then have the effect of reducing the number of groups arriving during the hours around mid-day. Mid-day rest periods such as those recorded at Karisoke (Harcourt, 1978) do not appear to be a feature of time-use in gorillas using the bai, though this is not to say that a tendency towards a mid-day hiatus in intensive feeding or travel may not be present for gorillas while in the forest. This may also contribute towards the apparent decline in arrivals during this period.

General reactions to the bai environment: Arrival

It was commoplace for the arrival of NOO group to be heralded by immature males Bayleaf, Parsley and Coriander running into the clearing, chest-beating and pirouetting. Parsley and other individuals also showed what appeared to be signs of considerable contentment at arriving at the bai by rolling on their backs with their feet in the air. Other groups, particularly infrequent visitors such as EME and DWA groups, enterd the bai cautiously and only progressed out into the main body of the clearing as greater numbers arrived and inched forwards towards the better feeding locations. The passage from the forest to the open spaces of the clearing did not appear to concern the vast majority of gorillas. One unusual exception (a frightened reaction to a dramatic cloud formation) is described in Appendix A3.1.

Reactions to observers

Reactions to the platform and the presence of observers varied between gorilla units and, to a limited extent, on the behaviour of observers. Usual protocol called for all observers to move slowly and carefully, and to keep noise to a minimum. Sudden movements or sounds almost always caused some apes to look up, and occasionally to flee the bai.

Groups that used the zones immediately around or opposite the platform were generally more relaxed in proximity to it than those that habitually used more distant zones. For instance, immature members of NOO group frequently crossed into Zone 5 (*see* map on page 92), and approached the platform to less than 30m, frequently looking up at researchers. Solitary silverbacks Vince and Dylan both occasionally fed, apparently unconcerned, almost directly below the platform. NOO group were observed entering the clearing and feeding peacefully on several occasions when vital repair work was being carried out on the platform, and remained in the bai even during hammering and chain-sawing. By contrast, members of SNO group, that preferentially used the more distant Zone 3, became visibly ill at ease on the few occasions that they drifted closer to the platform.

Locomotion within the bai: problems associated with the aquatic environment

Few gorillas above juvenile age appeared to encounter serious difficulty moving within the bai habitat. In the most open and waterlogged areas, rapid movement from one location to another was hampered, and individuals attempting to move too quickly occasionally floundered in mud and water and were obliged to haul themselves back onto the floating vegetation mat (usually young males during display interactions). Water as deep as one to one and a half meters appeared to present little challenge to adult gorillas, and bipedalism during the crossing of deep streams was universal. During deep stream crossings, most individuals held their arms above the surface of the water as they waded; this appeared to aid balance.

Plate 3.1 Silverback Bear (left) and blackback Bird (right) wade bipedally at Mbeli.

In young immatures, however, there was evidence that a semi-aquatic environment could be hazardous, or at least alarming. The following examples all show some indication of this phenomenon.

Moses, a motherless juvenile of approximately three years tried on two consecutive days, shortly after his mysterious solitary arrival in TSB group, to cling to the group silverback as he crossed small channels in the bai. On neither occasion did the male facilitate this, but some assistance was clearly gained in crossing. Eight months later, the same individual was observed trying to cling to a blackback after having encountered difficulty moving through thick mud. An infant slightly over two and a half years old was observed to become stranded on one side of a channel after his mother had crossed. She, however, responded to his cries for help and held her arm out over the channel for the infant to use as support. A juvenile slightly over three years also shrieked towards his mother when he experienced difficutly moving through a boggy zone, clogged with tall vegetation. His mother waited for him at a deep stream crossing, however, and carried him dorsally to the far side, where he dismounted and continued unassisted. Two months later the same individual encountered similar problems, but his shrieks were ignored. A similar scenario was played out in a four year old who began to panic at finding herself on the far side of a large pond from her mother. Finally, a one and a half year old infant was forced to climb high on her mother's shoulders as she crossed a stream bipedally. Only by clinging to her mother's head was she able to remain dry.

Insect pests

An extreme case of insect related events is discussed later in the chapter (pg 80). However, on a day to day basis, observations indicated that gorillas were often pestered by insects. In most adults, this was evident by the frequent swatting of one or other hand onto the shoulders or head. This was a rapid gesture performed many times during a given visit. Occasionally water would be splashed over the shoulders, though it is not certain if this was a deliberate action, or an accidental effect of feeding in a flooded zone. A visible increase in the frequency of swatting was observed among CLI group in May 1999 as a reaction to the presence of the small biting fly *Stomoxys* sp. Three days later, another group appeared so bothered by the flies that they hurredly fled the bai, constantly slapping and swatting at their shoulders. CLI group were bothered by honey-bees on one occasion. Most individuals were observed to swat above their heads from time to time, but juvenile Wendy became increasingly distracted and swatted frantically above her head before running screaming for several meters. Her mother immediately came to her aid and took the juvenile ventral, where she suckled. Appendix A3.2 gives details of what may be the only example of possible tool-use by the Mbeli gorillas, in which food plants appeared to be used as insect swatters by some individuals.

Direct effects of rainfall on gorilla behaviour

Although rainfall may at times be extremely heavy, and particular times of year receive significantly more rain than others, the overall chance of rain on any given day, averaged across the year, is actually quite low. Using the full-year data from 1998, it is found that rain falls once every five and a half days, or, on any given day there is an 18% chance of rain ('day' in these examples referring only to the hours of daylight). Therefore, although a common climatic phenomenon for the gorillas of Mbeli, it is by no means a daily or regular event. Gorilla reactions to rain, and in some cases lightning and thunder, varied across groups and individuals, and over time. Some individuals exited the bai, while others adopted a huddled posture and waited for the rain to ease off before a resumption of feeding. Examples of these and other reactions to daily weather conditions are given in Appendix A3.3.

The frequent observation of yawning by gorillas during prolonged and heavy rainfall prompted an examination of the yawning phenomenon in gorillas and other primates. Data were collected on the weather conditions coinciding with all cases of yawning by gorillas at Mbeli and analysis suggested two potential hypotheses. These are presented and discussed in detail in Appendix A3.4.

Encounters with other species

As described briefly in Chapter 2, the bai provides valuable resources for many different species, from elephants extracting minerals to black-shouldered kites (*Elanus caeruleus*) and marsh harriers (*Circus aeruginosus*) hunting for the apparently abundant numbers of rodents living in the waterlogged substrate. Not only does the bai represent a unique habitat in its own right, complete with its own set of complex inter-relationships and species, but it also provides a rare, if not unique, opportunity to view species of the forest that are seldom, if ever, seen in the open. With regard to gorillas, the bai offers an opportunity to record ape reactions to, and interactions with, other species that would be impossible to witness in the forest. Some of these interactions may be considerably more frequent in the bai, and the open habitat may alter the nature of some compared to what may take place in the forest, but they do provide an insight into the situations the gorillas (and other species) may perceive as threatening and those that appear to arouse something akin to curiosity or even indifference.

Elephant

At Lopé, gorillas have been known to move nest sites during the night to avoid the passage of elephants (*Loxodonta africana cyclotis* – pers. obs.). Gorillas at Lopé also made more tree nests than ground nests during a mast fruiting period for *Celtis tessmannii* (Ulmaceae) when the crop attracted gorillas and large numbers of elephants into the same limited area (Tutin et al., 1995). Aggressive auditory displays have also been exchanged during accidental meetings during daylight hours (pers. obs.). Elephant females have been known to be aggressive in defense of their young, and musth males can be unpredictable and dangerous (Estes, 1991; pers. obs.). Schaller (1963) observed no direct interactions between the species and noted that gorillas did not abandon their nests when an elephant passed less than 20m from the site. At Mbeli reactions were varied, but most showed at least the wish to monitor the location and activity of elephants. TSB group watched an adult female elephant feed 40m from them without incident, and on another occasion the silverback and blackback monitored an adult from 55m. For about five minutes, one of GEO group adult females watched two sub-adult bull elephants sparring, and the females of CLI group all stood bipedally to scan five elephants feeding noisily in the stream 300m from them. TSB group were particularly calm, and fed peacefully within 35m of a bull elephant, and Travis and Stockwell, who fed at 20m of a bull and a female, only occasionally glancing up.

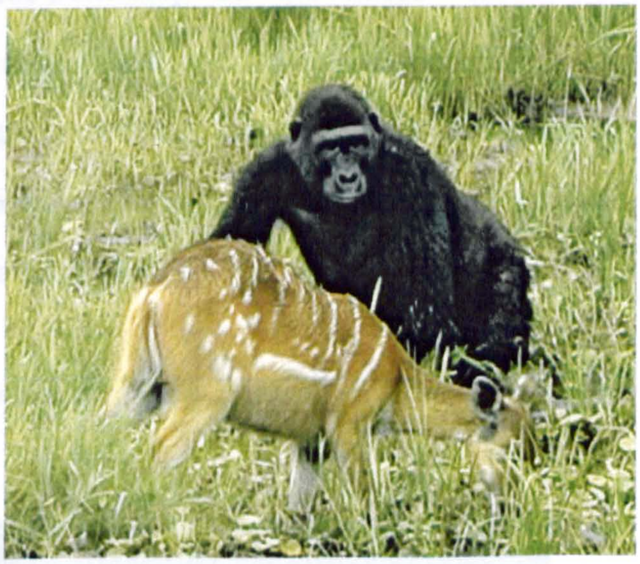
On four occasions, gorillas calmly moved away from elephants but remained in the bai, and on one occasion calmly exited the clearing. Where animals did react strongly, it was more often females and juveniles: one unknown female grabbed her offspring and placed it on her back before running directly away from the elephant she had just spotted 45m away. On seeing the elephant and her reaction, another female and infant, two sub-adults and a juvenile also ran away. The elephant in question ignored the gorillas completely. Only once the gorillas had formed a tight group at 75m did they turn and scan the elephant and resume feeding, albeit with frequent scans. All but one of Caravaggio's four females moved swiftly towards the bai edge on seeing an elephant enter 60m away: juvenile Kendal was particularly alarmed. In NOO group also, juvenile Dill was the only individual to begin a retreat towards the bai edge when an elephant approached to 25m. He stopped, however, when no other group members reacted other than to scan the elephant. Silverback George and blackback Homer both exited the bai rapidly on seeing elephants, the latter in some panic.

On only two occasions did elephants act aggressively towards gorillas. Caravaggio was observed crossing a corner of the bai very rapidly shortly after a female elephant and her juvenile daughter entered nearby. The juvenile then made several mock charges towards the bai edge where it is believed the rest of the gorilla group were, having only just exited. Caravaggio once back in the forest made two loud hoot-series chest-beats, to which the elephants raised their trunks to scan for scent. The juvenile elephant appeared agitated and exited the bai soon afterward, though the mother remained to feed. The other occasion involved an adult female elephant charging at solitary silverback Frank. Although an impressive display through shallow water, Frank did not respond with anything other than a glance, and the female halted 25m from him, turned and wandered back towards her offspring and other group members.

There can be little doubt that elephants have the capacity to severely injure or kill apes, and their occasionally aggressive and temperamental nature make them worthy of respect. In the forest, gorillas may have the added safety of access to the canopy, while in the bai they are at the same time more vulnerable to being chased and more able to monitor the location of elephants and adjust their own proximity accordingly.

Plates 3.2 Blackback gorilla feeding within 25m of an elephant

Plate 3.3 Blackback observes an adult female sitatunga at 3m.



Sitatunga

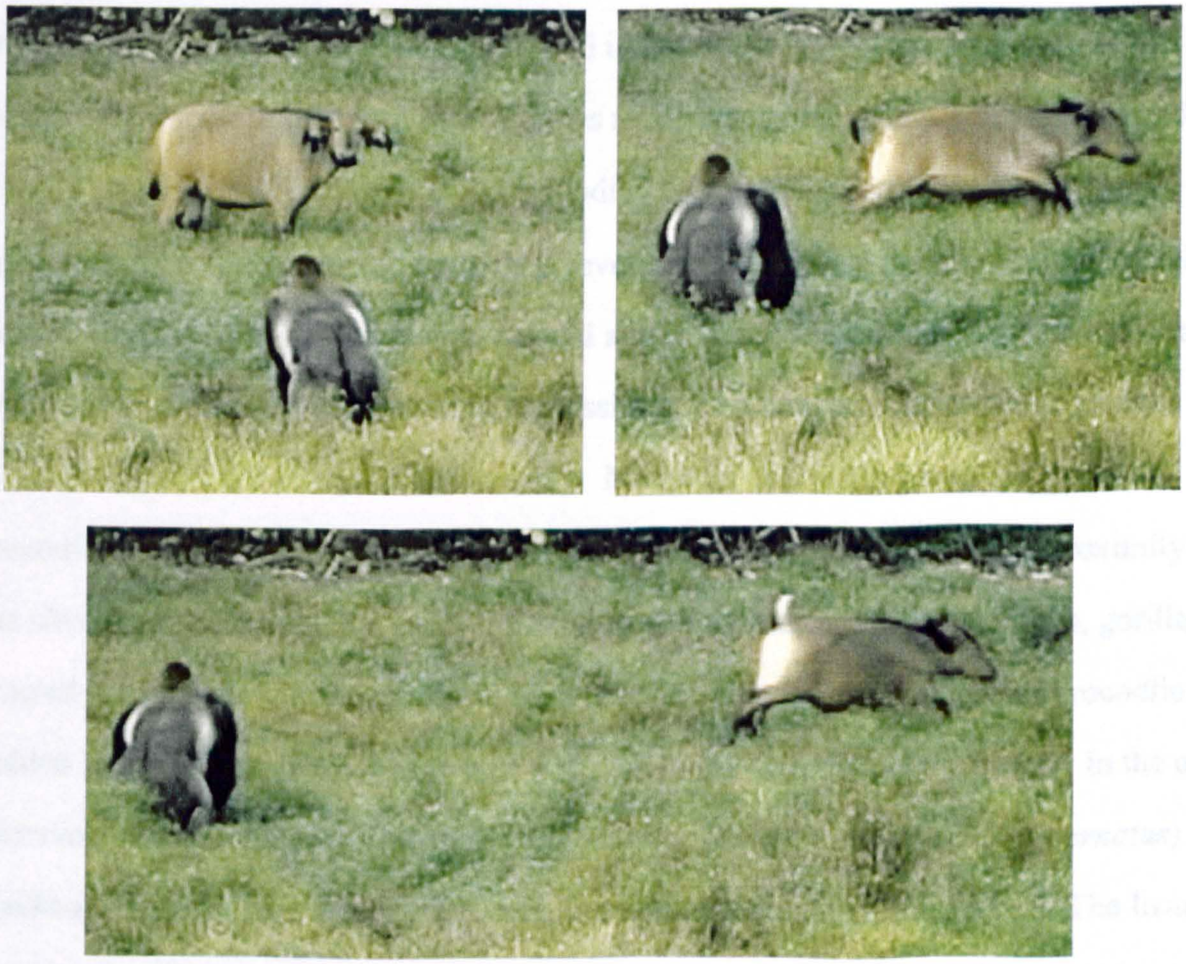
Unlike elephants, sitatunga antelope (*Tragelaphus spekei*) are resident at Mbeli, and their presence more ubiquitous. Sitatunga show considerable sexual dimorphism, with males much larger than females and sporting large pointed horns. Many reactions reflected a greater sense of alarm to males than females, and in some cases reactions were extreme (*see* Appendix A3.5).

Responses to the smaller, horn-less female sitatunga were generally very different. In several cases antelope and gorilla fed in very close proximity. On others, juveniles and females were observed watching sitatunga and some individuals clapped their hands towards them. Some bolder adolescent males were even observed chasing and displaying at female sitatunga (*see* Appendix A3.6).

Buffalo

Schaller (1963) records tolerance between gorillas and buffalo in the Virungas, though describes the apparent displacement of a buffalo by an adult female; a feat executed by merely ambling toward the other. At Mbeli, reactions to buffalo (*Syncerus caffer nanus*) were less numerous and mostly involved occasional monitoring or slight evasion. Solitary silverback Bear, however, displayed at buffalo on two occasions. On one of these, the buffalo ignored his tight-lipped lateral charge, though on another occasion his direct charge at a sub-adult caused it to flee into the forest (*see* Plate 3.4). On no occasion were reactions to ungulate bai visitors ever thought to be related to food competition (little overlap in food species was present) but appeared more to do with a general intolerance of proximity, potentially influenced by past experiences (likely in the case of Duke's group), and at times seemingly provoked by little more than whim.

Plate 3.4 Solitary silverback Bear charges at, and displaces, an adult forest buffalo



Crocodiles

The crocodile species primarily seen in the bai (*Crocodylus cataphractus*) was never observed feeding, but was of a size such that larger mammals were unlikely to be considered prey. However, even elephants appeared alarmed by their presence and displayed at them (pers. obs.). Gorillas were also very concerned at the proximity of this species. It is not inconceivable that a disturbed crocodile might take a defensive bite at an unsuspecting gorilla, however, the following observations are in most cases, probably examples of observational conditioning whereby young group members learn to fear crocodiles from the responses of older group members, though never having had any direct negative experience of them. The widespread fear of snakes in primates has been shown to be subject to transfer via such observational conditioning (e.g., Mineka et al., 1984; Cook et al., 1985) and this may also be an important factor in gorilla responses to crocodiles at Mbeli.

NOO group once became very alarmed and stared fixedly at a crocodile approximately 12m from them. Several individuals, including a blackback retreated rapidly from the area. The motherless juvenile Dill immediately sought the proximity of the silverback, who in turn barked several times at the crocodile. A sub-adult approached to 7m and stood bipedally to gaze at the crocodile, then retreated from the area. The silverback then cough-grunted towards it several times, causing no reaction. Eventually, it moved away and the gorillas slowly calmed and resumed feeding. Bones, the silverback of BON group was observed advancing aggressively with cough grunts towards another crocodile, which retreated and swam away. Members of Duke's group discovered a crocodile about 10m from them. Screams were heard and the group sought proximity to the silverback, who led them away from the area. On three separate occasions, gorillas reacted to crocodile vocalisations. In each case, the response, even with the crocodile well hidden almost 100m away, was to turn and scan in the direction of the sound. In the only observed interaction between a gorilla and monitor lizard (*Varanus niloticus ornatus*) blackback Bayleaf became slightly tense, but remained to watch it from 5m. The lizard continued on its course and did not flee at speed as would be expected from reactions to humans.

Other species

Bongo (*Tragelaphus eurceros*) have only ever been seen at Mbeli for a few weeks during a period of fly infestation (*see* pg. 80). As such, they may have been unfamiliar to some groups. This was evidenced by the reaction of NOO group to spotting them. The group had been feeding comfortably 25m from a group of buffalo when they spotted two bongo. The reaction of most of the group can best be described as one of consternation and fear. All but blackback Bayleaf rapidly fled the area. Bayleaf remained at 25m and fed, while scanning the bongo, then splash displayed (*see* Appendix 7) and charged, before rejoining his group. The bongo remained impassive throughout. TRA group also reacted strongly when two bongo strode through a stream in their direction. All group members fled rapidly for the forest edge, only the silverback lagging behind and turning frequently to monitor the bongo.

The incidence of **colobus** monkeys (*Colobus guereza*) in proximity to the gorillas was infrequent. On one occasion a silverback made a short run and chest-beat display towards the bai edge where a group of colobus sat in low bushes waiting to enter the clearing. On another occasion, a colobus approached MOS group and fed 4m from the juvenile Iook. All four gorillas stopped feeding to observe the monkey, the juvenile standing bipedal, and then resumed feeding.

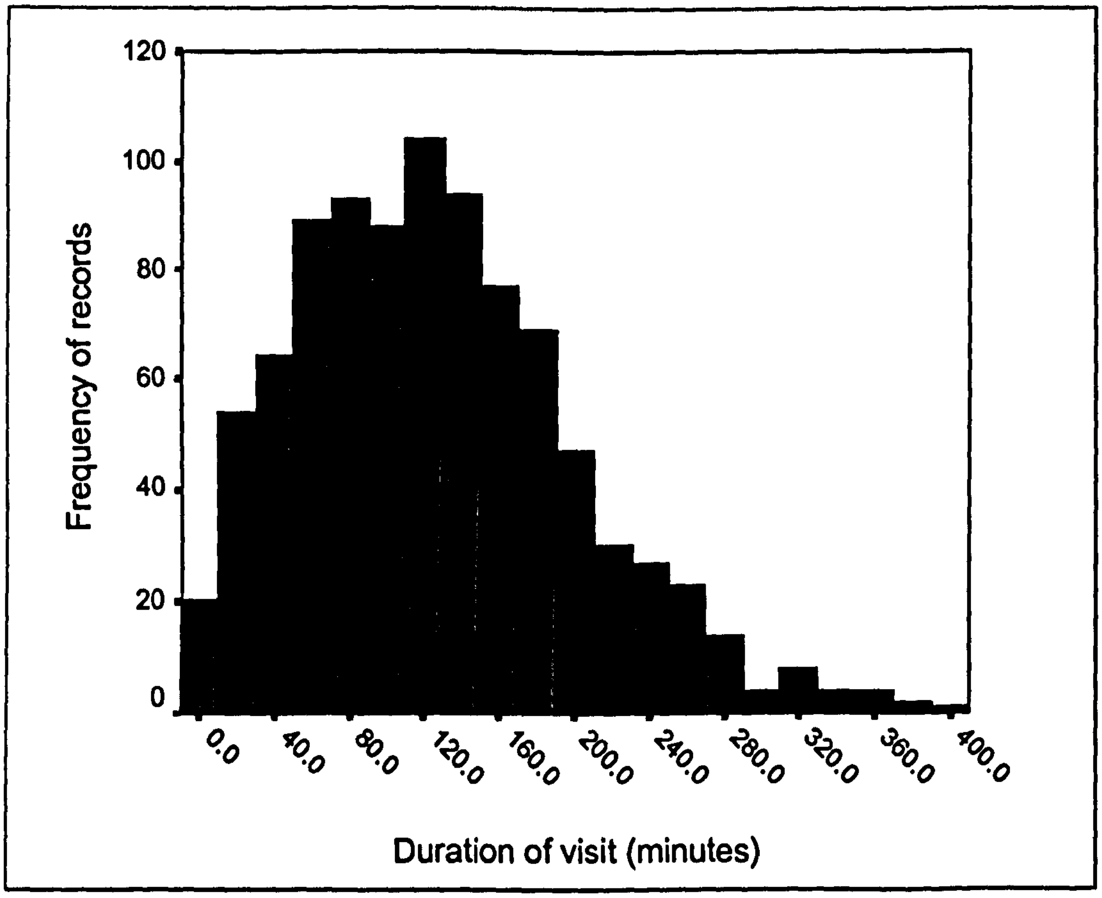
In reaction to the proximity of a **Congo clawless otter** (*Aonyx congica*), one blackback 5m away gently sloshed water towards it in an apparent attempt to provoke a reaction. Silverback Mosombo once barked at an otter that swam 3m from him and an adult female, and immature males Redstripe and Bogplant both watched an otter swim past them at 4m with what appeared to be mild interest before resuming feeding.

Insectivorous **birds** can benefit by feeding in the vicinity of mammals that disturb and flush prey during their passage. Ruggiero and Eves (1988) have shown that jacanas (*Actophilornis africana*) have a higher peck-rate in proximity to foraging gorillas than when alone. Jacanas are abundant at Mbeli and gorillas largely ignored their activities. Other birds such as eagles, herons and storks caused alarm in gorillas when landing unexpectedly near them. Details of such encounters are given in Appendix A3.7.

Visit duration

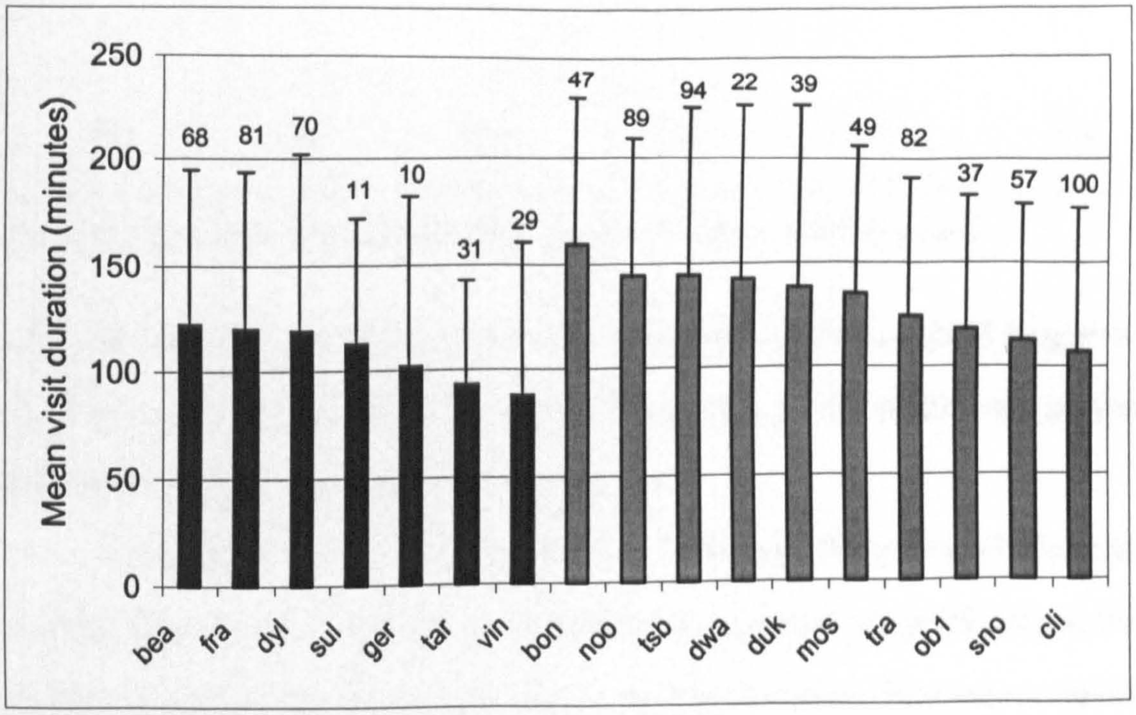
Using all records from January 1997 to October 1999, a total of 1066 bai visits by social units were used to calculate average visit length. Mean duration was 122 minutes (SD = 75, range = 1 to 405mins). Figure 3.5 shows the frequency of visits of different duration as a histogram.

Figure 3.5 Duration of bai visits by frequency



Mean duration was compared for groups and solitary males (excluding all units with less than 10 scores, and excluding GEO due the ambiguous nature of his unit and changeable numbers of individuals visiting the bai). Mean visit duration for solitaries was 114min (SD = 74, range = 4 to 350), and for groups, 131 (SD = 73, range = 3 to 393). The difference between means was significant (independent samples *t*-test; *t* (914) = -3.42, *P* = 0.001). One explanation for such differences may be that more efficient feeding (due to reduced scramble competition) in solitary males, allows them to be satiated more swiftly. Although no silverbacks were ever seen to be displaced from a feeding spot by a member of their own group, the harvesting of resources by other members in the vicinity of the silverback may force him to forage slightly further or longer. A Pearson's Correlation showed a significant positive correlation between the average size of each unit over the study period (weaned individuals only), and its mean visit duration ($r = 0.531$, N = 17, $P = 0.028$); thus units with more members stayed longer in the bai per visit. It should be noted, however, that when solitary males were excluded from the analysis, significance in the correlation was lost ($r = -0.103$, N = 10, $P = 0.778$). Figure 3.6 shows mean visit duration in minutes for seven solitary males and ten groups.

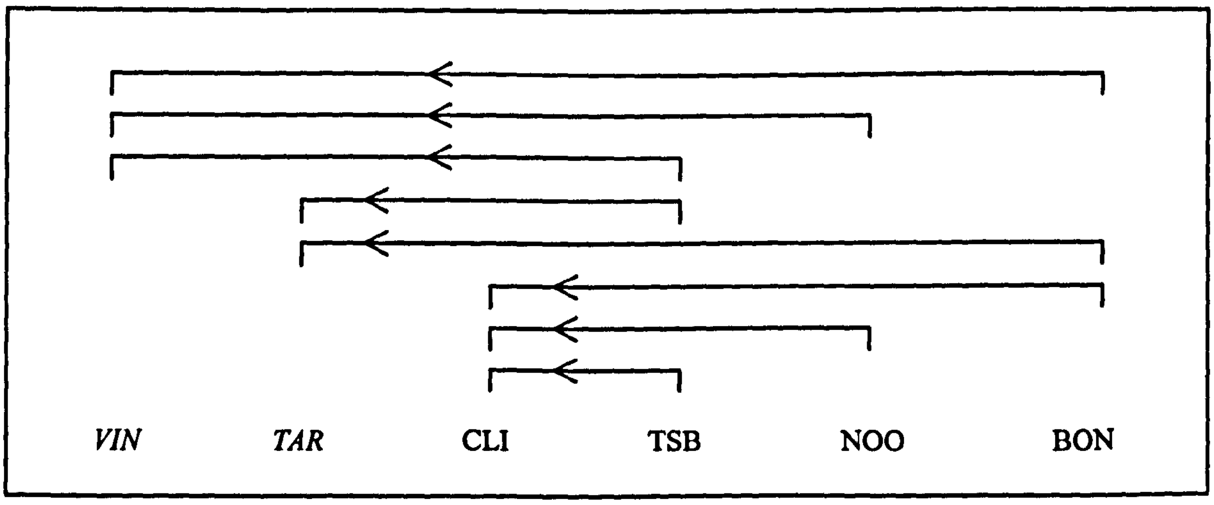
Figure 3.6 Mean visit duration per unit



N shown by the values above the error bars.
Error bars give standard deviation. ■ Solitary silverback; ▨ Group.

With all units compared (solitaries and groups), a one-way ANOVA indicated significant differences in visit duration: $F = 3.172$, df = 16, $P < 0.001$. Figure 3.7 (generated by Tukey post-hoc comparisons) illustrates where significant differences occurred. Only three of 16 units had mean durations significantly lower than the three units with the longest average duration (differences were significant at $P < 0.05$, except for CLI – BON and VIN – BON for whom $P < 0.01$); all other comparisons were non-significant. As illustrated, two solitaries and one group showed durations significantly lower than others. No solitary had a mean duration greater than a group. In the case of TAR, his very recent emigration to solitary status may have rendered him more cautious and fleeting in his bai-use. However, VIN had been solitary throughout the study and was at ease with proximity to researchers. His mean score suggests, however, that his tolerance for other gorillas or other aspects of the bai habitat may have been below average.

Figure 3.7 Significant visit duration differences following Tukey post-hoc comparisons



Arrows indicate direction of the significant effect. The solitary males are indicated in italics.

It may be difficult to satisfactorily examine why some units may spend longer in the clearing than others given the potential for idiosyncrasies of character and personal preference in silverbacks and other individuals.

Weather conditions may play a role in influencing the general characteristics of visit duration. Using all bai visits over the full study period, a significant positive correlation was found between temperature and visit duration (Pearsons correlation; $r = 0.138$, $N = 321$, $P = 0.013$). However, when the variables were plotted against each other in a scatterplot, it was evident that enormous variation was present, and that as it stood, little confidence could be placed in the test statistic.

As an alternative approach, another test took all visits where the weather conditions were given as 'full sun', and all visits recorded as 'heavy rain', and compared the mean visit duration for each set. No significant difference was found between the means ($t = 1.39$, $df = 48$, $P = 0.171$). A significant difference was found, however, by comparing visit duration for visits representing the bottom and top tenths of all temperature records for 1999. Mean duration for the low temperature visits was 105min (SD = 81) and for the high temperature visits, 151 (SD = 56); $t = -2.926$, $df = 76$, $P = 0.005$. Low temperature itself may be a factor, but it should be pointed out that of the low temperature sample, 54% (21 of 39 records) showed that it had rained during the visit, whereas the high temperature sample returned a 10% (4 of 39) record of rain (only one case of which was heavy, while 15 low temperature records were). This result suggests that gorillas may cut short their visits during cold, wet weather. The mean visit duration for the high temperature sample is above the mean visit duration, suggesting that high temperatures did not force gorillas from the bai.

In general, the data for visit duration show a surprising lack of variation, and a possibly more interesting question than trying to interpret individual unit traits is to consider why the mean visit duration was not higher, given the apparently abundant food resources available in the bai. Why do units not spend, on average, more than approximately two hours in the bai at a time? As the histogram in Figure 3.5 shows, relatively few units remained at the bai over approximately three to four hours. Furthermore, departures from the bai followed by re-entries on the same day were extremely rare.

Plant intake and water content: method

An important variable with regard to visit duration may be the nature of the food available in the bai. All of the plant species consumed by gorillas in the bai are aquatics, a characteristic of which is a high water content. In an attempt to gauge something of the energetics of feeding in a *Hydrocharis chevalieri* swamp, advantage was taken of a brief period of unavoidable human disturbance at the observation platform to harvest *Hydrocharis* plants.

A typical dense area of *Hydrocharis* swamp with relatively easy access from the bai edge was selected. Once in the center of the patch, the researcher obtained a compass bearing using random number tables. Facing in the direction of the bearing, the researcher tied a marker tape to vegetation at the point his fully stretched out arm reached in front of him (without bending forwards). Another tape was placed having turned 90° to the right. The researcher then harvested all *Hydrocharis* plants within the marked quarter segment. The sampling rationale behind this method was that the collected plants represented approximately one quarter of the *Hydrocharis* plants that an adult gorilla could harvest by remaining in the same location and merely rotating his or her body through 360°. The collected plants were then washed, drained of excess water, split into component parts (leaf and stem, root, rhizome), counted, weighed and then laid to air-dry in the sun on aluminium trays at Mbeli camp. The node connecting stems to roots and rhizomes was occasionally eaten by gorillas, but the rarity of this influenced the conservative decision to omit these parts from the analysis. Plants were re-weighed periodically until no further weight loss was recorded and the sample could be considered dry. At this point the entire sample was once again weighed and the water content calculated.

Results

Table 3.1 gives the wet weight values for each component part of the plants harvested, followed by an extrapolation to the weight for the whole area obtainable without changing location (calculated at 2.7m²). These are followed by dry weights for the same two cases. All values are in metric grams. As the table shows, an adult gorilla sitting in the location selected for the sample would have had available to it an astonishing 23.6kg wet weight of *Hydrocharis* without having to move. This translates to 1.8kg dry weight of food.

Table 3.1 Wet and dry weights of *Hydrocharis chevalieri* from a single feeding location.

Plant part	Sample wet weight (g)	Whole patch wet weight (g)	Sample dry weight (g)	Whole patch dry weight (g)
Leaves and stems	3276	13104	295	1180
Rhizomes	1130	4520	76	304
Roots	1376	5504	66	264
Shoots	129	516	7	28
TOTAL	5911	23644	444	1776

Time and disturbance constraints did not allow the harvesting of plants from other patches within the bai. However, as a rapid means of adding somewhat to the sample size, two other locations were selected using the same methodology. With these plots, however, plants were not harvested, but leaf bearing stems were counted. Counts made during the processing of the main sample showed that the ratio of stems to leaves and roots was fairly constant; thus by examining the proportion of stems from the new samples against the number from the weighed sample, it was possible to estimate the total biomass of edible parts represented by the number of stems. Two further such counts were made and both yielded lower numbers of stems, and thus total food weight. The weighed sample contained 543 stems while the subsequent two yielded 360 and 339 respectively (counting *in situ* probably underestimated the numbers of stems as compared to the complete harvesting method, but probably not enormously so). By reducing the weighed sample wet weight by the same proportional reduction observed in the number of stems, wet weight samples of 3901g and 3664g were derived. Multiplied to give values for the whole patch, these yield 15.6kg and 14.7kg wet weight respectively. Using the same reduction ratio observed through drying of the weighed sample, it is estimated that the new patches would have yielded 1.2kg and 1.1kg of dry weight food respectively. A sample size of three is clearly inadequate to describe vegetation density in any habitat type. However, mean values of 18kgs wet weight (SD 4.9) and 1.4kgs dry weight (SD 0.4) are probably a reasonable guide to the quantities of *Hydrocharis* that can hypothetically be consumed without changing position in an average density patch at Mbeli. Figures from the weighed sample, of 23.6kgs and 1.8kgs respectively, probably represent the upper limit of food availability in such a feeding patch.

Plate 3.4 *Hydrocharis* plant parts harvested from one sample plot at Mbeli

Gorillas are clearly able to consume large amounts of food speedily and with little energy expenditure while in a *Hydrocharis* marsh. The plants are not physically defended and require only moderate processing (Parnell, 2001). However with a water content averaging 94%, the food itself is inefficient in terms of the quantity that must be eaten to contribute a given dry weight of food. It is hypothesized then that the principal cause of homogeneity in the visit duration data may be the abundance of food and a relative lack of variability in the time taken for the gorillas to reach satiety. Using figures for stomach or gut capacity as a guide to intake and appetite is problematic due to issues of expansion, and transfer of ingesta to the small intestine. However, as a simple point of reference, Chivers and Hladik (1980) give a value for the volume of a gorilla stomach (from one sample) as 3370 cubic centimeters. Clearly, this is well below any capacity to deal with the weight of food available, based on the *Hydrocharis* harvesting sample. Under the satiety hypothesis, silverbacks, with their larger gut capacity should feed for longer than adult females (given equal processing times). At Mbeli, data were taken on the order of departure of individuals from the bai, but unfortunately this did not take into account the actual timing of departures or the activity of group members prior to departure. In some groups, it was evident that immatures and females stopped feeding well in advance of the silverback and rested or fed at a very reduced rate until he was ready to leave before departing the bai as a group. In BON group, the elderly and infirm silverback Bones was the first to leave the bai on 48% of 27 visits and was last on only 11%. Bones was often observed resting while his group fed, indicative perhaps of a reduced appetite or a disinclination to eat due to dental atrophy (the elderly silverback Porthos, on whom a post mortem was carried out at Lopé, was found to be suffering from multiple cases of tooth decay and abscesses which would have caused him considerable pain and may have led in part to his loss of condition and eventual death at the hands of another silverback – Tutin, pers. comm.). Another apparently elderly silverback, Mosombo, was also seen to leave the bai before the rest of his group on 50% of occasions, while leaving last on only six (N = 18). By contrast, Caravaggio, the silverback of SNO group, was last to leave the clearing on 87% of the 15 occasions examined and first to leave on only 7%. Caravaggio was frequently seen feeding in the clearing long after his females had left, and could occasionally be heard hooting in order to locate them when he finally re-entered the forest. Lack of precision with regard to actual feeding time and activity prior to departure therefore render this data set inadequate to verify the satiation hypothesis for visit duration. It is suggested that group composition, silverback age, and other personal idiosyncrasies may influence results. Future studies would do well to record the total time spent feeding, and the feeding rate for each age/sex-class.

In some species (e.g., wilderbeest – McNaughton, 1977), grazing has been shown to benefit the quality of the grassland utilised. It has been shown that gorilla foraging increases both the quality and density of herb food resources on a time scale relevant to gorilla patterns of re-visitation (Bullock, 1978, 1981; Watts, 1987). This is highly unlikely to be a factor influencing gorilla bai-use, however, due to the enormous level of range overlap, and the large number, and unpredictable visitation patterns, of the units concerned. It would nevertheless be useful in future to establish some fixed plots either at another site or close to the observation platform at Mbeli and measure growth rates and productivity in a protected area against one artificially 'grazed'.

Seasonal influences on bai-use

Figure 3.7 shows the number of hours gorillas were visible at the bai, for each year of the study period, expressed as a percentage of the number of hours of observer time at the bai. The number of hours represented by the columns range from 31 to 106, with a mean of 56 hours (SD 20). Interpretation of this data is not easy given the loss of the second half of 1997, and the termination of the study two months prior to the end of 1999. However, one potentially interesting feature can be discerned. For two years, gorilla presence drops dramatically between the first and second months of the year; a third year shows a slight increase. However, two years then show a marked drop in presence corresponding to April and May. A third year fails to show this drop, but remains at a relatively static level. Following the trough, all years rise towards August which is the peak month in one year. Two years then show a determined drop until October, when data stop for all but one year, which shows a recovery towards the end of the year.

Figure 3.7 Percentage of observer time that gorillas were visible

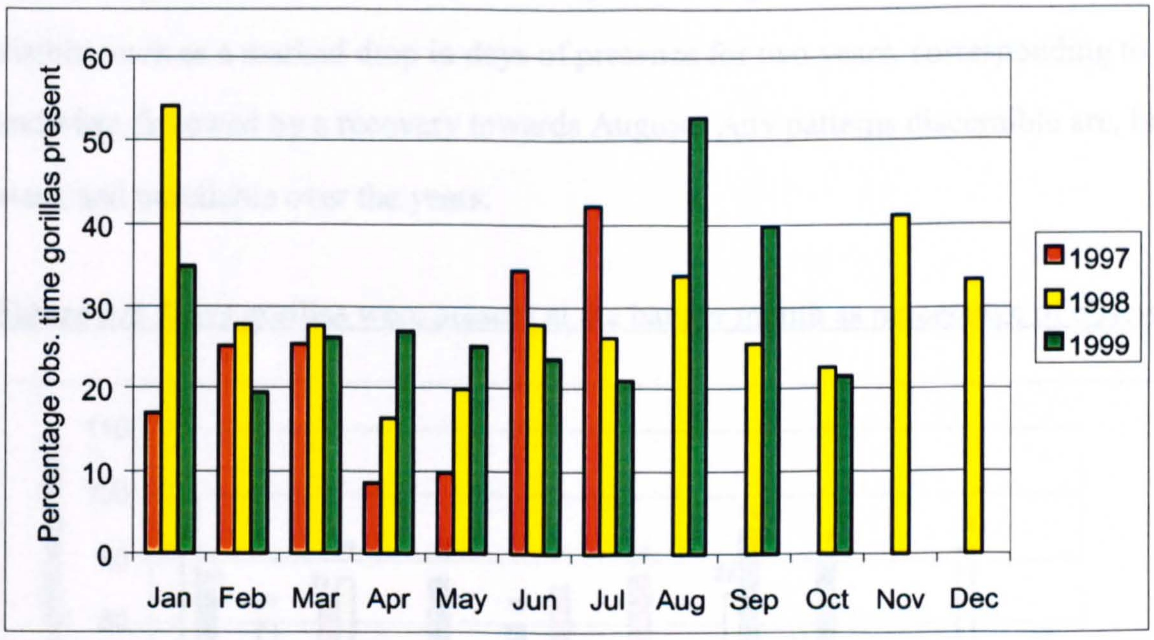
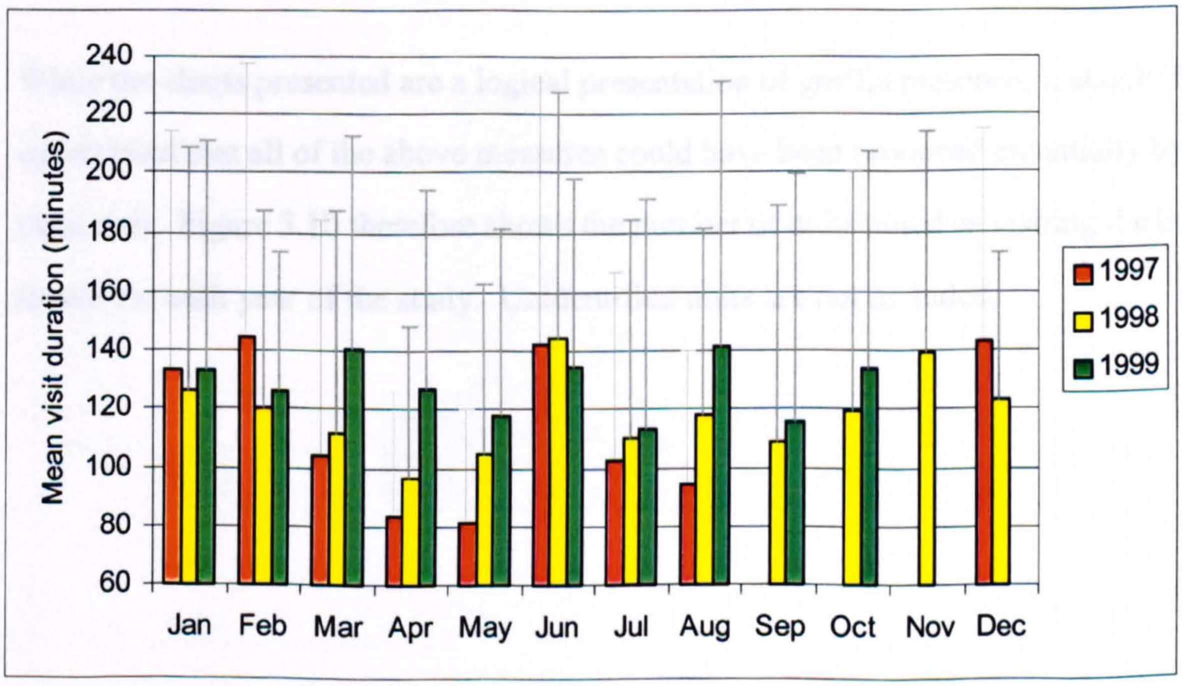


Figure 3.8 shows data over the same three years relating to mean visit duration per month. The chart indicates the same depression in gorilla presence in April and May and a subsequent rise in visit duration in June, but then shows duration falling off again in July, and for two years rising again in August and falling slightly in September. As for minutes of presence, visit duration appears to rise again towards the end of the year.

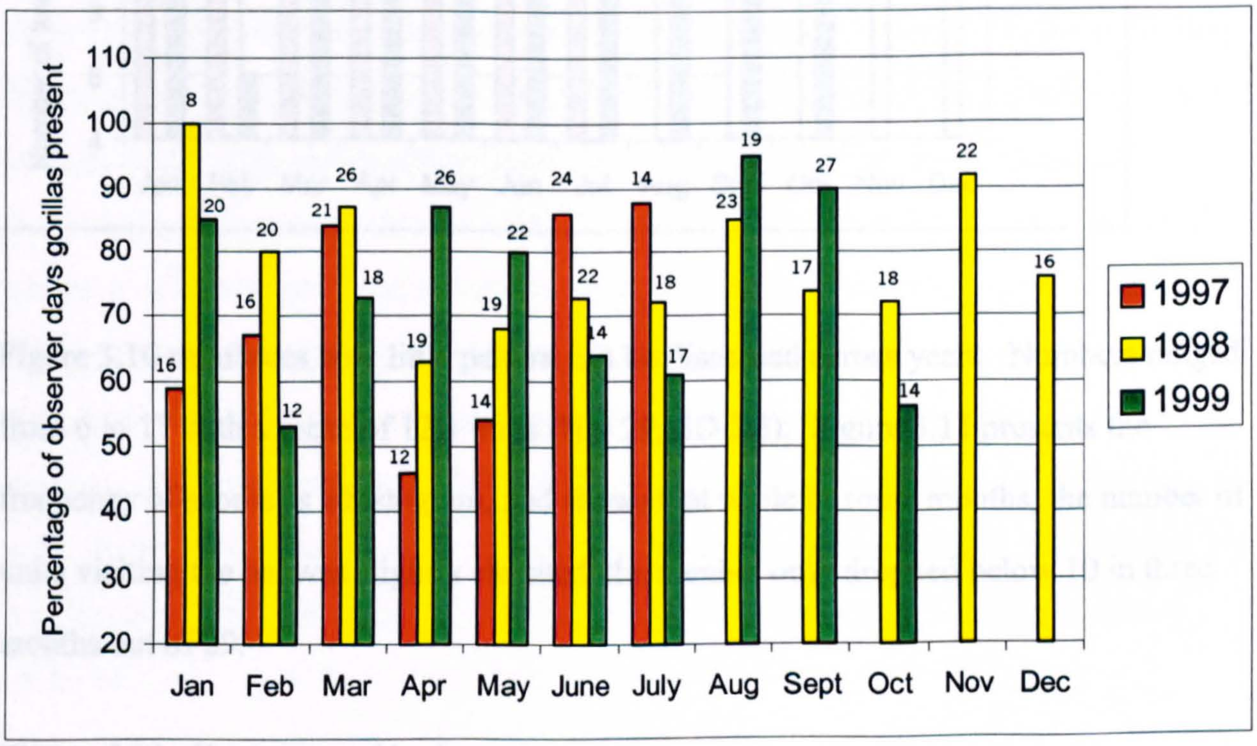
Figure 3.8 Mean visit duration per month (minutes) for each year of the study period



Error bars indicate standard deviation

Finally, Figure 3.9 shows the number of days per month gorillas were present at the bai as a percentage of the number of observer days. Once again, some similar patterns are visible, such as a marked drop in days of presence for two years, corresponding to April and May, followed by a recovery towards August. Any patterns discernible are, however, weak and unreliable over the years.

<u>**Figure 3.9** Days gorillas were present at the bai per month as percentage of observer days</u>



N given above each column

While the charts presented are a logical presentation of gorilla presence, it should be appreciated that all of the above measures could have been produced essentially by the same unit. Figure 3.10 therefore shows the number of units noted as visiting the bai each month for each year of the study. Unidentified units are not included.

Figure 3.10 Number of units to have visited the bai each month

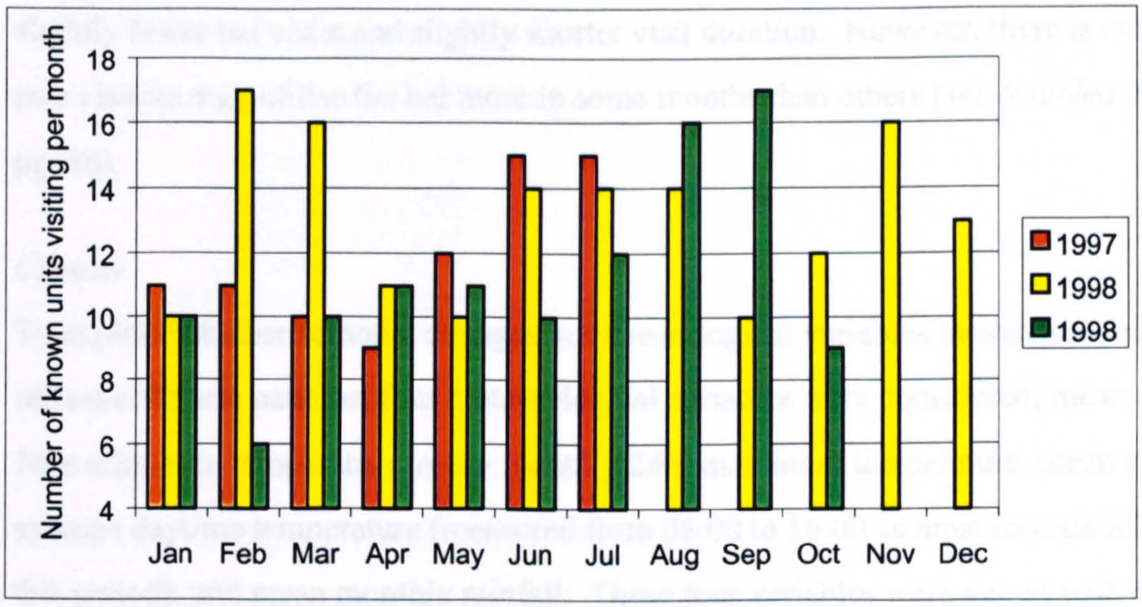
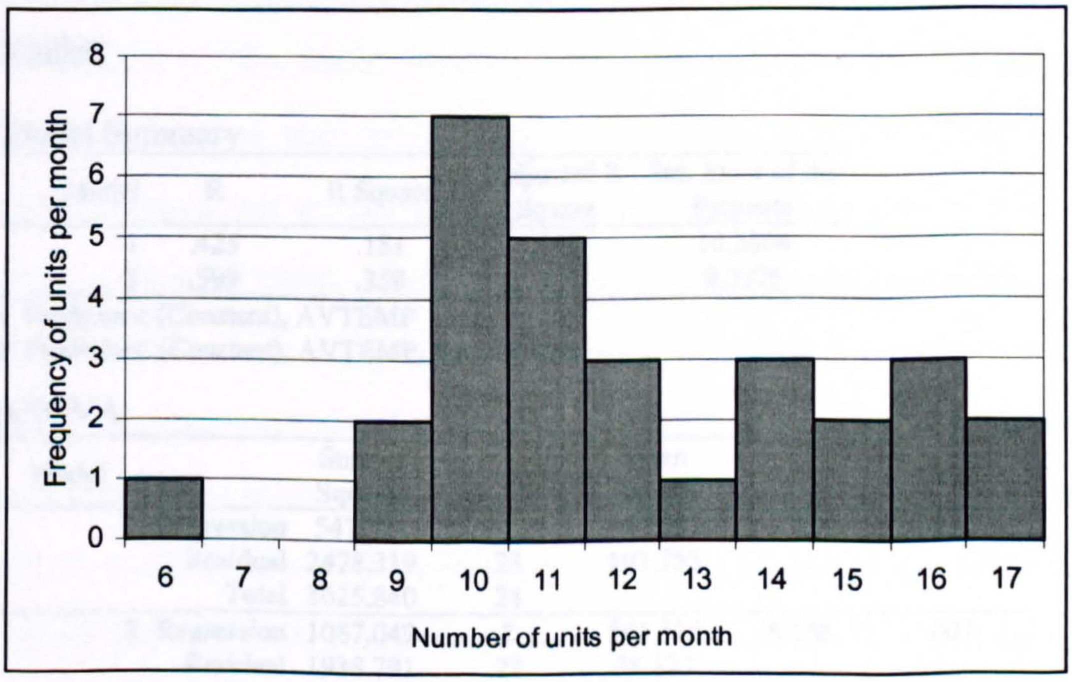


Figure 3.10 reinforces how little pattern can be discerned across years. Numbers ranged from 6 to 17 with a mean of 12.1 units (N = 29, SD 2.8). Figure 3.11 presents the frequency of scores as a histogram, and shows that while in some months, the number of units visiting the bai was slightly elevated, the number only dropped below 10 in three months out of 29.

Figure 3.11 Frequency of 'units per month' scores



This suggests that gorilla units are not generally leaving the area in any particular season, but that the low rates of presence associated with April and May result primarily from slightly fewer bai visits and slightly shorter visit duration. However, there is evidence that rare visitors may utilise the bai more in some months than others (*see Nauclea* fruiting – pg. 86).

Climate

To explore whether seasonal changes in meteorological variables themselves may have influenced these patterns, four meteorological variables were considered; mean monthly 24hr minimum temperature, mean monthly 24hr maximum temperature, mean monthly average daytime temperature (measured from 08:00 to 16:00 as most records fell within this period), and mean monthly rainfall. These four variables were paired with one of three measures of gorilla presence in turn (mean visit duration per month, gorilla minutes at the bai as a percentage of observer minutes expressed as monthly means, and number of units visiting the bai per month) and examined through stepwise multivariate regression analysis. No correlations were found with any variable and visit duration or numbers of units visiting the bai per month. However, as the results below indicate, a significant result was indicated with the variable 'gorilla minutes as a percentage of observer minutes' (grilmins).

Figure 3.12 Results of stepwise multivariate regression analysis for gorilla presence and weather

Model Summary

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.425	.181	.145	10.3804
2	.599	.359	.301	9.3876

a Predictors: (Constant), AVTEMP
b Predictors: (Constant), AVTEMP, RAINFALL

ANOVA

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	547.521	1	547.521	5.081	.034
	Residual	2478.319	23	107.753		
	Total	3025.840	24			
2	Regression	1087.049	2	543.525	6.168	.007
	Residual	1938.791	22	88.127		
	Residual	1938.791	22	88.127		
	Total	3025.840	24			
	Total	3025.840	24			

a Predictors: (Constant), AVTEMP
b Predictors: (Constant), AVTEMP, RAINFALL
c Dependent Variable: GRILMINS

Coefficients

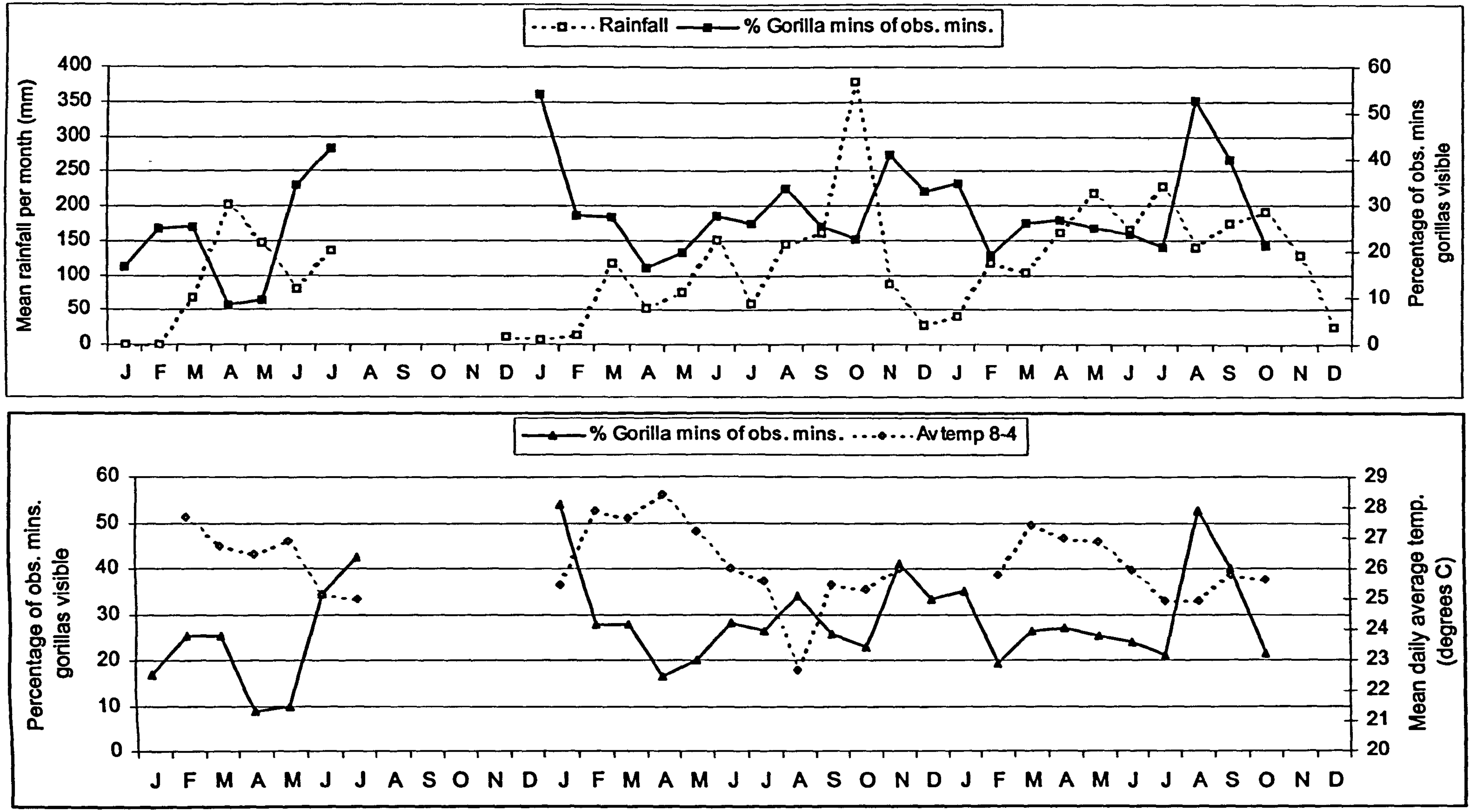
		Unstandardize Coefficients		Standardized Coefficients	t	Sig.
Model		B	Std. Error	Beta		
1	(Constant)	131.398	45.881		2.864	.009
	AVTEMP	-3.959	1.756	-.425	-2.254	.034
2	(Constant)	172.811	44.742		3.862	.001
	AVTEMP	-5.216	1.668	-.560	-3.128	.005
	RAINFALL	-6.372E-02	.026	-.443	-2.474	.022

a Dependent Variable: GRILMINS

As the results show, minimum and maximum monthly temperature did not significantly improve the model. However, this may have been because both are related to average daily temperature, and thus may not have been independent. Average temperature was the most important predictor of gorilla presence, with a significant negative effect shown. The model was significantly improved by the addition of rainfall data, also in a negative correlation. Thus, it appeared that gorillas were seen less during months with higher average daily temperatures, and months with higher rainfall. Figures 3.13 and 3.14 show average monthly temperature against gorilla presence and against rainfall. Data points are shown over the whole study period from January 1997 to October 1999.

The chart for average daily temperature appears to agree with the regression findings, showing reduced gorilla presence each year during the hottest period around April and May. The rainfall chart is harder to interpret, given the findings of the regression analysis. Certainly, there are two peaks of rainfall that appear to correspond with low gorilla presence, but at other times the two variables almost appear to follow each other (March to August 1998). Earlier analysis on visit duration suggested that gorillas might shorten visits on cold, wet days, however any link to rainfall in seasonal terms may be much less directly correlated to the disinclination to get cold and wet in the clearing, and be more likely to involve proximal mechanisms discussed shortly. The finding that hotter months predicted lower gorilla presence seems contradictory to the earlier finding regarding shorter visits at low temperatures, however some hotter months were not necessarily drier months; reactions to downpours and subsequent chilling on any given day may be independent of the overall average temperature of the period.

Figure 13 and 14 Rainfall and average daily temperature per month plotted with gorilla minutes visible as a percentage of observer minutes



Unfortunately, anomalies may be inevitable when dealing with so short a period as three years, especially when some data are missing. A short study period is also highly sensitive to stochastic events, or non-annual cyclic phenomena. A example of this is the 'fly plague' that hit the Ndoki area in April and May 1997.

Consequences of a major outbreak of biting flies in the Ndoki area

During the last week of March 1997, swarms of small, red-eyed biting flies were detected in the forest and at the bai. The flies were identified as a species of stable fly (*Stomoxys omega* - Huchzermeyer et al., in press), the only representative of its genus in Central Africa. The insects are blood-sucking and cause painful bites in humans. On the daily walk to the observation platform, researchers could amass well over 100 flies on the trouser legs alone in less than a minute. Fortunately, the flies did not follow researchers even to the modest height of 8m. Forest mammals were less fortunate, and distress, loss of condition and death were noted in bongo, sitatunga, and yellow-backed duiker (*Cephalophus sylvicultor*). The fly inundation ended suddenly on around the first of June, 1997. In the intervening two months, in the Ndoki area, 17 bongo were reported dead, 5 yellow-backed duiker, and at Mbeli, 4 adult male sitatunga. During April and May, sitatunga at Mbeli spent almost all daylight hours of every day trying to deter the flies. Head-turning and ear and tail flicking (sending sprays of water from the ears over the back), were performed repetitively but no method did more than send some of the flies airborne for a few seconds. The sitatunga spent considerably more time in the streams than usual.

All four resident adult male sitatunga (N = 4) disappeared during the fly outbreak and have not been seen since. Two of the four males were observed to lose condition over several weeks during the fly period prior to disappearing. Observations after the April-May period confirmed that 4 new adult males began to visit the clearing regularly. The female sitatunga population remained constant throughout April and May, and although their behavior changed markedly (constant head-turning, ear dipping and the majority of the daylight hours spent standing in open water) they were not observed to lose condition.

None of the adult females died or disappeared during the fly outbreak, although one newborn died.

During April and May, the resident Mbeli buffalo group took to spending almost all daylight hours lying in a deep pool in a tightly packed group. This may have maximised their insect swatting potential as the flicked ears of a neighbour or individual to the rear may have deterred flies from another individual's back without it having to turn around or use its tail as often. In a typical week during this period (May 23rd to May 29th), of 56 hourly behaviour scans performed, only eight found the buffalo doing anything other than sitting in the pool. By comparison, the seven days of scans between the June 4th and 12th (omitting two days when no buffalo were present in the bai) gave a total of 62 hourly scans, only one of which found the buffalo in the pool. Despite this extreme change in their behaviour, the nine regular buffalo at Mbeli showed few signs of distress and no signs of extreme weight loss during the fly period.

Bongo were observed in Mbeli bai for the first time in the project's history (three years of prior monitoring) on April 12th. The two most regular visitors were two adult males. For 15 consecutive days from May 12th – May 26th, hourly scan samples of the bongo's location, condition, activity and distance from other species were performed. The two males were the only animals scanned and contributed a similar number of scans for a total of 176 for the 15 day period. During the majority of their daylight hours (86%), the two bongo were standing with their legs partly submerged, in the stream in the same area of the bai. Almost all of their time was spent trying to prevent insects from biting their backs (head turning) (95%). In combination with this action a great deal of time was spent ear dipping, (84% - wetting of the ears in water, then flicking them to create a spray over the back). About half the scans taken showed them to be ruminating, though very few showed feeding (3%). In early May one of the bongos deteriorated in condition. The second male was also seen to lose weight during this period, but to a lesser degree. The weaker male was last seen at the clearing on May 25th and his body was found on May 29th, about 300m. east of the clearing. No signs of predation were found. The second male was last seen in the clearing on June 22nd in moderate condition (his survival, and the importance of the bai in such cases has been confirmed by a report that the same animal was sighted at Mbeli in April 2002, coinciding with another, more minor, fly outbreak [Stokes, pers. comm.]).

While ungulates seemed to spend more time in the bai than usual in order to seek respite from the flies in the water, gorilla behaviour altered surprisingly little during the outbreak, and few signs of overt discomfort were observed. However, as shown in the preceding charts, gorilla presence was down considerably. For all of the following variables, April and May 1997 were the lowest months recorded in the five years that data have been collected at Mbeli: minutes gorillas were visible as a percentage of observer minutes, visit duration, and percentage of observer days gorillas were present. *Stomoxys* flies are seen annually in the area during this period, which may in itself be a strong influence on the generally depressed level of bai-use shown each year during the study period (levels were less depressed in the two years preceding the study [Mbeli Bai Study, long term records]); the unprecedented intensity of the outbreak in 1997, merely reinforcing a weak annual trend.

It is thought that rainfall patterns may be connected to the life cycle of *Stomoxys* flies, and that unusual weather conditions in early 1997 triggered the unusually large numbers witnessed. A case of high mortality in the lions (*Felis leo*) of the Ngorongoro Crater, Tanzania in 1962, (Fosbrooke, 1963), due to *Stomoxys* flies was linked to a severe, prolonged dry-season followed by exceptionally heavy rainfall (conditions allowing several generations of flies to develop). It is suggested that similar climatic conditions triggered the outbreak at Ndoki. The dry season of the first two months of 1997 was particularly severe, and subsequent rainfall in April was twice the average for that period.

Without ranging data on the gorillas when not at the bai, it is impossible to know whether reduced gorilla presence in April and May is due primarily to the avoidance of a localised insect outbreak. *Stomoxys* flies were recorded in several other areas surrounding the Ndoki forest and while the outbreak appeared to be limited in its distribution, the area affected was likely to be too large for most gorillas visiting Mbeli to simply re-locate to a fly-free zone. More likely is that gorillas moved to areas with slightly lower fly densities, but also avoided open clearings where ungulate populations and other conditions may have favoured high fly densities. This must, however, for the time being remain conjecture. Further details of the fly outbreak are given in Elkan, Parnell and Smith (in press). The outbreak of *Stomoxys* flies at Mbeli is an example of the proximal effects of weather patterns. However, potentially the most important such effect with regard to the Mbeli gorillas is likely to be that of seasonal fruiting patterns.

Fruit availability

Although nutritional analysis of bai plants in different seasons has not yet been undertaken at Mbeli, there was no obvious external evidence that aquatic herbs were subject to seasonal changes in nutritional content. The production of the stems, leaves and piths representing the majority of the diet available to mountain gorillas in the Virungas is subject to very little seasonal variation (Schaller, 1963; Fossey & Harcourt, 1977; Watts, 1984). By contrast the greater fruit component in the diet of lowland gorillas makes them subject to considerably greater seasonal variation in food availability (e.g., Tutin et al., 1991; Tutin & Fernandez, 1993a, 1993b; Remis, 1997). Such variation has consequences for lowland gorilla ranging patterns, and units have been shown to alter their day range length and also to extend their home range size in order to exploit more distant fruit resources that are only available in certain seasons (Williamson, 1988; Goldsmith, 1996a, 1996b; Tutin, 1996). As the amount of fruit available to gorillas alters, so does their reliance on herb foods. Gorillas have been shown to fall back heavily on herb foods during the dry season when fruit foods are in short supply (Rogers et al., 1988; Nishihara, 1995; Remis, 1997). Such variation in food availability may have implications for patterns of bai-use for gorillas in the vicinity of Mbeli.

It should be stressed that the primary aim of the present study was to investigate the behaviour of gorillas while *in* the bai. A conscious decision not to undertake a phenological study of fruit availability in the surrounding forest was taken at the start of the study period. The rationale behind this decision was that, in order for a fruit phenology study to be worthwhile, at least three to four days per month would be required to walk phenology circuits. In addition to this considerable time demand, the initial location, mapping and establishment of circuits would have impacted heavily on the time available at the bai. Given that some groups only visited the clearing on one day in one or more months (MAX group were seen once per year) the risk of losing vital observations while conducting vegetation surveys was thought too great.

Some data on fruit and fibre availability and consumption in the region are available, however. Nishihara (1995) reports that the main fruiting season in the Ndoki region is between June and September and shows that these months correspond to the highest proportions of fruit remains recovered from gorilla faecal analysis. February was the poorest month for fruit consumption, but all months from November to May were low. Consumption of fibrous plants was higher in the non-fruiting season, but the protein-rich shoots of *Haumania danckelmaniana* and *Hydrocharis* roots were eaten more heavily during the fruiting season than at other times of the year. Remis (1997) reports on fruit consumption by gorillas in the Bai Hokou region, close to the Ndoki forest, and sharing general seasonal climatic patterns, with December, January, and February significantly drier than the rest of the year. At Bai Hokou, as at Lopé, fruit availability was not consistent across years, with some years better or worse than others. It has been suggested in this respect, that flowering in some species may be linked to a minimum temperature threshold, which, if exceeded, triggers flower production (Tutin & Fernandez, 1993; Remis, 1994). Nevertheless, the peak of fruit availability in each of two years was during the rainy season between July and September (in a third year, fruiting began early, with peaks in both May and July. During the dry season and in poorer fruit seasons, gorillas at Bai Hokou fed more heavily on leaves, stems and piths. However, swamp vegetation was rarer than at Ndoki, leading to the suggestion that during poor fruit months, gorillas at Bai Hokou would have more incentive to pursue fruit than gorillas with access to swamps, for whom such times are likely to be less critical. Although not yet investigated, the contribution of aquatic herbs to fibre intake may be underestimated through faecal analysis, as their high water content and increased digestibility may render them hard to detect (Nishihara, 1995). Blake (2002) reports on extensive and intensive surveys of fruit availability in the Ndoki forest, and while acknowledging that inter-annual variation may be considerable, observes that fruit abundance was significantly and positively correlated to rainfall.

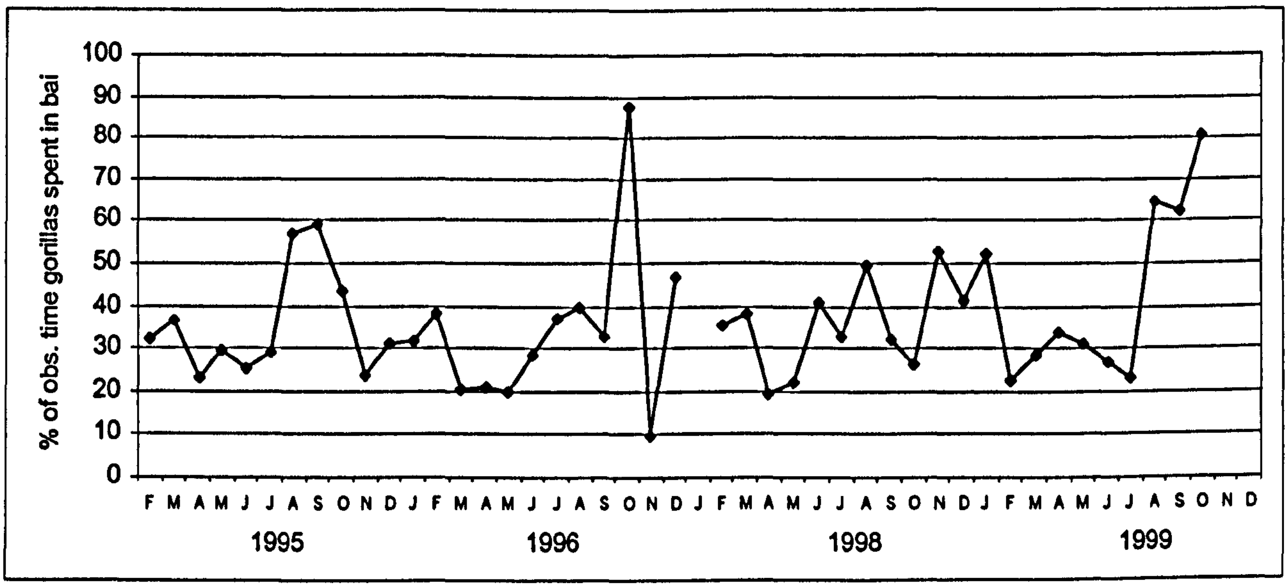
At Mbeli, the lowest levels of gorilla presence appeared to coincide with periods of low fruit availability (and high average temperatures). This seems counterintuitive, in that the inverse would be expected under the hypothesis that fibrous foods represent fall-back resources during periods of fruit scarcity. During fruit abundance, bai presence figures are increased, but not enormously so (it should be remembered that the range of values represented by the curves in Figures 3.13 and 3.14 is not great). Interestingly, Figure 2.9 in Chapter 2 (elephant presence) shows elephants to follow a similar trend of low bai-visitation. This however, is likely to reflect genuinely fewer elephants in the area. Blake (2002) reports that during periods of low rainfall, elephant density increased in the northwest of the Nouabalé-Ndoki National Park, due most probably to a higher presence of swamps, clearings and rivers.

A hypothesis that may be of interest, arising from the present study is that the drop in gorilla activity at the end of the dry season is linked to the avoidance of *Stomoxys* flies, and also a more intense search for high quality forage and rare fruits in *terra firma* forest. Raised levels of visitation accompanying periods of greater fruit abundance, may indicate that with high energy foods readily available, gorillas are more ready to top up their diet with highly digestible but exceedingly bulky aquatic plants that require a low energy expenditure to find and process. This hypothesis would be supported by the finding of Nishihara (1995) that *Hydrocharis* was eaten more during the fruiting season than at other times. It is proposed that aquatic plants alone, despite being high in protein compared to other terrestrial herbs (except *Haumania* shoots) might be nutritionally inadequate to maintain condition, due to their extremely high water content. More research on passage rates and intake will be required before such a hypothesis can be examined. Considerable variation across years, both in gorilla presence and climatic variables makes further interpretation perhaps foolhardy. Continued monitoring of gorilla presence at the clearing and of fruit availability and weather should indicate if and where genuine patterns are present. Fig 3.13 showed a marked peak in visitation corresponding with August and September 1999. The activity of the gorillas at this time provides a good example of the effects of fruit availability on ranging and activity.

Nauclea vanderguchtii: a mast fruiting event influencing gorilla behaviour at Mbeli

Figure 3.15 shows the number of hours all visiting units each month spent in the bai, expressed as a percentage of the total observer hours for the month. The years shown are 1995 and 1996 (Mbeli Bai Study long-term records; Olejniczak unpubl. data), followed by a gap for 1997, which is excluded due to missing data in the months of interest, then 1998 and 1999.

Figure 3.15 Total of all visiting units hours' in the bai per month, as percentage of observer hours



The number of contributing gorilla hours per month ranges from 25 to 254, with a mean of 81 (SD 42).

The chart clearly shows two peaks in bai-use; in October 1996, and from August to October in 1999. It is notable also that in the month of September 1999, eight visits were made to the bai by unknown units, plus 11 visits by the solitary silverback Sulatalu, whose entire history of visitation to the bai was limited to August and September 1999, and who disappeared in October 1999 and has not been seen since. The median rate of visitation for unknown groups during 1999 was 1 (range = 0 to 8 [19 including Sulatalu]). While these extraordinary periods do to a certain degree correspond with the main periods of fruiting in the Ndoki forest, the reason for such high levels of bai-use were more specific.

These periods corresponded to what might be described as 'gorilla-induced mast fruiting events' in a tree species of the Rubiaceae family, *Nauclea vanderguchtii*. These medium sized trees are known for their tolerance of swampy soils (White & Abernethy, 1997), and are found in high densities around the bai. By censusing the *Nauclea* canopies visible from the bai, during a walked circuit within it, 66 trees were recorded, 56 of which bore fruit in 1998. During October 1996, the gorillas spent large amounts of time feeding in the bai-edge *Naucleas*, but no systematic data were collected. It was noted however, that fruit-bearing trees sustained major damage to their limbs as a result of arboreal gorilla feeding. Repair from such damage is costly for a tree and in the following year, most trees carried little or no fruit. This effect has been noted in several other gorilla food tree species (*Diospyros sp.* - Williamson et al., 1990; *Tabernaemontana sp.* – Remis, 1994; *Dialium lopense* – Rogers & Parnell, 1991). Having missed a year, *Nauclea* fruit were once again abundant in the late rainy season of 1998, at which time detailed data collection took place. Space constraints do not allow for a full description of the exploitation of this crop at Mbeli.

Plate 3.5 Solitary silverback Vince eats fruit high in a *Nauclea* tree

Data on the density of *Nauclea* trees in the surrounding swamp forest await analysis, but it was clear that this species, although abundant around the clearing, was not confined to a bai-edge environment. It is thus hypothesized that gorillas preferentially selected bai trees in which to feed, as the abundance of fruit *and* the proximity of abundant fibre made the area a food-rich and energetically economical environment where these two aspects of their dietary requirements could be satisfied without extensive ranging. It should be noted that in 1996, as soon as the fruit crop was consumed (November) the gorillas deserted the bai, giving rise to the lowest ever recorded level of presence of any month in the project's history. Such abandonment of the area may have been linked to the depletion of resources, both fruit and fibre, due to the large numbers of gorillas having used it over a concentrated period, or may have indicated that the gorillas were exploiting *Nauclea* elsewhere within their range. As in the case of the *Stomoxys* outbreak, such events further suggest that caution should be exercised when interpreting resource-use data, especially from a limited data-set.

Zone of entry, visit frequency and synchrony: implications for ranging patterns.

Given that no attempts were made to contact or follow social units into the forest, the movements of the gorillas visiting Mbeli remain unknown. In addition to logistical and technical difficulties, it was thought undesirable to attempt the fitting of radio telemetry collars to gorillas. In the case of groups, this could only have been achieved by immobilising the silverback, who would otherwise aggressively protect his group members. The risk in this case of causing permanent damage or even death to a group leading silverback was deemed unacceptable, especially given the potentially disastrous effects the loss of a silverback may have on other group members through group disintegration and infanticide (e.g., Watts, 1989). The habituation of groups to observer presence on the ground, and rigorous post-visit tracking may have added somewhat to our understanding of ranging patterns, but the risk in this case of altering normal bai visitation patterns through contact was deemed too great.

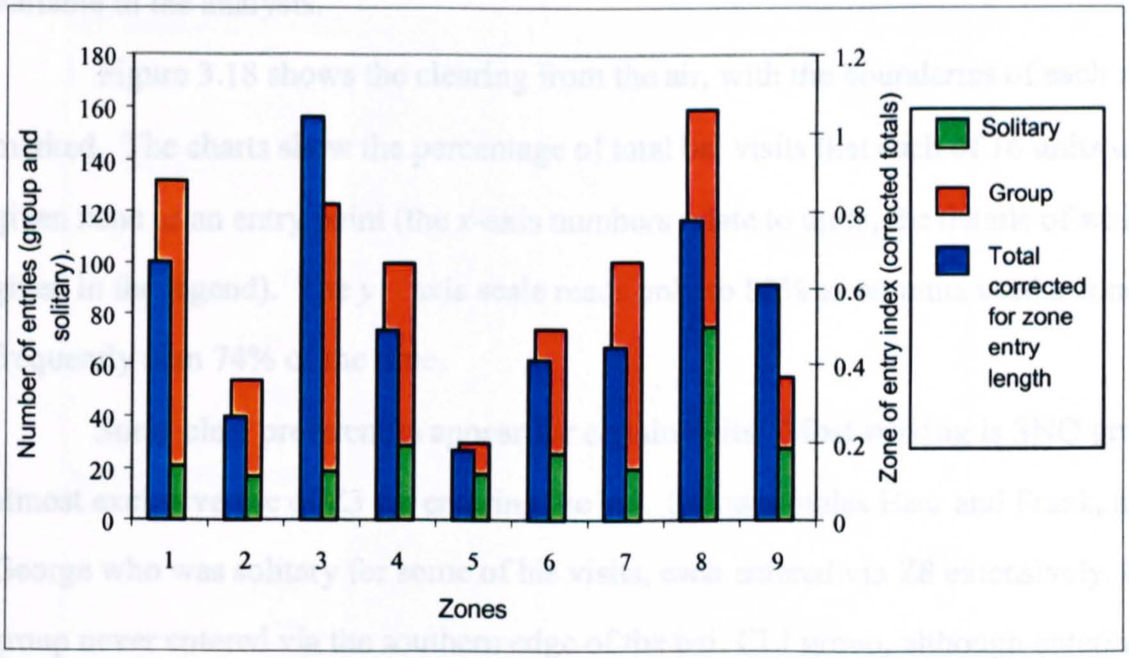
It was hypothesised, however, that information regarding the location of a unit's core range area might be obtained were units to show repeated use of the same zones to enter the bai. The fact that over 14 different social units have been recorded visiting Mbeli Bai proves indisputably that, like all other gorilla populations studied, the home-ranges of Mbeli gorillas overlap extensively (e.g., Watts, 1996; Tutin, 1996; Yamagiwa et al., 1996). However, it is highly unlikely that the bai is at the centre of most group's ranges. More probable is that for a few groups, it is relatively central, for others, peripheral, and for others still, represents a specific extension to a more distant range. This phenomenon of home-range extension for a particular resource is well documented in western lowland gorillas (e.g., Remis, 1994; Tutin, 1996).

Zone of entry

Figure 3.18 (pg. 92) shows an overhead view of the bai with the area visible from the observation platform divided into polygons (delineated in a previous study [Olejniczak, pers. comm.]). Natural features were used as guides to the location of zone limits. These areas or 'zones' were sub-divided into 4 quadrats corresponding to the cardinal points, allowing observers to record the relative location of a unit or individual with moderate precision.

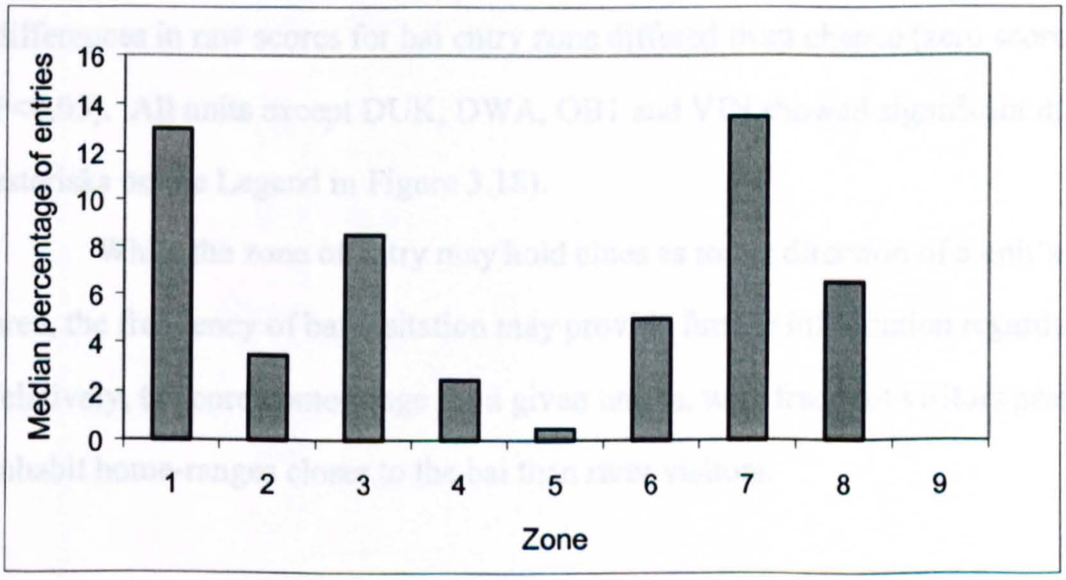
Zone of entry was recorded for every unit visit to the bai. If individuals from the same group entered in more than one zone, that used by the majority of members was recorded. Figure 3.16 shows the total number of entries per zone, sub-divided into solitary males and groups. Zone 5 (Z5) was clearly used the least, very possibly as the observation platform was situated in the middle of the zone's boundary with the forest. However, use of the remaining zones did not match the rank order of zone distance from the platform, with some more distant zones receiving less entries than closer ones; for example, the second most used entry zone was Z1, which was directly opposite and less than 200m from the platform. As the relative use of each zone might be a function of the area available to enter a zone, an aerial photo and GIS software were used to determine the straight-line distance across the face of each zone's boundary with the forest. An index was then obtained by dividing the total number of visits per zone by the straight-line distance across the entry to that zone. The resulting scores are represented by the blue columns in Figure 3.16, and reveal a slight change in rank order with Z8 losing first place to Z3, and the second smallest zone, Z9, rising to fourth place.

Figure 3.16 Number of bai entries via each zone, and number of entries as an index of total bai entry zones corrected for bai/forest boundary length per zone.



An alternative method of examining zone of entry is to plot the median percentage of occasions each zone was used by the 16 units. The results of this are given in Figure 3.17.

Figure 3.17 Median percentage of bai entries per zone (uncorrected for distance).



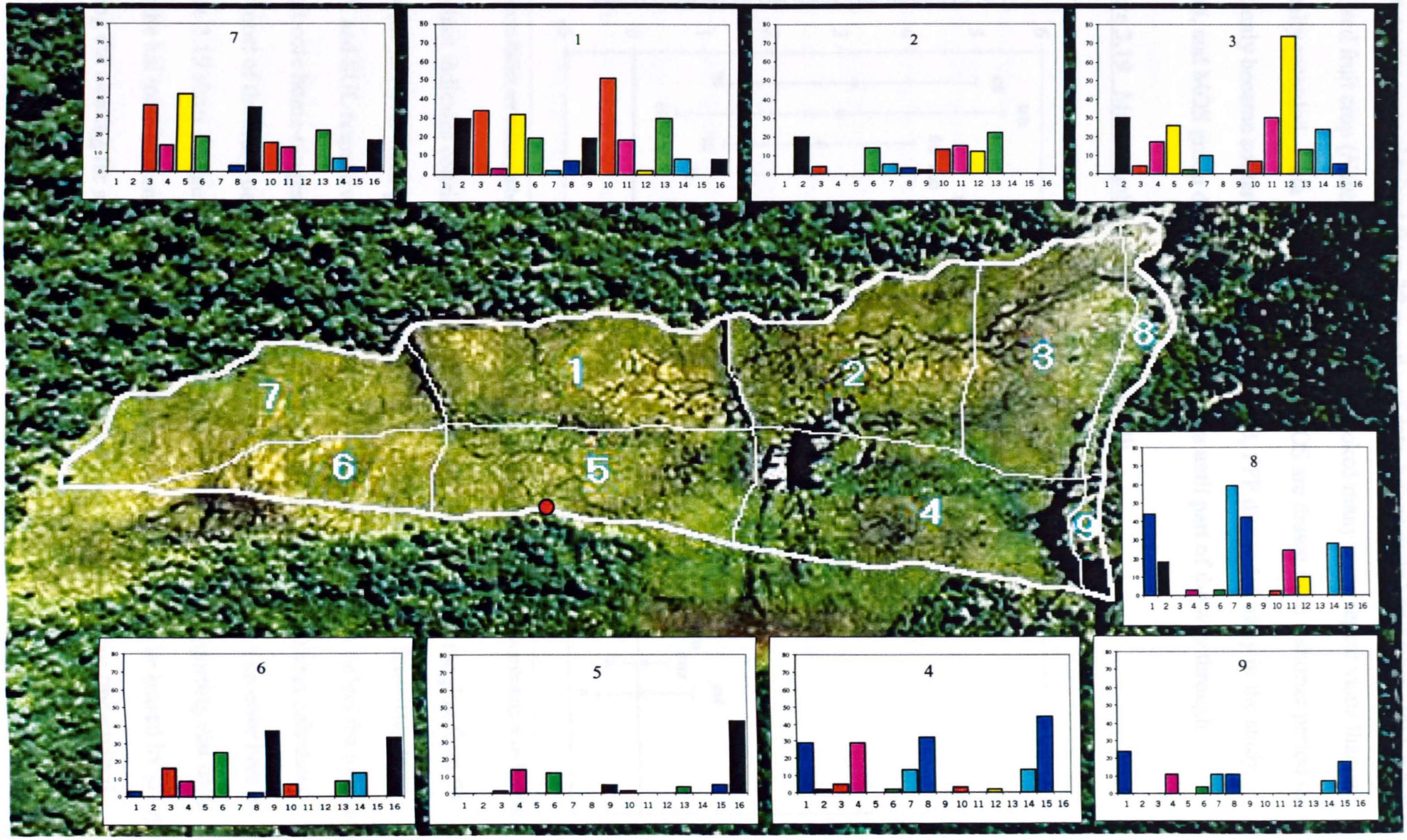
By taking the median of each unit's percentage score for each zone, the data are not swayed by extreme use or non-use of certain zones by certain individuals. Z9 has more non-users than users, resulting in a median score of zero, and the importance of zones 8, 3, and 4 appears much reduced. The value of an average percentage of zone use may be somewhat marginal, however, as the individual habits of units are the most interesting variable in the analysis.

Figure 3.18 shows the clearing from the air, with the boundaries of each zone marked. The charts show the percentage of total bai visits that each of 16 units used a given zone as an entry point (the x-axis numbers relate to units, the details of which are given in the legend). The y – axis scale reads only to 80% as no units used a zone more frequently than 74% of the time.

Some clear preferences appear for certain units. Most striking is SNO group's almost exclusive use of Z3 for entering the bai. Solitary males Bear and Frank, and George who was solitary for some of his visits, each entered via Z8 extensively. OB1 group never entered via the southern edge of the bai. CLI group, although entering via seven of the 9 zones, showed a clear preference for Z7 and 1, whilst solitary male Vince (VIN) was the only gorilla with Z5 as his most used entry point (Vince was the most frequently encountered gorilla on the path leading to the clearing and occasionally fed directly below the observation platform). NOO group entered via all zones except Z9, but showed a preference for Z1. A chi-squared test was run for each unit to determine if differences in raw scores for bai entry zone differed from chance (zero scores not included; $P<0.05$). All units except DUK, DWA, OB1 and VIN showed significant differences (*see* asterisks on the Legend in Figure 3.18).

While the zone of entry may hold clues as to the direction of a unit's core range area, the frequency of bai visitation may provide further information regarding how far, relatively, the core home-range for a given unit is, with frequent visitors predicted to inhabit home-ranges closer to the bai than rarer visitors.

Figure 3.18 Zones of Mbeli Bai and percentage of total bai entries that each social unit used each zone to enter the bai



x - axis
legend

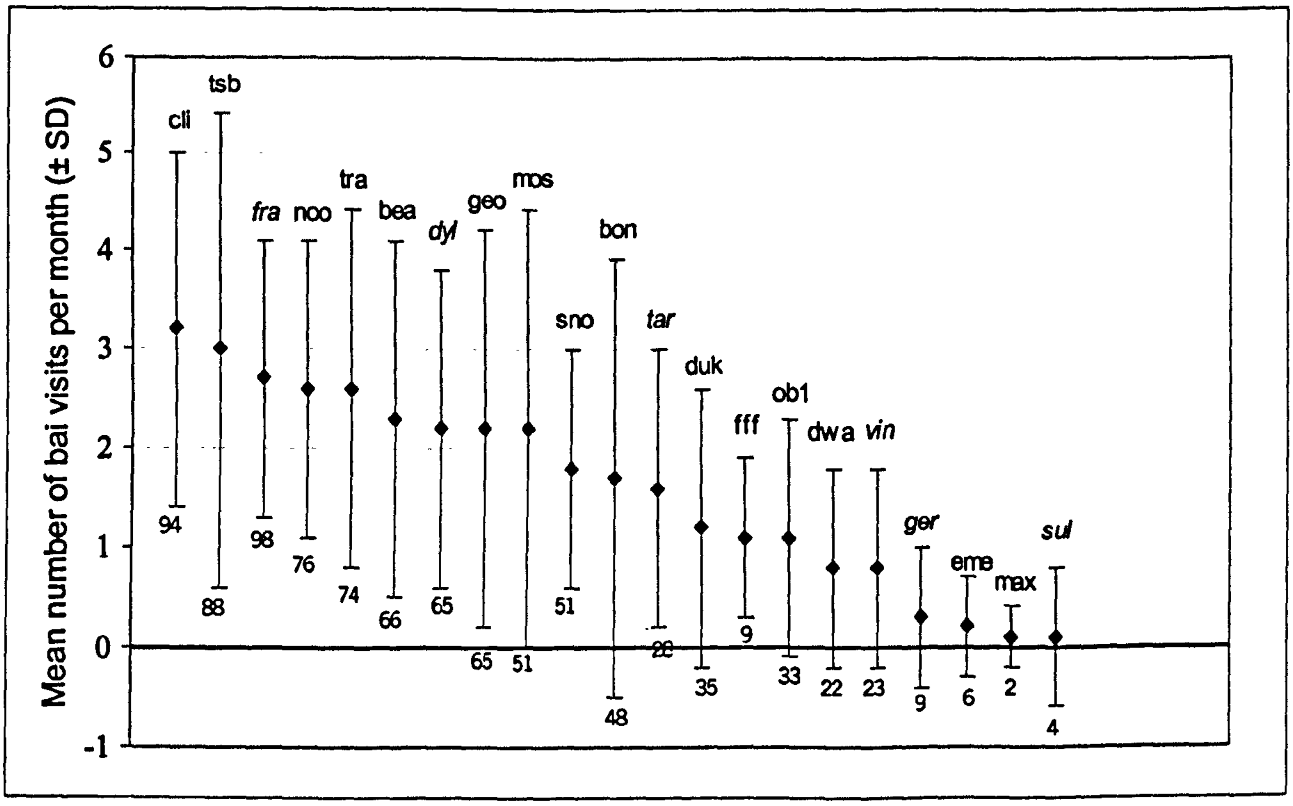
1. BEA*
2. BON*
3. CLI*
4. DUK
5. DWA
6. DYL*
7. FRA*
8. GEO*
9. MOS*
10. NOO*
11. OB1
12. SNO*
13. TAR*
14. TRA*
15. TSB*
16. VIN

y – axis = percentage of total visits that each unit entered the bai in the given zone. x – axis, see Legend. * Significant difference between raw scores for entered zones (χ^2 test, $P<0.05$)

Visit frequency

Figure 3.19 shows the mean number of bai visits per month for solitary males and groups. Mean scores were obtained from 29 months of data, but exclude September 1999, when a localised fruit crop (*Nauclea vanderguchtii*) provoked many more repeat visits than are typically recorded. Data from TAR, FFF, and MOS are drawn from a shorter period as TAR only became solitary late in the study period, FFF disbanded early in the study period, and MOS group did not come into the area until part of the way through.

Figure 3.19 Mean number of bai visits per month



Labels in italics are solitary silverbacks. Values below SD bars show the number of visits contributing to each mean.

The chart indicates considerable differences in overall visitation rates, ranging from 94 visits (or just over three per month) from CLI down to a mere two and four visits from MAX and SUL respectively. It is likely that some of these differences reflect the locations of unit core home-ranges relative to the bai; however, by expressing a mean calculated over most of the study period, important information may be ignored. The error bars in Figure 3.19 show a large variation about many of the mean scores, suggesting that units used the bai more in some months, and less in others, or that data may be biased by groups visiting the clearing for several days in a row before moving on. A more fine-grained examination of actual bai visitation patterns may thus be more informative. To facilitate an overview of visitation frequency and rhythm, Figure 3.20 marks the temporal location of every bai visit from 21 social units. The data come from the inclusive periods, January 1997 to July 1997, and then from February 1998 to October 1999. The black bars to the left of the rows mark the beginning of each consecutive month, each faint row represents a day, and the red dots mark a bai visit.

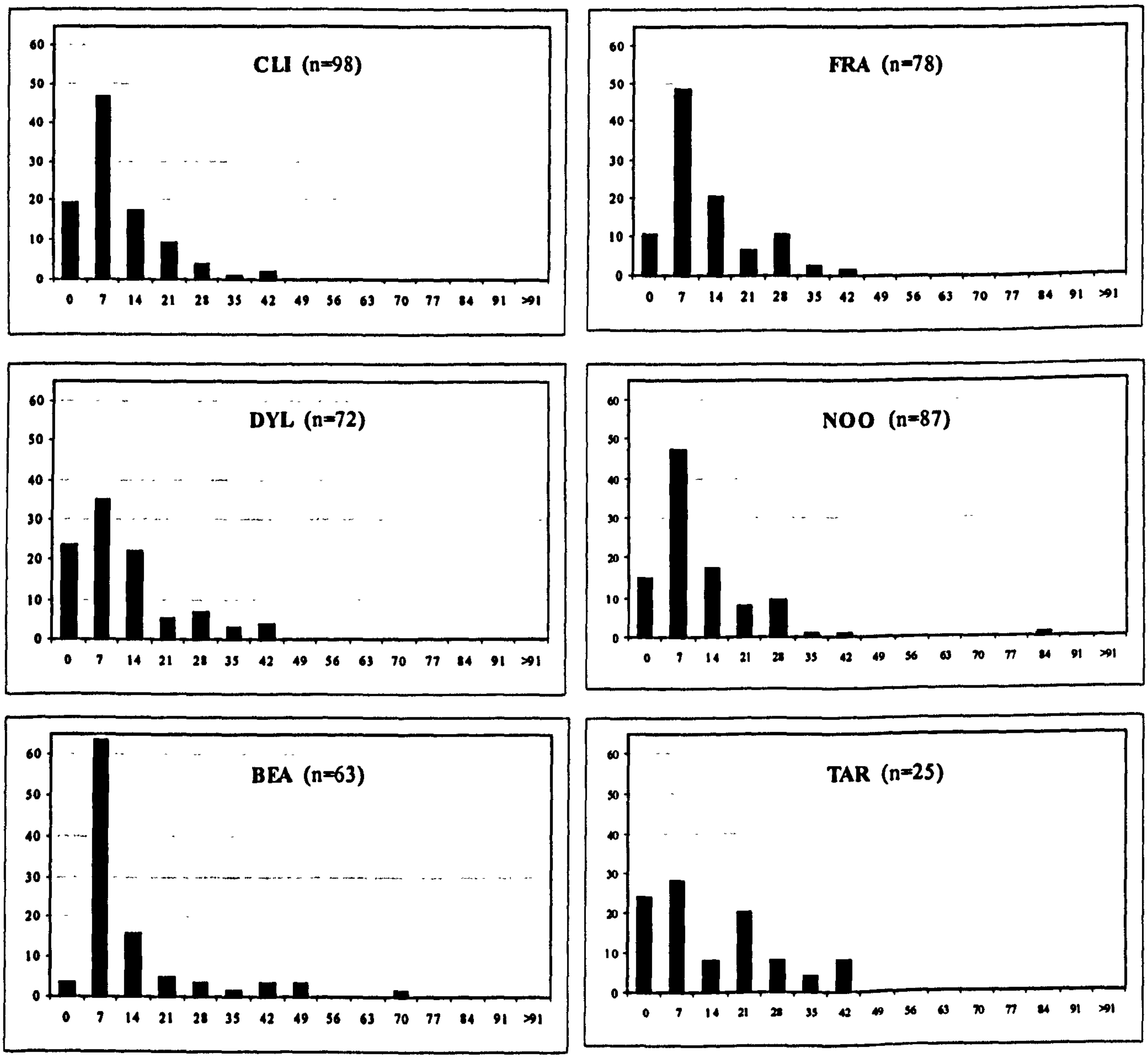
Although this presentation of the data may at first appear confusing, a vertical reading, taking each unit in turn from the top, clearly demonstrates the great variation in bai use patterns both between and within units. At one extreme are units such as the solitary males SUL and GER. SUL used the clearing quite intensively over a period of just over a month during the *Nauclea* fruiting season of 1999, but was never seen prior to, or following this period. The visits of GER were spread over a much longer period and were each separated by approximately 3 months. At the start of the period, the visits of solitary VIN averaged at around once a fortnight, but became very infrequent in the main body of the period. They then became frequent again during the *Nauclea* season of 1999. Solitary FRA and sometime solitary GEO were both much more regular and frequent visitors, generally maintaining at least one visit per month, and often more. Among groups, variation was similar. SNO group visited the bai throughout the period, and were among the more regularly spaced groups, with most visits being between two and four weeks apart, and lasting only a single visit. By contrast, both TRA and TSB showed a relatively similar regularity in their visits, but often visited the bai every day for several days before disappearing again. There also seemed to be a suggestion of synchrony between these groups, with several of their consecutive day visits taking place simultaneously, potentially signaling that these groups may, on occasion, range together or in close proximity.

The use of mean scores is not desirable for such data, as its flattening effect hides any patterns that may be present, especially in the case of a unit visiting the bai daily for several days before moving on. Taking such visits as a single bout representing presence in the area might remove some imprecision from average scores, but this presents a new problem with regard to assigning criteria regarding what defines a 'bout' (i.e., consecutive visits, or consecutive visits plus visits separated by only one or two days etc.).

Figure 3.20 Timing and interval of gorilla visits to the bai for 21 units (one day per row)

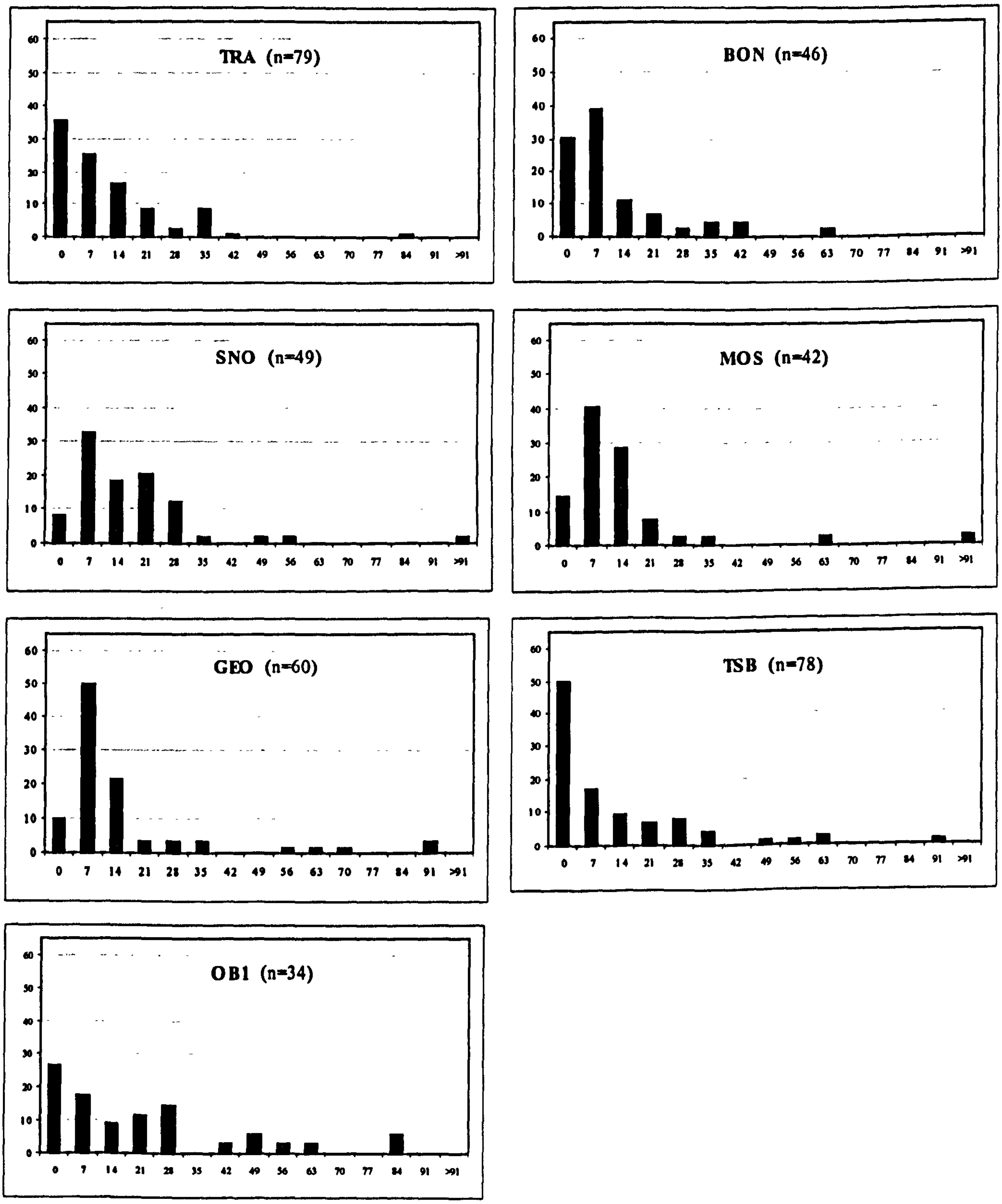
The solution given in the following figures is to present the intervals between visits for each unit as frequencies, in histogram form. The x-axis starts with a 'zero' category to record visits on consecutive days, and then increases in increments of one week (7 days) up to three months. A final category (>91) combines all intervals over three months. The y-axis gives the percentage scores for each interval band. Total visits are given in parentheses).

Figure 3.21 Frequency of inter-visit interval for 21 social units at Mbeli (expressed as percentage of all intervals within each interval band)



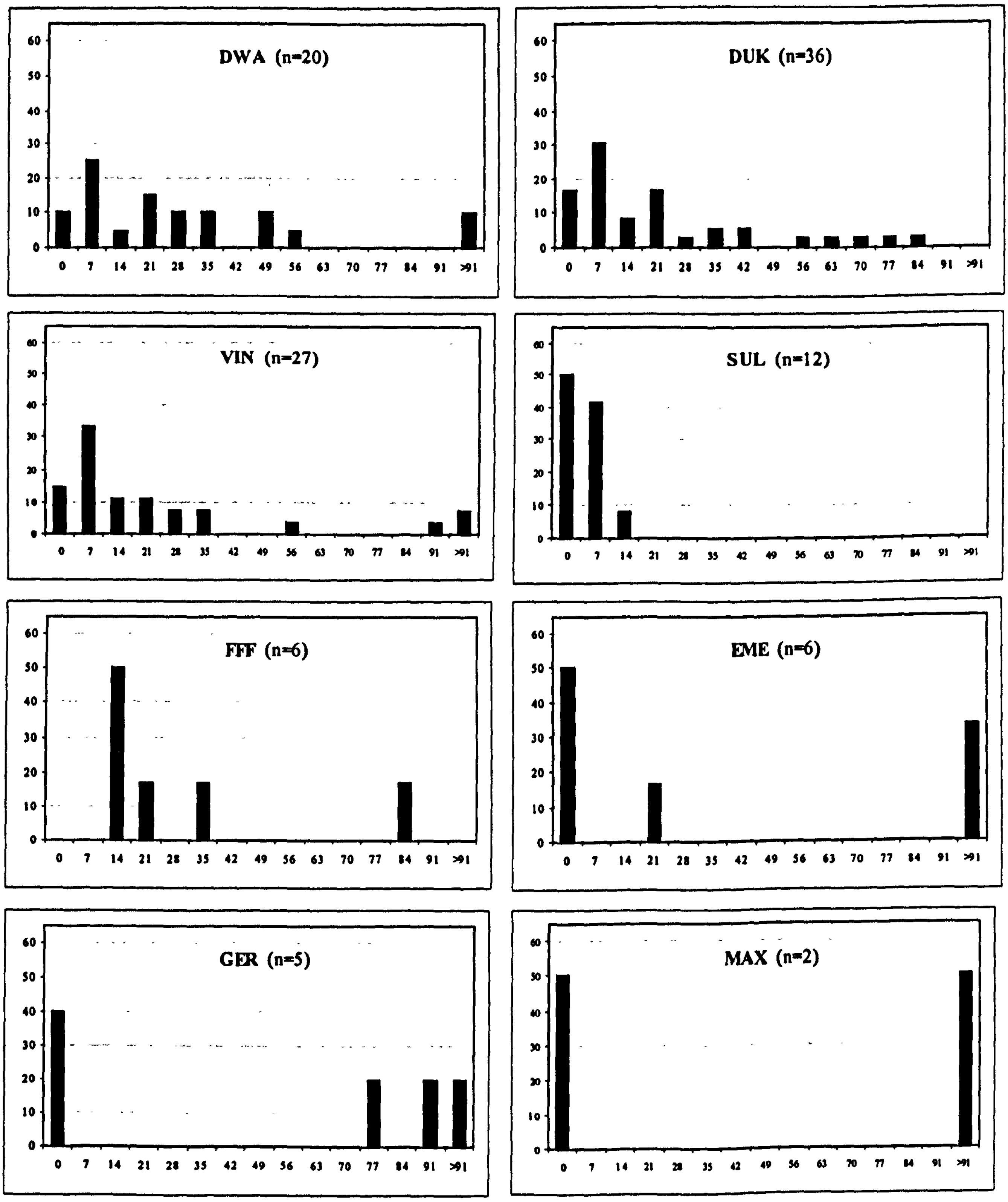
Units described in the preceding charts are the most frequent and regular visitors to Mbeli. In the charts below, visits become more widely spaced. The chart for TSB group is particularly interesting in that it sheds light on a reason for the group's high mean visit per month ranking in Figure 3.19. TSB are here shown to be rather less frequent visitors than seemed apparent, but visit the bai for several consecutive days when they are in the area.

<u>**Figures 3.21** *continued.*</u>



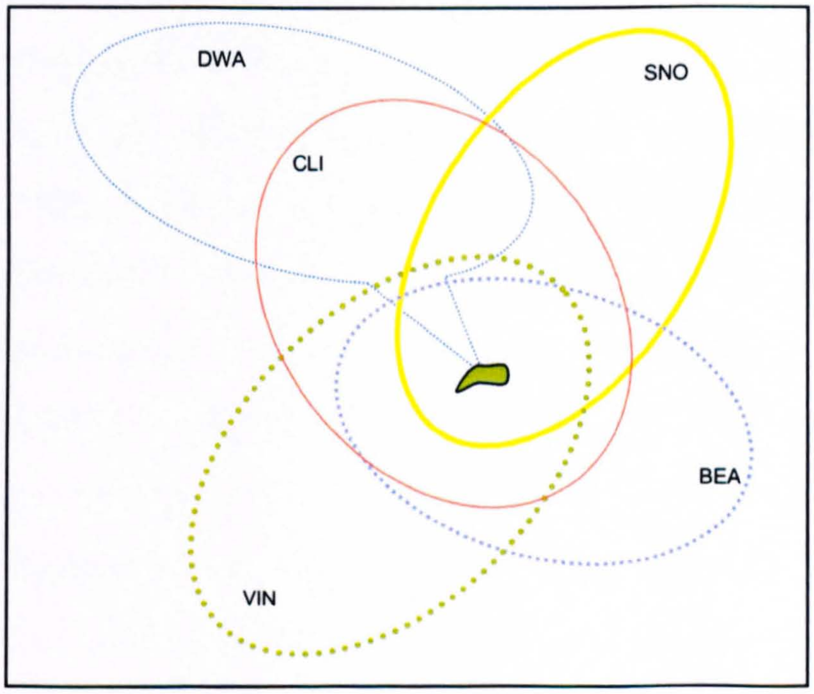
Finally, the charts below describe units with greater frequencies of long inter-visit intervals than all others. Also shown are units visiting the bai over a brief period only.

Figures 3.21 *continued.*



It may be unwise to attempt to draw too much inference from bai entry zone and visit frequency data, as, without physical corroboration through the location and identification of nest sites or radio telemetry of individuals, theories regarding ranging and core home-range location must remain speculative. It is unlikely however, that precise data on home-range will ever be obtainable for more than one or two of the units using Mbeli, and speculation based on the few clues available may be as far as exploration into this area can progress. By combining information from bai entry zone and visit frequency, it is possible to make the following predictions: of groups, the home ranges of CLI and NOO overlapped the most extensively with the bai, and they may have encountered each other frequently in the forest. The ranges of solitary males FRA, BEA and DYL may also have overlapped considerably with the bai, though both FRA and BEA were skewed slightly to the east and may have overlapped with each other rather more frequently in the forest. Solitary FRA entered the bai from the same general direction as his putative natal group TSB, although their core range may have been slightly more distant than his. Recently emigrated solitary TAR also used the same zones of entry as his natal group, NOO (in mountain gorillas, solitary males have been known to remain within their natal group's core range area following emigration [Caro, 1976]). Solitary VIN was something of an anomaly: his preferred zones of entry (5 and 6) and visit frequency suggested occasionally distant ranging to the south-east, yet even during long periods when he did not use the bai, he was often seen in nearby forest. Furthermore, his preferential use of zones 5 and 6 may have had more to do with his tolerance for humans and the vacuum created by other group's apparent avoidance of them than an actual ranging pattern skewed towards the south-east. GEO, who ranged both as a solitary and as a group silverback showed a skew towards the south-east and may have overlapped with BEA, TSB and FRA but may occasionally have ranged considerably further from the bai. TRA, SNO, MOS, GEO, TSB and OB1 were all regular visitors to the bai, but may have had areas within, or extensions to, their ranges that occasionally took them away from the area for considerable periods. The centre of the core home-range in the case of SNO group was very likely to have been to the north-east of the bai. The core home-ranges of DWA and DUK were unlikely to have included the bai, and their visits probably constituted occasional range extensions into the area. Solitary males GER and SUL only visited the clearing for a limited period and may have been in the process of searching for a new area in which to establish a home range and acquire a group (SUL is also known to have stayed in the vicinity of the bai only during *Nauclea* fruiting period of 1998), while groups EME and MAX probably inhabited home-ranges quite distant from the bai. It seems unlikely that their extremely infrequent sweeps into the area were made specifically in order to exploit the bai, but were probably linked either to the exploitation of some other food resource, or to a social purpose such as group expansion. Figure 3.22 presents a graphical view of the suggested relative positions of some of the Mbeli social units.

Figure 3.22 Speculative approximation of home-range location and overlap with the bai for five selected units (the green island represents the bai)



Discussion

This chapter has presented data on what time of day gorillas visit Mbeli and when they leave. The effects of day to day weather patterns have been considered, particularly in terms of how gorillas cope with the changes they encounter. The physical characteristics of the bai, as encountered by gorillas traveling into and out of the clearing have been described, including interactions with other species with which they may share the resource. Seasonal effects on bai visitation have been explored, and while trends are hard to detect reliably within so short a time-span, particular events, correlated at least partially with the climate, have been identified. Unfortunately, without data on gorilla activity when not at Mbeli, it is difficult to consider such observations within the context of the majority of a gorilla's time. In particular, the nutritional contribution of the bai cannot be gauged without knowing the circumstances of the gorillas when elsewhere. Do they travel from bai to bai, making swamp vegetation a central element in their diet, or do visits to places such as Mbeli represent rare, special events in the ranging patterns of most gorillas? The chapter is, however, a valid piece in the puzzle of understanding what it means to be a gorilla in the vicinity of Mbeli Bai. Several of the findings described may be important for the study of gorillas elsewhere, and even those that appear specific to the bai environment, may hold clues to other aspects of gorilla life that would otherwise remain hidden. Certainly with regard to Mbeli, we now know that even the most frequent visitors spend less than three percent of their daylight hours at the site. Of the population's total daylight hours, an average of just one percent is spent at Mbeli. Further study, expanding our knowledge of the gorillas into the surrounding forest, and observations made at other bais in the vicinity may begin to fill in the enormous gaps between Mbeli visits.

Little bias was evident in the gorillas time of arrival at the clearing. Relative to the size of a given unit's home range, Mbeli is a tiny feature, and gorillas are unlikely to time their visits with regard to particular daily conditions. More likely is that gorillas may target Mbeli for a visit, either specifically, or when their ranging patterns happen to bring them into the area. As such the timing of visits is probably a simple function of when a unit arrives in the immediate vicinity. Gorillas left the bai before sun-down, almost certainly in order to find a suitable nest site before dark, and this influence may synchronize some morning visits. The most 'popular' hour to be in the clearing was 14:00hrs, however this too is likely to be a simple function of morning arrivals and standard visit duration time leading through a cumulative effect to the highest presence corresponding with this time period (14:00hrs also represented the period of highest gorilla presence at Maya bai [Magliocca, 2000]). Unlike at Karisoke (Harcourt, 1978b), gorillas visiting Mbeli do not show a marked mid-day rest period. Rather their entire time in the bai seemed geared to satisfying the appetite and then leaving. Differential times to satiety and natural age-specific predilections to certain behaviours probably allow younger individuals to spend part of their bai-time in social pursuits or resting, but the occasional nature of bai-visits indicates that they are special events, linked to feeding, and not a regular part of any group's day, conditional on climatic or other conditions.

Other bai-users may alter the behaviour or mental state of some gorillas. Magliocca (2000) examines the likelihood of species using Maya Bai encountering each other, and concludes that gorillas, sitatungas and giant forest hogs, by merit of their overlap in food species, may potentially be competitors within the clearing (no examples of behaviour indicative of this are detailed however). While there may have been some scope for scramble competition between certain species at Mbeli, the responses of gorillas to proximity with other species showed no sign of this being a concern of the gorillas. Gorillas treated elephants with calm caution but never extreme fear. Elephants for their part, mostly ignored gorillas, though both species showed signs of locating the other, either visually or through olfaction. Sitatunga, who were resident at the bai, paid little attention to gorillas, though there was a suggestion that certain male gorillas acted aggressively towards them. Gorilla reactions were mixed, with some groups paying little or no attention, and others reacting with extreme alarm to the proximity of male sitatunga. By contrast, female sitatunga were almost universally ignored or in a few cases, chased, in what anthropomorphically bore an uncanny resemblance to 'recreation'. The mutual tolerance of proximity between female sitatunga and gorillas indicates a long history of non-aggression. The alarmed reaction of gorillas to bongo suggested either that unfamiliar animals cause fear, or that negative experiences have been assimilated from elsewhere. By far the most consistent reaction to any other species was that towards the long-snouted piscivorous crocodile (*Crocodilus cataphractus*). All gorillas appeared alarmed by this animal, keeping it in sight and even displaying aggressively at it. This suggests strongly that crocodiles have given gorillas reason to fear them, probably by snapping at them when taken by surprise. No such incident was observed at Mbeli however, and it is intriguing to consider the learned or cultural aspect of such reactions (e.g. Mineka et al., 1984). Young gorillas paid more attention to other species than adults, and an incipient curiosity was evident in some situations. Gorillas, while unperturbed by the presence of most other species, are clearly not 'masters of their world', but appear aware of the capacities of other species, and may be influenced in their reactions to them by past experiences or learned patterns.

On a daily basis, the duration of bai visits was shorter on the coldest ten percent of visits than the hottest ten percent, however overall, gorillas did not show any great sensitivity to short-term changes in the weather. Rainfall caused clear discomfort in some gorillas, evidenced by attempts to cover the head with the hands. Heavy downpours caused a cessation of feeding and in some cases, a departure from the bai. Those animals remaining characteristically sat motionless in a hunched position; a reaction also noted in mountain gorillas (Schaller 1963). The possible correlates of this reaction in connection to yawning have been discussed at some length in the main body of the text, and while the proposed mechanisms involved remain the thoroughly untested hypotheses of the author, yawning was shown to be at least proximally correlated to poor, or changeable, weather conditions. This trigger for yawning appeared considerably more reliable and frequent than any resulting from a tense mental state. Agonistic display of the canines was all-but ruled out as a function of yawning in the Mbeli population.

Significant differences in visit duration were noted between some units. There appeared to be little pattern to which groups remained the longest and which the shortest. One recently emigrated young solitary male was among those with the shortest visits, but so was another older solitary and a breeding group. Two of the groups with the longest visits were among the most frequent visitors, but a third group only had an average visitation rate; thus nervousness or familiarity in the bai environment, while a possible factor, did not account for much of the variation.

Overall however, there was little variation in visit duration. It is suggested that this may result from homogeneity in the time taken to satiety. Given that the primary activity of gorillas in the bai is feeding, it can be envisaged that the time spent in the bai will roughly equal the time taken to reach satiety by the individual with the largest gut capacity (assuming that this individual is either confident enough to remain feeding after other members have left the bai, or is in a position to influence the duration of a visit by merit of its social rank). In the case of gorillas, gut capacity and social rank converge upon the silverback, who has the necessary power to restrain or hurry other group members should he so wish. Pilot work at estimating the wet and dry weight of *Hydrocharis* plants indicated that not only was it possible to harvest an enormous weight of food with very little energy expenditure, but that this preferred food has a water content of approximately 94%. While the importance of the high mineral and protein levels found in such plants cannot be ignored (Nishihara, 1995; Magliocca, 2000), they may represent an extremely bulky food source. Even given the probable high digestibility of these species, they may not represent an energetically sound alternative to terrestrial herbs. Support for this is tentatively offered through the finding that gorilla presence at the bai was actually lower during periods of low fruit availability than when fruit were abundant; the inference being that gorillas can afford to 'take it easy' and consume more aquatic herbs, allowing for their high water content, when the bulk of their nutritional needs are easily met through the consumption of fruit. More research in this area would be of considerable interest.

At Maya bai, gorilla presence was depressed during the drier months of January, February, and August; an effect that Magliocca (2000) suggests may be linked to the drying of soils supporting aquatic vegetation and its subsequent negative impact on food quality. The presence of *Santira sp.* fruit in the forest during August was also linked to the reduction in visitation. At Mbeli, while the dry season lowered the water table, most of the bai remained waterlogged, and there was little evidence that a major change in food-plant quality occurred (though nutritional analysis remains to be carried out). The effects of the major fruiting season on bai visitation are not yet clear, especially as the drop in gorilla presence potentially attributable to dry season effects on fruit availability may in fact have more to do with the effects of *Stomoxys sp.* flies. One major outbreak of these irritant biting flies took place in April and May of 1997, with catastrophic impact on several ungulate species (Elkan, Parnell & Smith, in press), and the flies have been noted as present, though at lower numbers, each year. Such events confuse the interpretation of presence data with regard to food availability and data will be required from more years before these variables can be explored independently.

As already noted, the rise in gorilla presence apparent as fruit becomes more available may be linked to a reduced need for extensive ranging to exploit higher quality herbs. At Lopé, however, day ranges were significantly longer during good fruit months than bad (Tutin, 1996), though the high availability of terrestrial herbs in the dense Marantaceae forest of Lopé may have influenced these figures. At Mbeli, extremely high presence rates in 1996 and 1998 were clearly shown to be due to major fruiting events of *Nauclea vanderguchtii.* In 1996, the fruit of this species became ripe in October, while in 1998, ripe fruit were already available in late August. It is therefore not inconceivable that some of the rise in gorilla presence at the bai towards the second half of the year may be linked to the monitoring of the *Nauclea* crop for abundance and ripeness (Olejniczak 1997). *Nauclea* was clearly of considerable importance to gorillas: frequently visiting groups increased their average rate of visitation, and the arrival and departure of several unknown units coincided exactly with the availability of fruit at the bai edge. Due in all probability to canopy destruction by feeding gorillas, *Nauclea* did not fruit heavily each year, but in the years covered, showed a bi-annual cycle. More data are now required to explore the influence of this species on bai-use patterns at Mbeli.

An attempt was made at using bai visitation patterns and zone of entry to gain insight into the relative locations of unit home ranges. While some units showed little preference for one zone over another, there were clear examples of others using some zones preferentially. It is hypothesised that in some cases, these preferences may reflect the angle of travel of the unit in question during its journey to the bai, and thus, the direction of its core home-range. However, such observations must remain purely conjectural until further field study into gorilla presence at other clearings, or the tracking of units, are undertaken. Similarly, the analysis of visitation rate can only provide clues to relative home-range location. Extreme variation between units was evident, with some groups highly likely to have the bai relatively central within their core range, and others having to make considerable home-range extensions to reach the area. The combination of entry zone and visit frequency may allow a 'theoretical' map to be drawn of relative home range locations of units, and to consider social relationships between units with such a map in mind, however, it is impossible to escape the ultimate limitations to our knowledge of these units in this regard, which are set the moment the gorillas exit the bai.

Chapter 4

Social Structure and Organisation

Introduction

Gorilla life revolves around the group. Whether an individual is in a group, looking for a new one, or trying to build one from scratch, the influence of the group is all-pervading. The group shapes the character of developing individuals, influences dispersal patterns, and impacts upon reproductive success. The group not only facilitates genetic survival, but in some cases, that of the individual itself (e.g., Harcourt, 1978a; Harcourt & Stewart, 1981; Watts, 1989, 1996).

An understanding of the way in which gorilla society is structured is fundamental to any further investigation, whether it be of social interaction, behavioural ecology, or even physiology. Furthermore, with many gorilla populations in areas threatened by human disturbance in the form of war, bushmeat hunting, human transmitted disease and habitat destruction, the monitoring of population trends is becoming increasingly important. The informed interpretation of census results relies on a sound knowledge of how, from a demographic perspective, undisturbed, healthy populations should look. The processes involved in mediating demographic change must also be understood if abnormalities in the social structure of a population are to be detected. Such an understanding has remained firmly out of reach for as long as the social organisation of western lowland gorillas has remained a mystery. This chapter offers, for the first time, an accurate description of social structure and organisation in a large population of western gorillas; information that is indispensable to any attempt at a comparative approach to an understanding of this and other primate species, and the effective monitoring of threatened populations.

This section will begin with an overview of the main shaping influences on group life, before summarising what is already known of social organisation in gorillas. After stating the aims of the chapter and describing the methods used in data collection and analysis, a full description of the Mbeli population will be given, detailing group size, composition and type. Comparisons with other populations will be made where applicable and the Mbeli data discussed in relation to existing hypotheses for group formation and type. A further sub-section of the chapter will comment briefly on birth and mortality rates at Mbeli, followed by a description of male and female dispersal patterns.

Group Living

The formulation of any strategy inevitably involves a weighing up of potential benefits against potential costs. This remains so whether the weighing up is a conscious process or a behaviour under evolutionary selection pressure. For group living to have evolved as such a widespread reproductive and survival strategy, it can be assumed that in many species, the benefits to the individual outweigh the costs. Benefits may include increased protection from predators, either through the dilution effect (e.g., Hamilton, 1971; Calvert et al., 1979) or through increased vigilance (e.g., Dimond & Lazarus, 1974; Pulliam et al., 1982), protection from dangerous conspecifics (e.g., Watts, 1989), and a range of benefits related to the location, acquisition, and defence of food resources (e.g., Gartlan & Struhsaker, 1972; Garber, 1988). The costs of group life may involve increased competition for food (e.g., Janson, 1988), harassment by other group members, and increased incidence of disease or parasite transmission (e.g., Hoogland,1979).

Understanding the forces generating and shaping group structure in a given species may frequently involve unravelling a complex web of costs and benefits. Within the Primate Order in particular, a large variation in grouping patterns can be discerned, and it may be impossible to isolate a single factor responsible for generating the social system of a given species (Clutton-Brock & Harvey, 1977a). Furthermore, the factors influencing group structure and size may be different from the original selection pressures that promoted group living. Finally, the social system observed in a given species may differ from the mating system exhibited (Dixson, 1998).

In primate societies, various conflicting theories, concerning the relative importance of food acquisition, predators, and infanticidal conspecifics have been suggested for the evolution of group living. Grouping may have evolved as a strategy for the efficient acquisition of food resources (Wrangham, 1979). Female primates invest more heavily in their offspring than do males. Females carry their offspring during gestation and are then responsible for their feeding and care until, and sometimes beyond, weaning. Reproductive success in females is thus predicted to be limited first and foremost by the quality and availability of food resources. Males, however, may invest very little in their offspring, and their reproductive success is principally limited by access to breeding females. Such differential levels of parental investment (Trivers, 1972) generate intra-sexual competition among males (for access to females) and among females (for the best males).

Wrangham (1979, 1980) proposed that females living in groups would be better able to maximise their survival and reproductive capacity than solitary individuals. This paradigm, based upon the effects of inter-group feeding competition, predicts that groups of females may find greater success at gaining access to, and defending food than solitary females. Female membership of these groups is likely to be life-long, facilitating the development of strong affiliative bonds. As male reproductive success is limited by access to females, males are predicted to be distributed around these groups of females so as to best maximise their chances of obtaining mating opportunities. However, although many primate species fit into this model, others, including mountain gorillas, show females forming groups but without close bonds developing and with female emigration as a norm.

Another theory for group formation in primates relates to predation pressure (Alexander, 1974; van Schaik, 1983). It claims that in most cases, there are no feeding advantages to group living and that in fact, any gains through the improved defence of food resources are outweighed by the effects of intra-group feeding competition. The theory proposes that selection for group living has operated only via the decreased chance of being killed by a predator while living in a group (van Schaik, 1983). Between these two poles lies a middle ground, in which predation is acknowledged as an important factor, but where improved feeding also plays a role (e.g., Jolly, 1972; Clutton-Brock, 1974; Pulliam & Caraco, 1984).

Finally, group living has been hypothesised as a mechanism for the reduction of infanticide risk (Hrdy, 1974; Watts, 1989; van Schaik & Kappeler, 1997). In many species, including primates, males kill unrelated infants in order to trigger a resumption of oestrus in females, allowing for mating to take place with the infanticidal male (e.g., langurs – Sugiyama, 1965; lions - Packer & Pusey, 1983; colobines – Struhsaker & Leland, 1987).

The Social System of the Gorilla

The core of this section, by default, describes the social system of the mountain gorillas at Karisoke, Rwanda, for almost everything we know of gorilla society is based on this tiny and isolated population. A brief mention of western lowland gorilla social systems is made at the end of the section, but until now, only disparate and vague reports for this sub-species have been available.

As mentioned above, there may be differences between an observed social system and the mating system in operation. Mountain gorillas provide a good example of this (Dixson, 1998). The mating system described for the sub-species is that of female defence polygyny. In this system, a single adult male maintains a harem of adult females over which he is able to control breeding access. In theory, all offspring born into these groups will have been sired by the silverback. In practice, many groups contain more than one silverback and although most offspring are still thought to have been fathered by one dominant silverback, covert matings by subordinate males may be responsible for some births within a group (Robbins, 1999).

Groups with more than one silverback are common in the Virungas. Weber & Vedder (1983), using 1978 census data, found 37% of groups to be multi-male (7/19), although the maximum number of silverbacks per group remained at two. Sholley (1991) found 25% of groups (8/32) to contain more than one fully adult silverback. In such groups, the additional males are usually sons of the dominant silverback.

Male natal emigration at, or just prior to full maturity at 14-15 years of age is common. However, Harcourt (1978a) found that 40% of males in a small sample of groups (N = 6) did not emigrate from their natal group, and in an analysis of 25 years of demographic data from the Virungas, Robbins (1995) found that 4 of 11 males (36%) remained in their natal group. The decision of whether or not to emigrate, though yet to be shown definitively, is thought to be linked to the number and ratio of females and males in the natal group, group size, and the past history of males' relationships within the group (Robbins, 1995; Harcourt & Stewart, 1981). Males remaining in their natal group may obtain covert or tolerated mating opportunities, and in some cases may become dominant should the previous silverback die or become infirm (Harcourt & Stewart, 1981; Fossey, 1982; Stewart & Harcourt, 1987; Watts, 1990a). Data are as yet insufficient, but it is suggested that lifetime reproductive success is greater for males remaining in their natal groups than for those emigrating and becoming solitary (Robbins, 1995; Watts, 2000).

Between natal emigration and first acquisition of females, virtually all males spend a period of time travelling alone. Males do not appear able to leave their natal groups and usurp leadership from the silverback of another group in order to establish a group of their own. The mean age of emigration for Karisoke males is 13.5 ± 1.2 years (N = 9, range 12 - 15 yrs: Robbins 1995), and most emigrant males toward the upper limit of this range are likely to become solitary until able to acquire females. Solitary males frequently follow established breeding groups and may interact agonistically with them in order to attract the attention of potentially migrant females. Encounters with these groups are often violent and may lead to the wounding of the silverbacks involved (Harcourt, 1978b). Such competition for females among males is thought to have contributed heavily to the extreme sexual dimorphism shown by the species (Stewart & Harcourt, 1987).

Younger males, and especially those in single-silverback groups collapsing after the death of a silverback, may seek to join an all-male (or 'bachelor') group in which to continue their development in a social environment potentially offering a reduced risk of predation and conspecific harassment (Yamagiwa,1987a; Robbins, 1995). Such all-male groups are rare however, and in most cases, males emigrate from them on reaching maturity, much as they would from a natal group.

Female gorillas are unusual among primates in that most leave their natal group (Harcourt et al., 1976; Harcourt, 1978a; Watts, 1990b). This movement is directly from one group to another, or directly to a solitary male, and as such, is known as 'transfer' rather than 'emigration' (Pusey & Packer, 1987). This is presumed to be a response to an increased risk of predation for solitary females. Furthermore, the young offspring of females not accompanied by a silverback are at high risk of infanticidal attack from other males (Fossey, 1984; Watts, 1989). Natal transfer in females appears to be voluntary (Harcourt et al., 1976; Harcourt, 1978b), and mostly takes place between menarche (median age = 6.33yr, range 5.75 to 7.1yr) and the time of first breeding (median age at first parturition = 10.05 years, range 8.67 – 12.75; Watts, 1991a). Some females, however, remain within their natal group and breed with males other than their father. These individuals may remain within the group or may subsequently transfer to breed again in other groups (Harcourt, 1978a; Watts, 1996).

Secondary transfer is common in female gorillas, and an individual may breed in several groups during her lifetime (Watts, 1991a). The purpose of female transfer appears to be initially, the avoidance of inbreeding, and subsequently the optimising of infanticidal-male/predator protection, and to a lesser extent, the reduction of feeding competition (Watts, 1990b). Factors thought to influence a female's transfer choices include the number of males in the current group, current and prospective group size, composition and sex ratio, past success at raising young, and perceptions of male ability to protect offspring from predators and particularly, infanticidal males. The overall population structure is also likely to affect the choices open to, and selected by, females (Watts, 1989).

New groups are formed when females transfer from their natal or subsequent breeding groups to join a solitary male, or when breeding groups fission permanently into two units (Harcourt, 1978a). Groups in which a silverback dies and in which no other mature males are present are liable to collapse, with females and younger offspring transferring into other groups, and immature males either becoming solitary or especially in the case of younger males, joining an all-male group (Schaller, 1963; Yamagiwa 1987a; Robbins, 1995).

About 90% of the mountain gorilla diet is comprised of stem, leaf and pith foods (Schaller, 1963; Fossey & Harcourt, 1977; Watts, 1984). The plants providing this resource are abundant and quite evenly distributed temporally and spatially throughout the range. As such, the defence of feeding access is neither necessary or practical, either at an inter-group or intra-group level. There is some evidence that feeding competition may have a small influence on a female's decision to emigrate (reproductive success is slightly lower in larger groups), and thus have an impact on group size, but competition for the protective proximity of a quality silverback may be as, if not more, important (Watts, 1985, 1990b). In general, proportionally more females transfer from large groups than small and it has been suggested that small to medium sized groups are optimal for female survival and reproductive potential (Watts, 1990b).

Eastern lowland gorillas exhibit similar dietary preferences to mountain gorillas, though a greater fruit component is included at lower altitudes within their range (Casimir, 1975; Goodall, 1977; Yamagiwa et al., 1996). Western lowland gorillas, however, range in forest types containing considerably more succulent fruit, and are correspondingly more frugivorous than either eastern sub-species (Sabater Pi, 1977; Tutin & Fernandez, 1985; Williamson et al., 1990; Nishihara, 1995; Remis, 1997). The fruit of six plant species are known to be consumed by mountain gorillas (Watts, 1990b), compared with over 100 species for western lowland gorillas (at Lopé, Gabon; Tutin & Fernandez, 1993a). Fruit production in tropical forests is seasonal and may fluctuate annually in both species and quantity of fruit available (Tutin & Fernandez, 1993a). While terrestrial herbs still represent a stable base in the western lowland gorilla diet, the more patchy distribution of herbs, and the temporal and spatial variability of fruit foods have been suggested as factors responsible for increased home range sizes (Tutin et al., 1992) and reduced group cohesion (Mitani, 1992; Goldsmith, 1996a; Remis, 1997).

Despite the considerable differences reported between mountain and western lowland gorilla diets, in most respects, their social structure has appeared similar. Groups are known to be either single or multi-male, and female transfer and male emigration have been reported. However, as Doran & McNeilage (1998) point out, all-male groups have yet to be reported in western lowland gorillas. Furthermore, Magliocca et al. (1999) describing a large population of gorillas visiting Maya Bai in the Republic of Congo found that no groups contained more than one silverback. There can be little doubt, however, that most of the little we know of western lowland gorilla social organisation has been gleaned from secondary evidence (trail and nests) and from too few groups for robust conclusions to be drawn.

Aims

Although broad in approach, the overall aims of this chapter are straightforward and involve the description of social organisation for a large population of western lowland gorillas. Thorough demographic study of long-lived species such as apes cannot be achieved within the usual time-span of field-work for a thesis, but may take decades. This work draws on three years of observation, and benefits from two years of monitoring prior to the start of the study (Olejniczak, unpubl. data). With the unique observation conditions at Mbeli, this is sufficient time in which to confidently describe social structure in cross-sectional terms, and to begin the process of understanding how demographic processes work through individual life-strategies to create the social 'landscape' of the population.

Ecological data from outside the bai were not collected systematically and as such, a detailed analysis of how social parameters such as group size are influenced by forest type and food availability is not within the scope of this thesis. However, by adopting a comparative approach with other studied populations, some mention of this topic will be made. Fundamentally though, the chapter is descriptive in nature and designed to provide a firm reference base for the sub-species and a robust data-set for comparative analyses with mountain gorillas and other well-studied populations.

Subjects covered include the following:-

- Group Size:

  What is the range of group sizes and the average group size for the Mbeli population?

  How does group size at Mbeli compare with that from other populations?

  Is group size an important factor in the selection of groups by transferring females?

  Does group size have limiting effects on reproductive success or survival?

- Group Composition:

  What is the range and average composition of groups at Mbeli?

  Are multi-male groups present in the population?

  Are all-male groups present in the population?

  How does the composition of the Mbeli groups compare with other populations?

  What factors cause the variation in the group sizes and composition observed?

  To what extent does group size and composition change with group longevity?

- Dispersal Patterns:

  Is there evidence of male and/or female emigration and transfer in the Mbeli population?

  Why and when do individuals leave their groups?

  What are the consequences of emigration in males and females?
- Group Stability:

  Does the Mbeli population offer any evidence of flexible grouping patterns such as fission-fusion or temporary sub-grouping?

Methods

The methods used in data collection for this chapter follow those detailed in the earlier general Methods chapter. All observations were made from the observation tower at the edge of the bai, and no attempts were made to follow gorillas into the forest after a contact.

Most of the groups used in these analyses were present from the start to the end of the study period, though some groups collapsed and new groups formed. No attempt is made to describe a group by expressing average size or group composition generated from scans made throughout the 3 year period. Instead, these parameters were taken as those evident either at the end of the study period (November 1999), or, if a group broke up during the study period, on the last occasion it was seen functioning as a discrete social unit. By allowing the greatest possible time to pass before making a description, the most precise identification of individuals and groups can be guaranteed.

Clearly, when describing population size and composition, each gorilla is counted once only. However, when describing group composition and stability, there was some overlap, with some individuals transferring from one group to another. In the case of BON group, all members transferred into NOO group upon the death of their silverback. FFF group also broke up following the death of their silverback, with a young silverback becoming solitary (DYL) and the remaining individuals joining two unknown males (a silverback and what is thought to have been his almost mature son) to form MOS group. Thus, when considering grouping patterns, some individuals will be counted twice in the same analysis. Such use of different groupings from the same population as independent sample units is statistically sound and has been used many times in animal grouping studies (e.g., Altmann & Altmann, 1977; Caraco, 1979; Watts, 1985).

Fourteen groups are used in most of the following analyses. Only groups in which size and composition were known with complete confidence were selected. In most cases, these represent the most frequent visitors to the bai. Of the three groups that were seen on less than 20 occasions but remain in the analysis, one (MAX) was comprised mostly of females that were previously known to observers (having transferred from a well known group as sub-adults); individuals from FFF group transferred into other Mbeli units and so remained in the population, and confidence in the identification of the other group (EME) was greatly assisted due to a highly conspicuous mark on the silverback's shoulder.

Before presenting the data and analysis from Mbeli, a brief critique of the methods used to investigate social organisation at other study sites is offered. This is required in order to fully appreciate the value of certain comparative analyses presented in the Results. Table 4.1 gives reference details of the studies featured in population comparisons in this chapter.

Table 4.1 Details of study sites and periods of data collection used in comparative analysis

Name	Region	Sub-species.	Nation	Period of Collection	Data source	Reference
Rio Muni	Mt. Alen & Ab.-An.	wlg	Equatorial Guinea	1967-8	n.c./obs.	Jones & Sabater Pi 1971
Ndoki 1	Nouabalé-Ndoki N.P.	wlg	Republic of Congo	1991	n.c./obs.	Mitani et al. 1993
Ndoki 2	Nouabalé-Ndoki N.P.	wlg	Republic of Congo	1991-2	n.c./obs.	Nishihara 1994
Mbeli	Nouabalé-Ndoki N.P.	wlg	Republic of Congo	1997-9	obs.	This report
Lossi	Odzala N.P.	wlg	Republic of Congo	1997-8	n.c./obs.	Bermejo 1999 (2001?)
Maya	Odzala N.P.	wlg	Republic of Congo	1996-7	obs.	Magliocca 1999
Ndakan	Nouabalé-Ndoki N.P.	wlg	Central African Republic	1987-8	n.c.	Fay 1997
Lopé	Lopé Reserve	wlg	Gabon	1989-90	n.c./obs.	Tutin et al. 1992
Mikongo	Lopé Reserve	wlg	Gabon	2000	n.c./obs	Bermejo 2001
Kahuzi	Kahuzi-Biega N.P.	elg	Dem. Republic of Congo	1990	n.c./obs.	Yamagiwa et al. 1993
Virungas 1	Mt. Mikeno	mg	Rwanda	1959-60	n.c./obs.	Schaller 1963
Virungas 2	Mt. Mikeno	mg	Rwanda	1976	n.c./obs.	Weber & Vedder 1983
Virungas 3	All sectors but Mikeno	mg	Rwanda	1978	n.c./obs.	Weber & Vedder 1983
Virungas 4	Mt. Visoke	mg	Rwanda	1981-2	n.c./obs.	Yamagiwa 1999
Virungas 5	All sectors	mg	Rwanda	1989	n.c./obs.	Sholley 1991
Bwindi	Bwindi Impenetrable N.P.	mg	Uganda	1997	n.c./obs.	McNeilage et al. 2001

wlg – *G. g. gorilla*. elg – *G. b. graueri*. mg – *G. b. beringei*. n.c. - nest counts. obs. - direct observation.

Methodological issues associated with past reports and their implications for comparative analyses

As outlined previously, the difficulties encountered in observing western lowland gorillas directly have forced researchers to concentrate on secondary evidence (trail, nests and faeces) when investigating ecology, ranging and social structure. Traditional methods of assessing group structure in western lowland gorillas have met with mixed results. Nest counts have frequently been used as a census tool and as an alternative method for estimating group size and structure (e.g., Tutin & Fernandez, 1984; Mitani et al., 1993; Remis, 1993; Nishihara 1994; Fay, 1997; Mehlman 2001; Blom et al., 2001). However as Tutin et al. (1995) point out, in their study of 373 nest sites at Lopé, only a third of the sites attributed to their main study group accurately reflected the number of weaned individuals in that group: this was despite an intimate knowledge of the study site, considerable experience at locating nests, and a low proportion of 'zero construction' nests (5%) which are harder to locate. Nest site census technique fails to show the number of infants in a group accurately, as individuals in this age-class do not make their own nests and their dung is easily overlooked or absent (Fay, 1997). Unfortunately, it is not always clear in past reports whether results are limited to weaned individuals only.

The diameter of faeces found in night nests is often used to determine the age-class of an individual (e.g., Schaller 1963; Harcourt and Fossey, 1981; Weber & Vedder, 1983; Yamagiwa et al. 1993). However, confusion may arise when important age differences are not revealed by faecal diameter. It is not possible, for instance, to differentiate between some blackback males (8-12 years) and adult females (≥8 years) using this method, and the faeces of young silverbacks (12-15 years) may be identical to those of fully developed silverbacks (pers. obs.; Williamson, pers. comm.). Furthermore, the quantity of fruit in the diet of western lowland gorillas renders their faeces generally softer and less reliable as age-indicators than those of mountain gorillas (Tutin et al., 1992; Parnell, 2000b).

Even direct observations obtained at bais should be interpreted wisely when describing social structure. Whether bai data represent full and accurate descriptions of group structure or more general census estimates, will depend on the number of occasions and length of time each group is observed. For example, Magliocca et al. (1999) give details of group size and composition for 31 gorilla groups at Maya Bai, Congo. However, their data reveal that 32% of groups were seen on only one occasion (mean visits per group = 3.29 [SD 2.41, range 1-11]). At Mbeli, complete confidence in group size from a single observation could not be achieved (it is common for some individuals to remain in the forest edge in the early stages of habituation [Olejniczak, pers. comm.]), and even three to five visits did not guarantee error-free description of group composition (Parnell, 2002).

It is necessary to reiterate another point made in the Methods chapter relating to age-class definitions. There is considerable variation in the protocols employed in the published literature (e.g., Schaller, 1963; Harcourt et al., 1980; Weber & Vedder, 1983; Watts & Pusey, 1993; Magliocca et al., 1999), such that inter-site comparisons may in fact be comparing different age-groups, limiting their value considerably. This appears particularly to be the case with sub-adults and silverbacks.

Analyses of group size and composition, and inter-site comparisons, may be weakened due to invalid assumptions regarding the homogeneity of the data. Given the low sample sizes commonly presented in gorilla research, variance will frequently influence mean or median values unacceptably, such that apparent differences between populations may be statistical artefacts rather than the result of real influences such as sub-species or habitat type (Dunbar, 1987). Mean values on demographic parameters such as group size and composition should be used only after an assumption regarding normality in the distribution of group types has been validated. The small number of groups that frequently constitute a sampled population in gorilla research make such assumptions problematic. Median values, while more appropriate, may also suffer small sample effects, such that caution should be used when interpreting results.

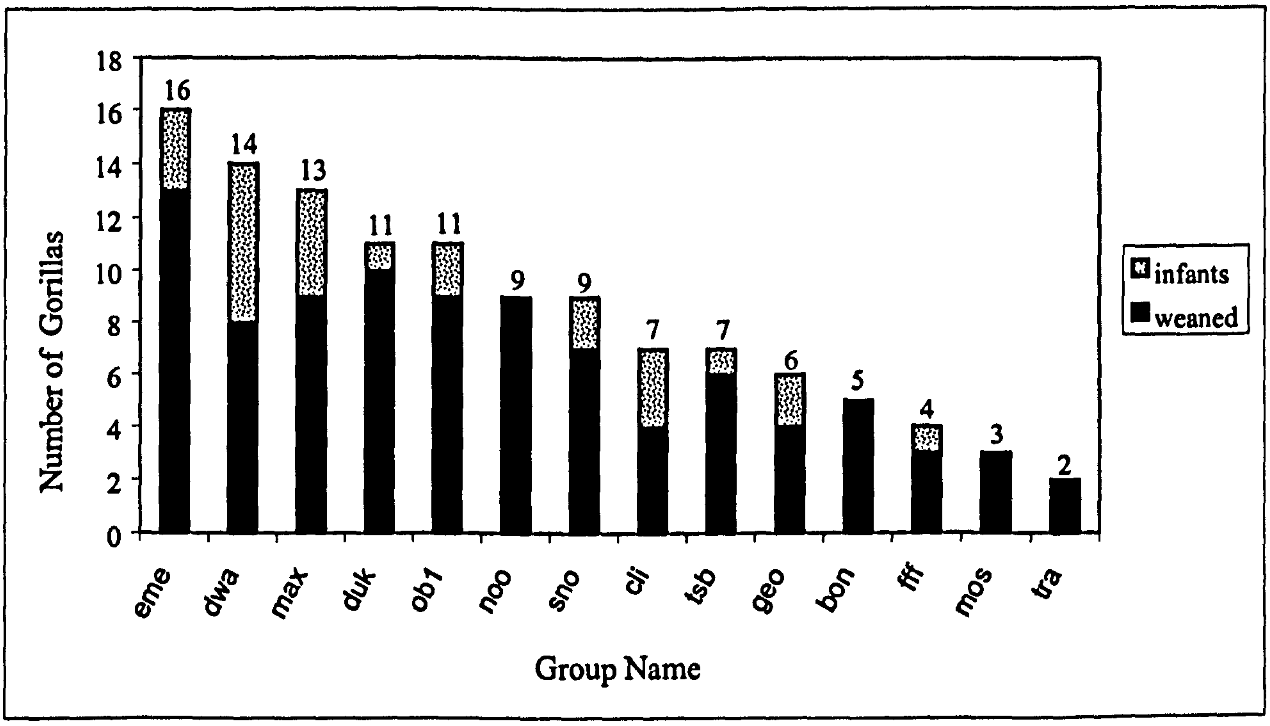
Results

Group Size

Group size at Mbeli

Figure 4.1 shows the total group size for the 14 well-known groups at Mbeli. In order to permit comparisons with data collected using nest sites, the columns are split into weaned individuals and those under three years of age. Total group size ranged from 2 to 16, and the mean for the 14 groups was 8.36 ± SD 4.3 (median = 8, IQR 6.75). The number of weaned individuals per group ranged from 2 to 13, with a mean of 6.57 ± SD 3.2 (median = 6.5, IQR 5.25). Weaned individuals accounted for a mean of 81.6% of total group individuals (± SD 15.4).

Figure 4.1 Weaned and total group size for fourteen groups at Mbeli



Group size compared across sites

Despite some concerns regarding the accuracy of some of the data, the only other large population of western lowland gorillas for whom whole group counts (including infants) are available is that studied at Maya Bai in the Odzala National Park, Republic of Congo (Magliocca, 1999). All other studies include data that are to a greater or lesser extent derived from nest census results. As such, they either underestimate, or in many cases, completely fail to account for infants. At Maya Bai, total group sizes ranged from 2 to 22, with a mean of 11.16 ± SD 4.9 (median = 11, IQR 9). With weaned individuals only, groups ranged from 2 to 18 with a mean of 8.9 ± SD 3.9 (median = 9, IQR 6). Neither weaned nor total group size differed significantly between sites (Independent Samples *t* – test: weaned individuals; *t* (43) = 1.94, *P* = 0.059, total individuals; *t* (43) = 1.84, *P* = 0.073) though for weaned individuals, Maya's larger groups only narrowly failed to do so.

Further comparisons between populations must rely on non-parametric statistical tests due to occasional low sample sizes and abnormally distributed data. Confusion and imprecision may arise from the results of several populations being obtained by a combination of direct observation and nest counts. Subsequently, it is not possible to know with confidence whether numbers for infants are nest-count underestimates or accurate observational counts. In order to remove this potentially confounding effect, the following analysis concentrates primarily on weaned group size, omitting the 'infant' age-class altogether. Unfortunately, data from the Ndakan site in the Central African Republic (Fay, 1997) and the early results from Rio Muni, Equatorial Guinea (Jones & Sabater Pi, 1971) are omitted as the lack of group composition data from these sites means that no corrections for infant numbers can be made.

Table 4:2a presents average numbers of weaned individuals (≥3years of age) from 14 studies (for reference, Figure 4.2b gives total published group sizes including infants). Five data sets are given for the Virunga gorillas, covering the area as a whole, some areas as distinct from others, and data from the same areas at different times. Rather than attempting to analyse such fine-grained differences, this has been done in order to best represent the population as a whole. Mountain gorillas are also represented by the geographically and genetically isolated Bwindi population in Uganda. Only one data-set is presented from eastern lowland gorillas, while six study sites are represented for western gorillas (two sets from Ndoki).

Table 4.2a Average group size compared between study sites (weaned individuals only).

Site	Mean gp. size and S.D.	Median	IQR	Range	No. of gps
Ndoki 1	6.14 ± 2.3	6	5	3-9	7
Mbeli	6.57 ± 3.2	6.5	5.25	2-13	14
Ndoki 2	6.60 ± 2.5	7	4	3-10	5
Lopé	8.25 ± 3.3	8.5	6.25	4-12	4
Maya	8.87 ± 3.9	9	6	2-18	31
Mikongo	10.25 ± 4.0	10	7.75	6-15	4
Lossi	13.50 ± 6.1	13.9	7.6	5.4-25.4	8
Kahuzi	9.16 ± 5.7	7	7.75	2-21	25
Virungas 2	7.67 ± 4.4	6	8	3-15	9
Virungas 5	7.88 ± 6.0	6	5	2-23	32
Virungas 3	7.11 ± 2.5	7	4	3-13	19
Bwindi	8.00 ± 4.3	8	8	2-16	28
Virungas 4	8.00 ± 1.7	8	2	6-12	11
Virungas 1	12.30 ± 5.2	13	7.5	4-21	10

IQR – Inter-quartile Range.

Table 4.2b Average group size from other study sites (all individuals).

Site	Mean gp. size and S.D.	Median	IQR	Range	No. of gps
Ndoki 1	7.29 ± 3.5	6	8	4-12	7
Rio Muni	6.85 ± 3.2	7	5.5	2-12	13
Mbeli	8.36 ± 4.3	8	6.8	2-16	14
Ndoki 2	7.80 ± 2.2	9	4	5-10	5
Lopé	9.25 ± 4.6	9	8.8	4-15	4
Maya	11.16 ± 4.9	11	9	2-22	31
Ndakan	11.67 ± 7.9	10.5	14.3	3-24	6
Mikongo	12.75 ± 4.57	12.5	10	8-18	4
Lossi	17.00 ± 7.7	17.5	9.5	7-32	8
Kahuzi	10.00 ± 6.3	8	9	2-24	25
Virungas 2	9.00 ± 6.1	6	10	3-21	9
Virungas 3	8.68 ± 3.4	7	6	3-15	19
Virungas 5	9.47 ± 7.1	7	6.5	2-34	32
Virungas 4	9.91 ± 3.0	9	4	6-16	11
Bwindi	9.89 ± 5.8	10	9.5	2-23	28
Virungas 1	16.90 ± 7.0	18.5	11.5	5-27	10

Group composition data are only available for one of the eight Lossi groups, and it was noted that infants represented 22% of this group. In order to include the important results from Lossi, it was decided that an equivalent reduction should be made from the other Lossi groups, as an estimation of weaned individual numbers. However, it was felt that using a reduction value of 20.5% (proportion of infants), calculated from the 31 groups at the Maya Bai site, 50km to the west, would be a safer procedure than basing such a reduction on a single group, albeit from the population in question.

Initially comparing groups of weaned individuals for western lowland gorillas, the Kruskal-Wallis test revealed a significant difference in median group size ($\chi^2 = 14.13$, df = 6, $P = 0.028$) that can be attributed with confidence to the large groups at Lossi. When comparing weaned group size across all species/sub-species and studies, a significant difference was narrowly missed ($\chi^2 = 22.17$, df = 13, $P = 0.053$). The western lowland gorillas of Lossi and the mountain gorillas recorded by Schaller (1963) in the Virungas stand out as the populations with the largest groups, and both mountain and western gorilla populations also shared the smallest group sizes. Judging from its total group size average, the western lowland population at Rio Muni (Jones & Sabater Pi, 1971) would have retained its distinction as that with the smallest average group size, had composition data been available.

The conservative approach of analysing group size using only weaned individuals is perhaps the most appropriate way of maximising the comparability of diverse data sets. However, historical demographic pressures may have created conditions such that proportions of the younger age-classes in some areas may be unusually high or low, affecting group sizes considerably (McNeilage et al., 2001). Table 4.2b presents group size for all group individuals at all sites and studies (including Fay, 1997, and Jones & Sabater Pi, 1971). Although the nature of some data-sets make such analyses suspect, the same Kruskal-Wallis test performed on medians for total group sizes returns a highly significant difference between samples ($\chi^2 = 30.54$, df = 15, $P = 0.010$), with Lossi (median = 17.5) and Schaller's (1963) census (median = 18.5) once again implicated in producing this level of significance.

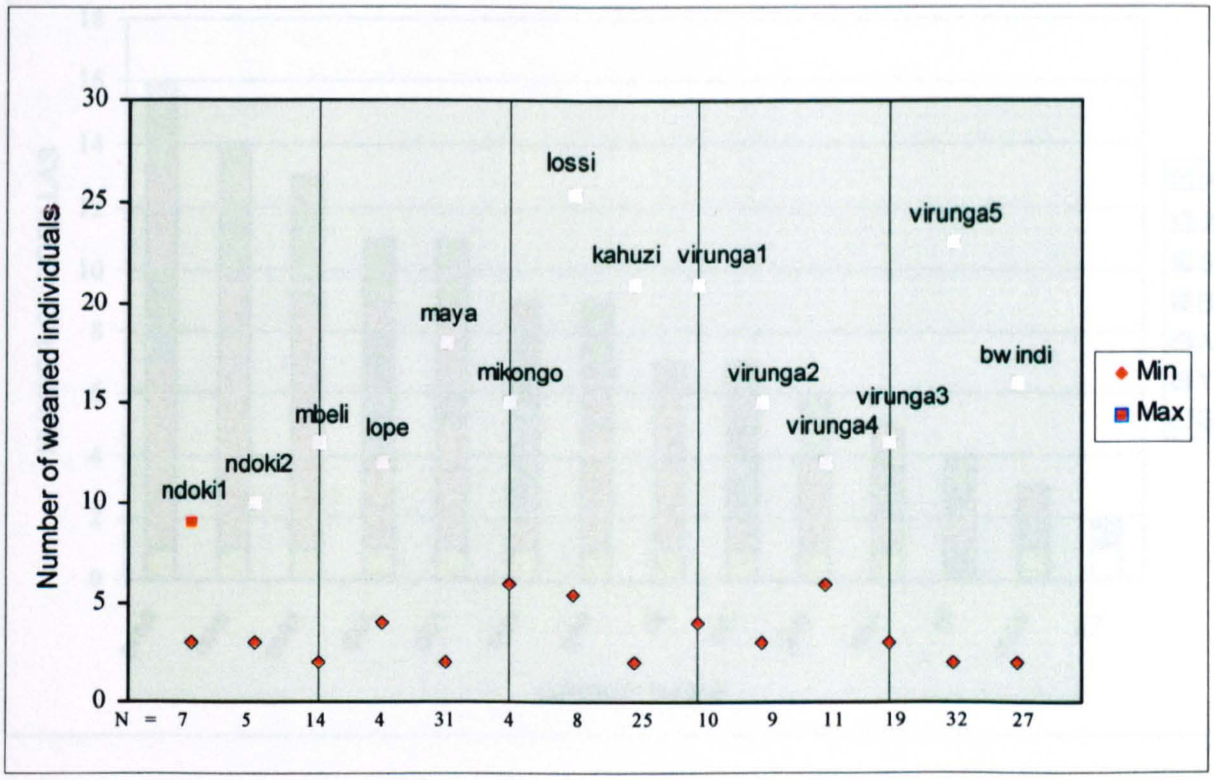
Minimum and maximum group sizes compared

Most comparisons of group size concentrate on average scores. However, information may be lost through ignoring the range and in particular the extreme ends of the range of group sizes in each population. It is suggested that if sufficient groups are sampled, most populations will be found to contain the lowest group size possible; that of two individuals. This is because most groups are formed by the initial association of a single male with a single female. Groups of two may also represent the final period of a group's existence, comprising only a silverback and a young silverback son (*see* 'Group Type' section). Minimum group size may then reflect little more than sampling efficiency (note that in Table 4.2b, the four samples with the highest number of groups censused all show minimum group sizes of two). Maximum group size, on the other hand will have no ceiling other than that created by socioecological variables such as food availability. For this reason it is potentially of more interest than minimum and possibly even average group size.

In this analysis, it is once again necessary to examine numbers of weaned individuals only, and the important data from Lossi are again included by reducing total group size by 20.5%. Figure 4.2 plots the largest and smallest group sizes for each of 14 data-sets. There were more large scores among the data for mountain and eastern lowland gorillas although the highest score was from Lossi. The lowest maximum group size was from western lowland gorillas at Ndoki (Mitani et al., 1993), being a little over two and a half times smaller than that at Lossi. When the distribution of median scores for maximum group size was examined, no outliers were present, suggesting that overall, differences were not extreme.

Group size range (the difference between minimum and maximum group size) was also examined for each site. In Figure 4.2 it appears that more eastern gorilla populations (mountain and eastern lowland) have larger group size ranges than western gorilla populations. However, the distribution of sample sizes (given below each pair of data points) suggests a more worrying trend.

Figure 4.2 Minimum and Maximum Group Size (weaned).



Refer to Table 4.1 for site details. From the left, all points up to and including 'lossi' are western lowland gorillas; those to the right of this are eastern lowland and mountain gorillas.

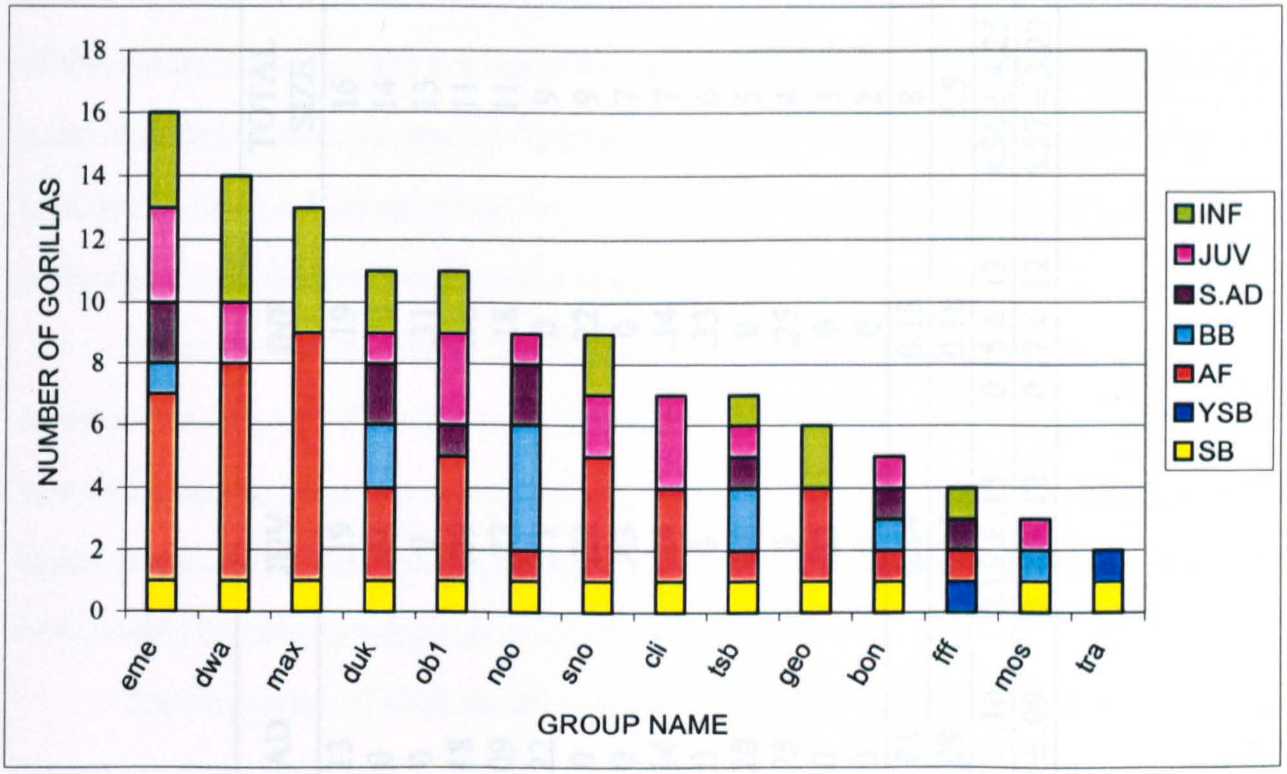
Sixty-four percent of the 14 samples have minimum group sizes of 2 or 3 individuals and even the higher minima vary little from the median of 3. Thus, differences in range are primarily due to the size of the largest groups. Using a Spearman Rank Correlation, a significant positive correlation was found between weaned group size range and the number of groups sampled per data-set ($r_s = 0.581$, N = 14, $P = 0.029$). While by no means certain, this does suggest that the observed differences in group size parameters sometimes ascribed to ecological variables may at least in part be due to differential sampling effort and thus may be a statistical artefact.

Group Composition

Group composition at Mbeli

Figure 4.3 gives the age/sex-class composition of 14 groups at Mbeli (age-class definitions are given in Chapter 2). Solitary males are not included.

Figure 4.3 Number of individuals per group in each age/sex-class at Mbeli



At Mbeli, the oldest male in one group (FFF) was a young silverback (age approx. 13 years) who remained in the group following the death of the group silverback until its eventual collapse. All other groups contained only one, fully mature silverback male (15 years). When summarising the population as a whole (including solitary males), adult silverbacks represented just over a tenth of group composition.

The median number of adult females in all group types was 3.0 (IQR 3.5, N = 14, range 0 to 8). For breeding groups only (those containing adult females), the median number of adult females remained at 3.0 (IQR 5.0, N = 11, range 1 to 8: one group containing a single young silverback was omitted from this analysis as the only adult female in the group was likely to have been his mother). Table 4.3 shows age/sex-class numbers as proportions of total group size.

Table 4.3 Proportion of individuals per group in each age/sex-class

GROUP	SB	AF	YSB	BB	S.AD	JUV	INF	TOTAL SIZE
EME	.06	.38	0	.06	.13	.19	.19	16
DWA	.07	.50	0	0	0	.14	.29	14
MAX	.08	.62	0	0	0	0	.31	13
DUK	.09	.27	0	.18	.18	.09	.18	11
OB1	.09	.36	0	0	.09	.27	.18	11
NOO	.11	.11	0	.44	.22	.11	0	9
SNO	.11	.44	0	0	0	.22	.22	9
CLI	.14	.43	0	0	0	.43	0	7
TSB	.14	.14	0	.29	.14	.14	.14	7
GEO	.17	.50	0	0	0	0	.33	6
BON	.20	.20	0	.20	.20	.20	0	5
FFF	0	.25	.25	0	.25	0	.25	4
MOS	.33	0	0	.33	0	.33	0	3
TRA	.50	0	.50	0	0	0	0	2
MEDIAN	0.11	0.32	0	0	0.05	0.14	0.18	8
B.G.	0.11	0.38	0	0	0.09	0.14	0.18	6.5
MEAN	0.15 ± .13	0.30 ± .19	0.05 ± .14	0.11 ± .15	0.09 ± .10	0.15 ± .13	0.15 ± .13	8.36 ± 4.25
B.G.	0.11 ± .04	0.36 ± .16	0	0.11 ± .15	0.09 ± .09	0.16 ± .12	0.17 ± .12	6.57 ± 3.23

B.G. – total values when only breeding groups are considered (i.e., groups with adult females: N = 11)

The use of proportions in the place of absolute numbers controls for the effect of group size when comparing groups. However the necessary use of medians in summarising data of this nature means that the average proportions for the 14 groups are not proportional to each other and as such, an 'average' group cannot be constructed from the data. Means are included in Table 4.3 for reference, and as both silverback and adult female proportions are normally distributed, the consideration of these data is permitted.

For all group types, adult females constitute approximately a third of all group members and almost 40% in breeding groups. Only two groups contained no adult females when their composition was recorded, though one of these was known to have done so earlier in the study. The silverback/adult female sex ratio was, for all groups, 0.31 (N =14), and in breeding groups only, 0.27 (N =11).

The proportion of adult females per group correlates positively with total group size (Spearman Rank Correlation: $r_s = 0.625$, n=14, $P = 0.017$). However, significance is lost when only breeding groups are included in the analysis ($r_s = 0.405$, n=12, $P = 0.192$). While it can be argued that the former result may indicate a disinclination for females to be part of small groups, this logic is likely to be circular, as the small groups not containing adult females at Mbeli may have become small *due* to female emigration. It is safer and more rational to consider breeding groups only, and this analysis suggests that larger breeding groups do not contain proportionately more adult females. Transfer patterns are more liable to indicate group size preferences among females.

In the 12 Mbeli groups containing adult females, the overall ratio of young immatures (0-6 yrs.) to adult females (≥8yrs.) is 0.90. Young immatures are present in all but one group, whether a breeding group or not, and represent a little over one third of all group members.

Young silverbacks are the least represented age-class in the population. The mean scores for these individuals are particularly misleading, as the small size of the two groups in which they were present inflates the overall population mean disproportionately. Clearly the median score of zero also fails to accurately portray their representation in the population, though less so than the mean.

Adult female/immature ratio

The relationship between the number of young immatures (0-6 years) per adult female both to total group size and to the number of adult females per group was examined as a possible indicator of the costs of different group sizes for reproductive success (Watts, 1990b). Table 4.4 shows the median number of young immatures per female against total group size. The two low median scores among the larger group sizes may be of interest, but a similarly low score is recorded for an intermediate sized group also. The relationship between these variables is not significant (Spearman Rank Correlation taking each group as an independent sample point: $r_s = -0.184, N=12, P > 0.567$). Similarly, in Table 4.5, which examines reproductive success against the number of females in a group, despite low scores for the larger numbers of females, the correlation coefficient is non-significant ($r_s = 0.485, N=12, P = 0.110$). Clearly though, with only one group representing several of the cases, few conclusions can be drawn from these tests. Furthermore, the individual group histories responsible for the scores observed may have a much greater effect on these parameters than feeding competition (Watts, 1990b).

Table 4.4 Median number of immatures per adult female in relation to group size (*sensu* Watts, 1990b).

Group size	Median no. of infants and juveniles per adult female
4 (1)	1.00
5 (1)	1.00
6 (1)	0.67
7 (2)	1.50
9 (2)	1.00
11 (2)	1.13
13 (1)	0.50
14 (1)	0.86
16 (1)	1.00

Numbers in brackets are the number of groups with the given group size.

Table 4.5 Median number of immatures per adult female in relation to number of adult females.

Number of adult females	Median no. of infants and juveniles per adult female
1 (4)	1.00
3 (3)	1.00
4 (2)	1.13
6 (1)	1.00
7 (1)	0.86
8 (1)	0.50

Numbers in brackets are the number of groups with the given number of adult females.

In an alternative test that simply plotted the ratio in absolute numbers of young immatures to adult females for each group against total group size, no significance was found (Spearman Rank Correlation: $r_s = -0.184$, $N = 12$, $P = 0.567$).

All-male ('bachelor') groups

When group compositions were recorded at the end of the study period, two groups were found to contain no adult females. However, one of these was known to have contained a female a few months prior to the census being taken, and the presence of a juvenile and sub-adult in the other group strongly suggests that it too was previously a breeding group. The Mbeli population did not, and has never in the history of the study, included true all-male groups.

Group composition compared across sites

The scope for making useful comparisons of group composition between sites is limited by the number of differing age-class definitions that have been used in the past. However, by concentrating on the more distinct age-classes, some comparisons can be made.

Silverbacks: single- or multi-male?

None of the 14 Mbeli groups could be considered 'multi-male' in the sense of their containing more than one mature silverback. Table 4.6 gives the percentage of multi-male groups in each reported study and the frequency of groups with varying numbers of silverbacks. All eastern populations contained multi-male groups, with proportions for representation ranging from 8% to 46%. Though data from different reports are not all independent, out of a possible 109 groups, 39 (36%) were multi-male. Among the western lowland studies complying with the conditions necessary for inclusion in the current comparative analysis, only two reports describe multi-male groups (Mitani et al.,1993; Tutin et al., 1992). This translates into a meagre two multi-male groups of a possible 65 (3%). Multi-male groups have also been described, however, at the Bai Hokou site in the Central African Republic (Goldsmith, 1996c; Remis, 1997).

Table 4.6 Single- and multi-male group representation across sites and studies

Site*	Number of Silverbacks (frequency) 2	3	4	Percentage of multi-male groups	Number of groups
Ndoki 2	-	-	-	0	5
Mbeli	-	-	-	0	14
Maya	-	-	-	0	31
Mikongo	-	-	-	0	4
Ndoki 1	1	-	-	14	7
Lopé	1	-	-	25	4
Kahuzi	2	-	-	8	25
Virungas 5	7	-	1	25	32
Virungas 1	1	-	2	30	10
Virungas 4	4	-	-	30	10
Virungas 3	7	-	-	37	19
Virungas 2	3	1	-	44	9
Bwindi	8	5	-	46	28

* See Table 4.1 for study references.

Adult females and young immatures

Table 4.7 shows the median proportion of adult females and young immatures per group for several studies, including Mbeli. Data from some studies are omitted due to variations in age-class definition (i.e., Schaller, [1963] does not differentiate between sub-adult and adult females: McNeilage et al. (2001) class juveniles and sub-adults together). With the exception of Weber and Vedder (1983) where corrections are already provided, no attempt is made to re-distribute sex-unknown adults into adult female and blackback classes; rather, only groups where the sex of all adults is known are used. In the case of McNeilage et al. (2001), only one group met this criterion, therefore the population is not included in the analysis.

Table 4.7 Median proportions of adult females and young immatures (juveniles and infants) per breeding group.

Location	No. of Groups	AF	IQR	JUV & INF	IQR
Ndoki 1	6	**0.29**	0.26	**0.29**	0.35
Lope	4	-	-	**0.33**	0.39
Mbeli	11	**0.38**	0.30	**0.33**	0.16
Maya	29	**0.33**	0.13	**0.36**	0.15
Mikongo	4	-	-	**0.40**	0.05
Ndoki 2	3	-	-	**0.44**	0.19
Kahuzi	11	**0.46**	0.17	**0.39**	0.21
Virungas 2	9	**0.33**	0.03	**0.20**	0.27
Virungas 3	18	**0.33**	0.16	**0.25**	0.19
Virungas 4	10	**0.32**	0.16	**0.33**	0.10
Virungas 5	16	**0.31**	0.19	**0.36**	0.23
Virungas 1	10	-	-	**0.46**	0.11

AF: adult females (≥8yrs.) JUV & INF: juveniles and infants (0 – 6yrs). Proportions in Weber & Vedder (1983) have unsexed adults redistributed into blackback male and adult female categories (sensu Harcourt & Fossey, 1981).

In non-parametric tests, medians for adult female proportions narrowly failed to differ significantly between studies (Kruskal-Wallis test: $\chi^2 = 14.02$, df = 7, $P = 0.051$). A highly significant difference was evident among proportions of young immatures (Kruskal-Wallis test: $\chi^2 = 29.88$, df = 11, $P = 0.002$), with Schaller's (1963) groups from Mt Mikeno showing the highest proportion of young immatures, and Mitani's (1993) data from Ndoki showing the lowest.

As a comparative measure of reproductive health, the ratio of young immatures to adult females was calculated for several studies, by dividing the total number of young immatures in breeding groups by the total number of adult females in the same groups. The results are listed in sub-species rank order in Table 4.8.

Table 4.8 The ratio of young immatures to adult females (breeding groups with fully known composition only).

Location	No. of Groups	Ratio of young immatures to adult females
Mbeli	12	0.90
Ndoki 2	2	1.00
Ndoki 1	5	1.15
Maya	29	1.19
Lope	2	1.20
Kahuzi	11	0.93
Virungas 3	18	0.72
Virungas 2	9	0.81
Virungas 4	10	1.16
Virungas 5	16	1.26

Mbeli exhibits the lowest ratio among western lowland gorillas, although two mountain gorilla censuses recorded scores that were lower still. Of the results from the Virungas, the two highest scores are from the earliest and most recent censuses. As mentioned earlier, Schaller (1963) did not differentiate between sub-adult and adult females. However the score for this study is included to represent a minimum figure. Had it been possible to divide off the sub-adult category, the young immature/adult female ratio would have been increased, potentially equalling or even surpassing the score calculated from the Virungas 5 data (Sholley, 1991). While incompatible methodologies may still play some part in explaining the differences between scores, it is probable that the 'U' shaped curve described by the immature/adult female ratio over time reflects a relatively healthy population during Schaller's study, coming under severe hunting and other human disturbance pressure during the seventies and early eighties before recovering again due to more effective protection.

Solitary males

Table 4.9 shows the number of solitary males in each population where the number of groups in the sample was over 10. Also given is the percentage of solitary males of all individuals, the ratio of solitary males to groups, and the percentage of multi-male groups per population.

Table 4.9 Representation of solitary males from seven studies

Study Name	No. of solitary males	Percentage of population	Ratio of solitaries to groups	% multi-male groups.
Mbeli	7	5.4	1 : 1.86	0
Maya	18	5.0	1 : 1.72	0
Kahuzi	9	3.5	1 : 2.77	8
Virunga 2	7	2.7	1 : 4.00	44
Virunga 4	2	1.8	1 : 5.50	30
Virunga 5	6	1.9	1 : 5.33	25
Bwindi	7	2.5	1 : 5.00	46

Once again, caution should be exercised in the interpretation of these results due to differences in detection rate. Nest count census techniques are likely to underestimate numbers of solitary males due to the lower probability of spotting single nests, whereas bai studies offer accurate counts. Another potentially confounding factor may arise should bais attract a disproportionate number of solitary males. The frequency with which bais are visited by a large variety of groups may make them ideal places for solitary males to contact groups with a view to attracting female emigrants.

However, these figures may relate to the observed number of multi-male groups per population. While a negative correlation between the percentage of solitary males and the percentage of multi-male groups in each population did not reach significance (Spearman Rank Correlation: $r_s = -0.703$, $N = 7$, $P = 0.078$), it may be useful to note that the populations with the fewest multi-male groups also had the highest proportion of solitary silverbacks.

Group histories

The previous analyses drew primarily upon the status of gorilla populations derived from census data. In other words, they describe the size and composition of groups at a particular moment in time. While this approach is unavoidable for the rapid assessment of a population, and is also necessary for drawing inter-site comparisons, it ignores the fact that group-living gorillas, like all social primates, exist in a state of perpetual social change. Groups ultimately serve individuals, and the social and physical needs of individuals change with their age, social status, sexual condition and the age/sex-class composition of the groups in which they live. These changes may even alter the character and to some degree, the function of a group. Even long standing relationships within a group are likely to evolve subtly over time. The immigration, emigration or death of individuals, the birth of infants, and the development of immatures are all potential causes for shifts in the nature of intra-group, and ultimately inter-group interactions. For these reasons, an appreciation of the dynamics of gorilla group life is essential to an understanding of how the social system functions.

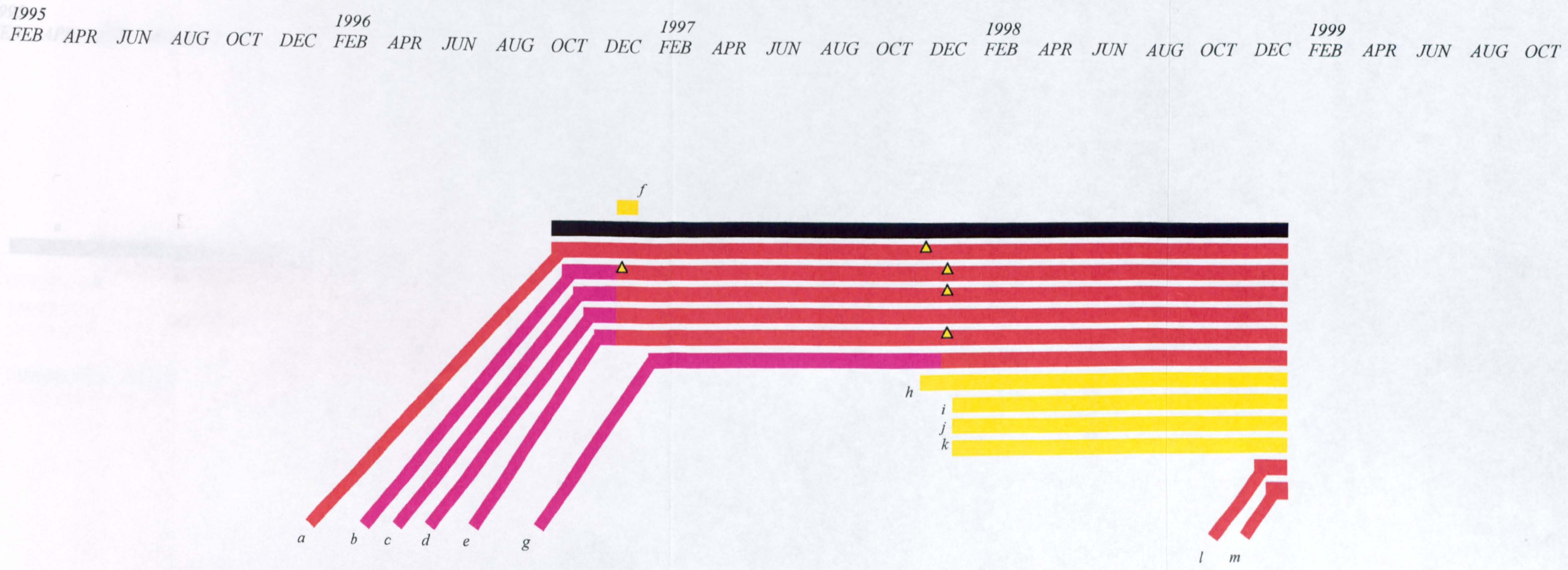
The most effective means of presenting and appreciating group dynamics is through the flowchart. The 14 groups at Mbeli are all represented in the figures that follow. The purpose of these is less to indicate individual fortunes (most individuals are not named) than to show the extraordinary variation in group histories. Births, deaths, immigration and emigration, the representation of age/sex-classes, and especially the changes in group size over time can be appreciated at a glance. To add greater perspective to the charts, data from February 1995 to December 1996 (C. Olejniczak, unpubl. data & Mbeli Bai long-term records) are included. A legend to the charts is provided on the rear of this sheet and can be left folded out while each sheet is examined in turn.

LEGEND FOR GROUP HISTORY FLOWCHARTS

🟨	Infant, 0 – 3 years.
🟩	Juvenile, 3 – 6 years.
🟪	Sub-adult female, 6-8 years.
🟥	Adult female, ≥ 8 years.
🟦	Sub-adult male, 6 – 8 years.
🟦	Blackback male, 8 – 12 years.
🟫	Young silverback, 12 – 15 years.
⬛	Adult silverback, ≥ 15 years.
▨	Sub-adult, unknown sex, 6-8 years.
▨	Adult, sex unknown (female ≥ 8 years, male 8 – 10 years.
▨	Adult female. Date of transfer uncertain.
▨	Infant. Date of birth uncertain.
△	Indicates parturition in a given adult female.
▁╱	Emigration or transfer from group by a given age/sex-class.
╱▔	Transfer into group by a given age/sex-class.

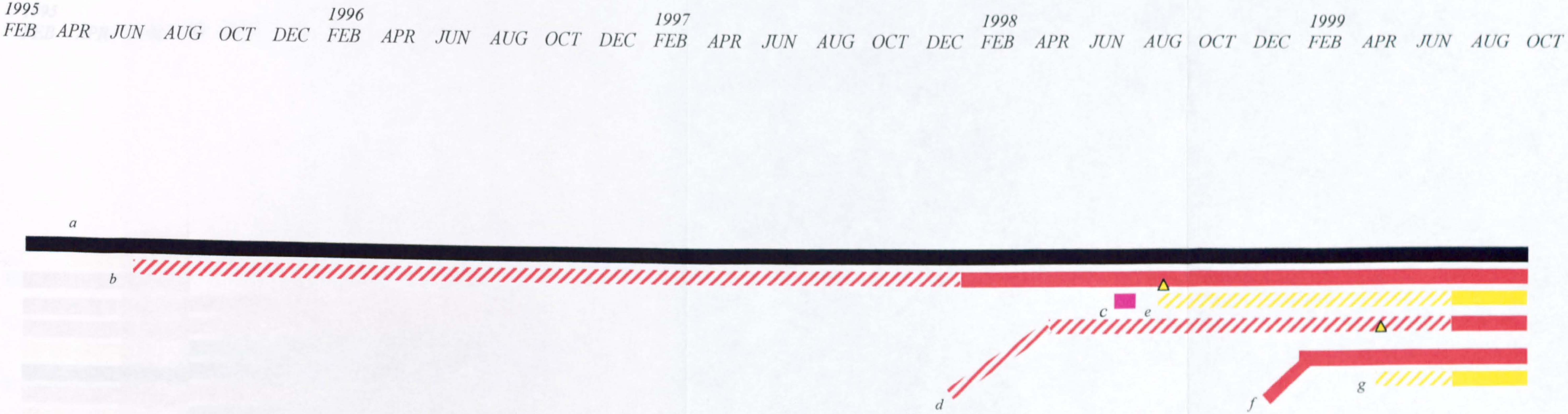
An abrupt start to a horizontal line indicates the birth of an infant, or, if most group members are thus represented, the start of observations on the group. The abrupt ending of a line indicates a death, or in the case of the whole group, the end of the study period (October 1999).

MAX GROUP



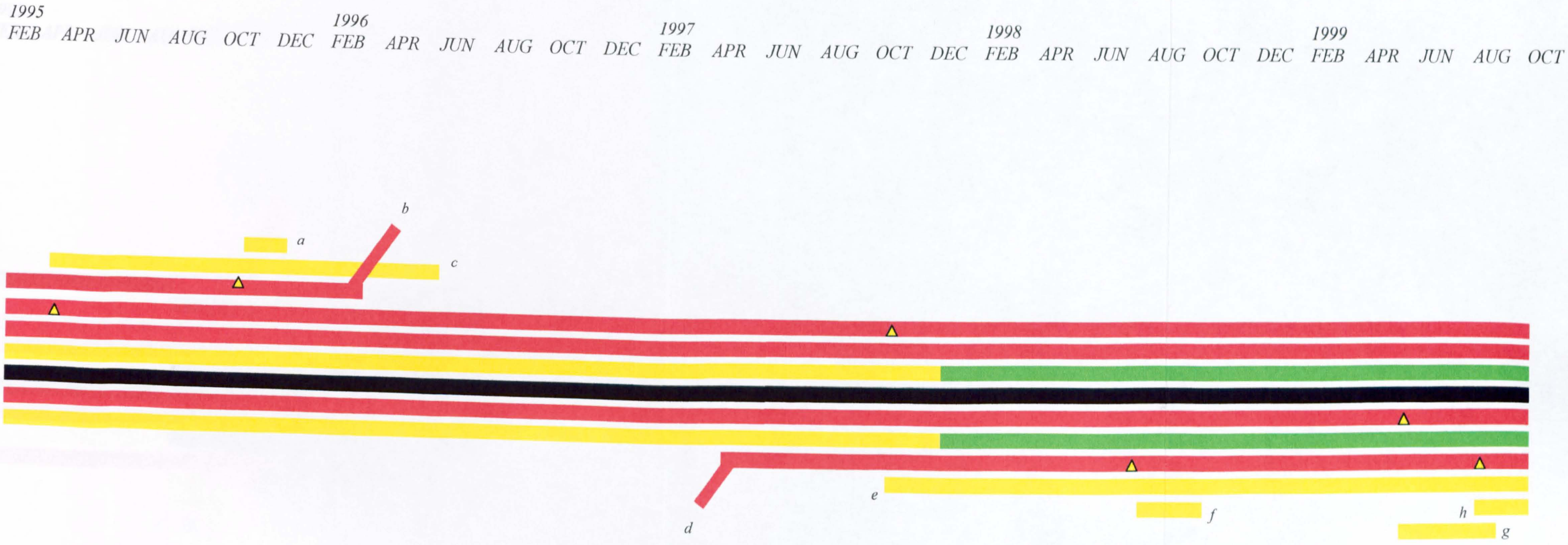
a. Adult female, fff, joins silverback, Max, who is presumed to have been solitary prior to this. Previously in FFF group. Seen once with solitary silverback, Vince, between leaving FFF and joining Max.
b. Sub-adult/adult female, Beetle transfers into group after leaving Clive's group.
c. Sub-adult/adult female, 'osaf' transfers into group after leaving Clive's group.
d. Sub-adult/adult female, Mia transfers into group after leaving Clive's group.
e. Sub-adult/adult female, 'nsaf' transfers into group after leaving Clive's group.
f. Sub-adult/adult female, Beetle seen with decaying remains of what is believed to be her first infant. Possibly still-born or killed by silverback Max.
g. Sub-adult female, Cumin, transfers into groups after leaving Noodles groups.
h. Infant born to 'fff'.
i. Infant born to Beetle.
j. Infant born to 'osaf'.
k. Infant born to 'nsaf'.
l. Adult female, AF6, transfers into group. Origin unknown. May have joined at any point since May 1997.
m. Adult female, AF7, transfers into group. Origin unknown. May have joined at any point since May 1997.

GEO GROUP



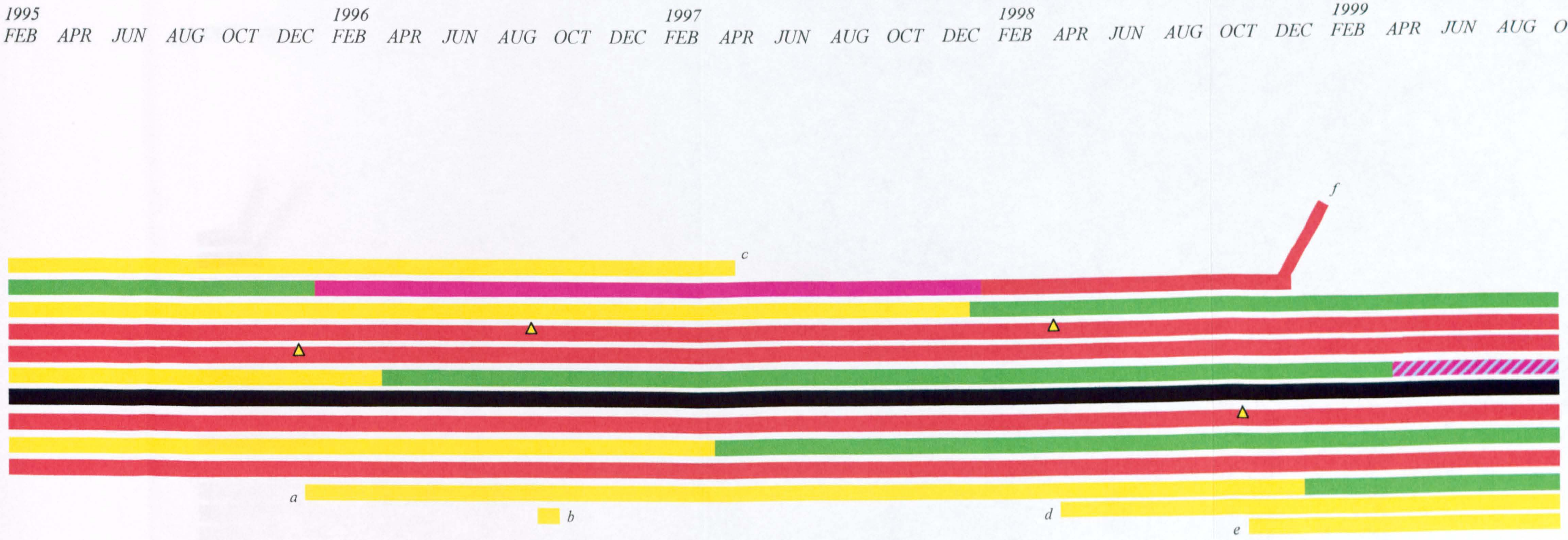
- *a.* Silverback, George, thought to have been solitary for most of study period. However, it seems he may have had one or more females with him for much of this time.
- *b.* Adult female, AF1. May have been with George since March 1995.
- *c.* Unknown sub-adult female seen once only with George.
- *d.* Adult female, AF2. Date of joining group unknown but thought to have been after AF1.
- *e.* Infant born to AF1.
- *f.* Newly-turned adult female, Leah, transfers into group from OB1 group.
- *g.* Infant born to AF2.

SNO GROUP



a. Infant born to adult female AF4. Dies 2 months later.
b. AF4, disappears following the death of her infant. Transfer presumed.
c. ‘Albino’ infant born to adult female, Salmonberry. Dies 14 months later.
d. Adult female, Drift, transfers into group. Origin unknown.
e. Infant, Spoonface, born to adult female, Salmonberry.
f. Infant born to Drift. Dies 3 months later.
g. Infant born to Caroline. Dies 5 months later.
h. Infant born to Drift.

OB1 GROUP

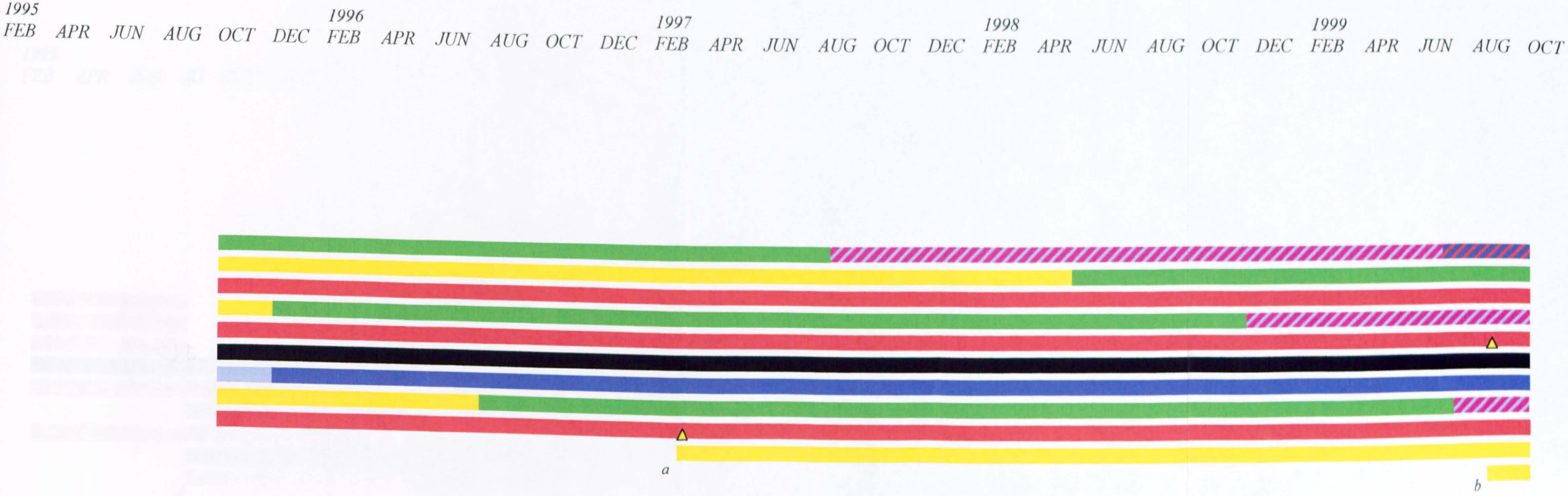


a. Infant, Elvis, born to Misty.
b. Simone gives birth but the infant dies a day later.
c. Infant of Sylvia dies.
d. Infant, Sunbeam, born to Simone.
e. Infant, Sapwood, born to Sylvia.
f. Recently turned adult female, Leah, transfers to George's group.

DWA GROUP

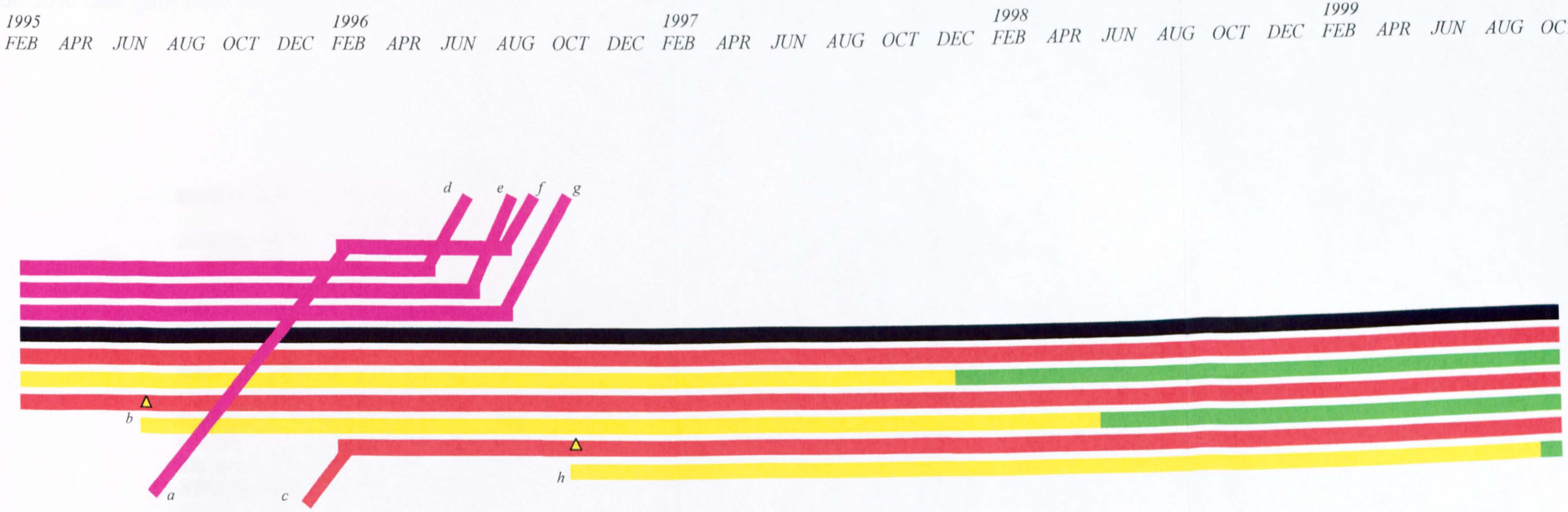
a. Sub-adult female, Lucy, transfers out of the group at the same time as fellow sub-adult Lobelia.
b. Lobelia transfers out of group at same time as Lucy.
c. Infant born to Pansy. Dies 8 months later.
d. Infant born to Bluebell.
e. Infant, Peapod, born to Petunia.

DUK GROUP



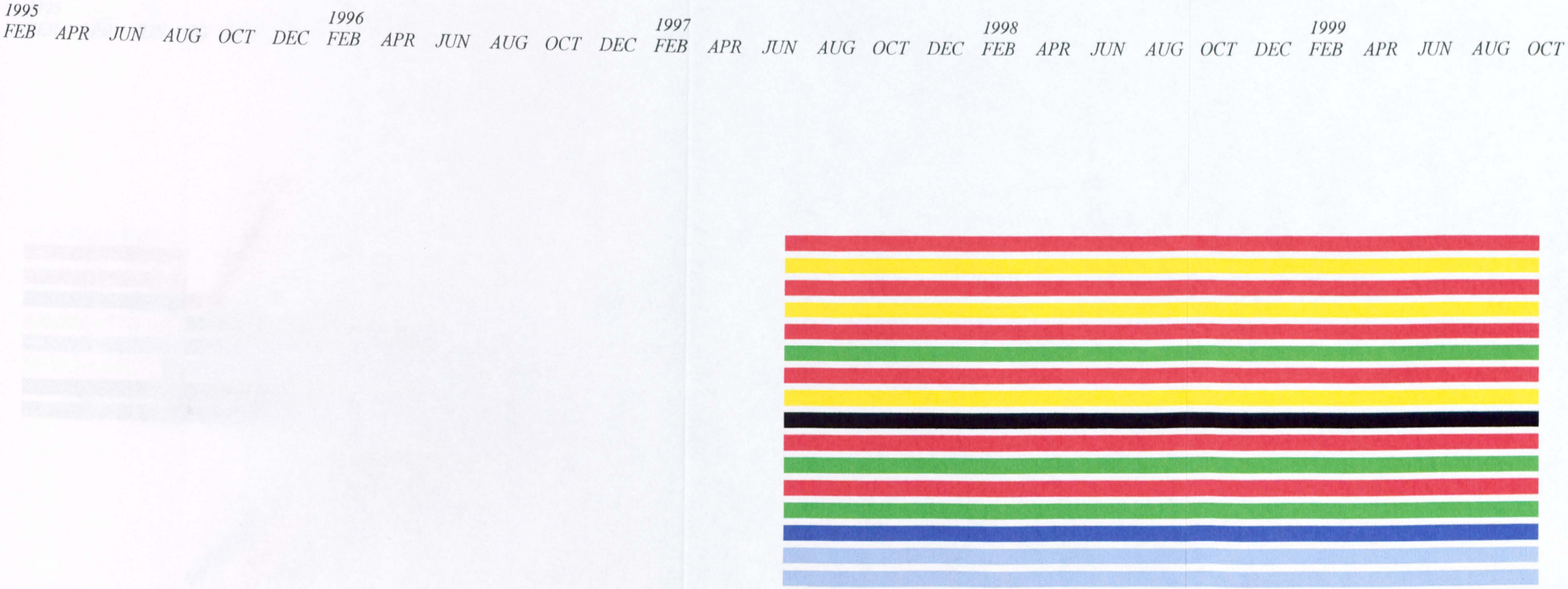
a. Infant, Satchmo, born to Butch.
b. Infant, Billie, born to Bessie.

CLI GROUP



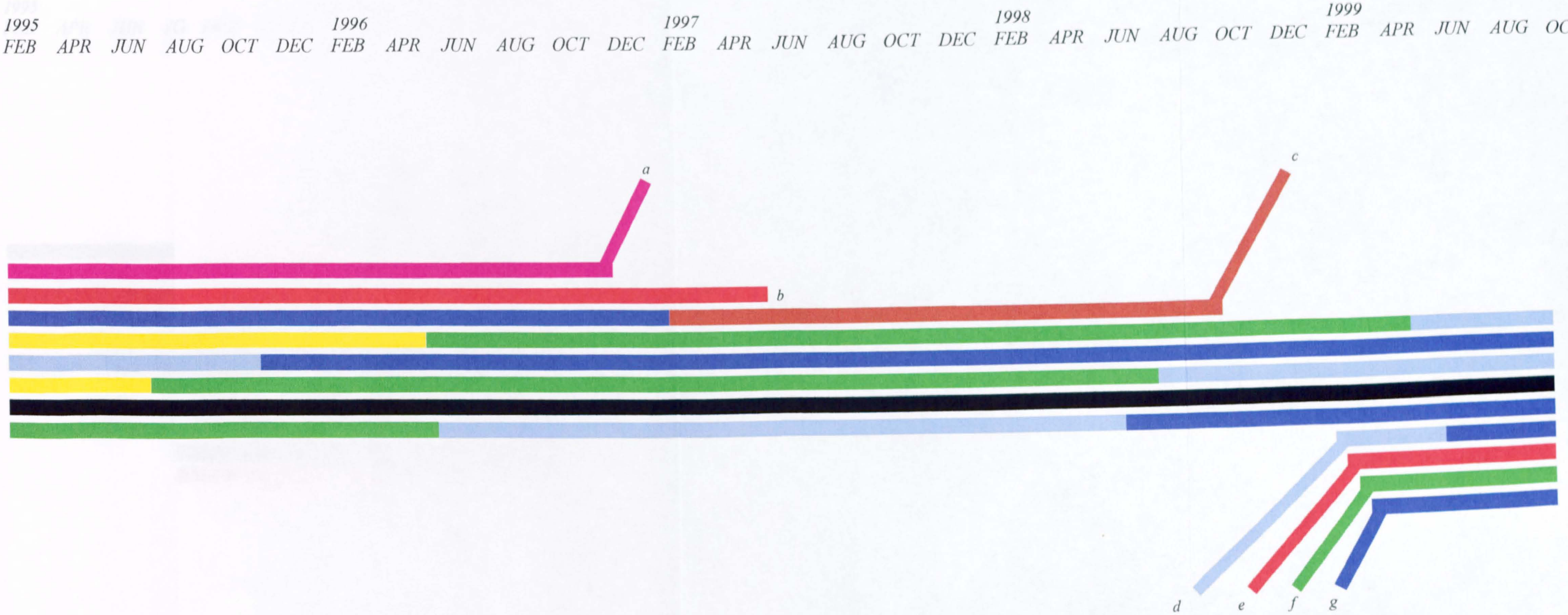
a. Sub-adult female, 'nsaf', transfers into group. Origin unknown.
b. Infant, Peter, born to Jewel.
c. Adult female, Jodie, transfers into group. Origin unknown. Gives birth 9 months later.
d. Sub-adult female, Beetle, transfers out of group and joins MAX group.
e. Sub-adult female, 'osaf', transfers out of group and joins MAX group.
f. Sub-adult female, Mia, transfers out of group and joins MAX group.
g. Sub-adult female, 'nsaf', transfers out of group and joins MAX group.
h. Infant, Lyle, born to Jodie.

EME GROUP



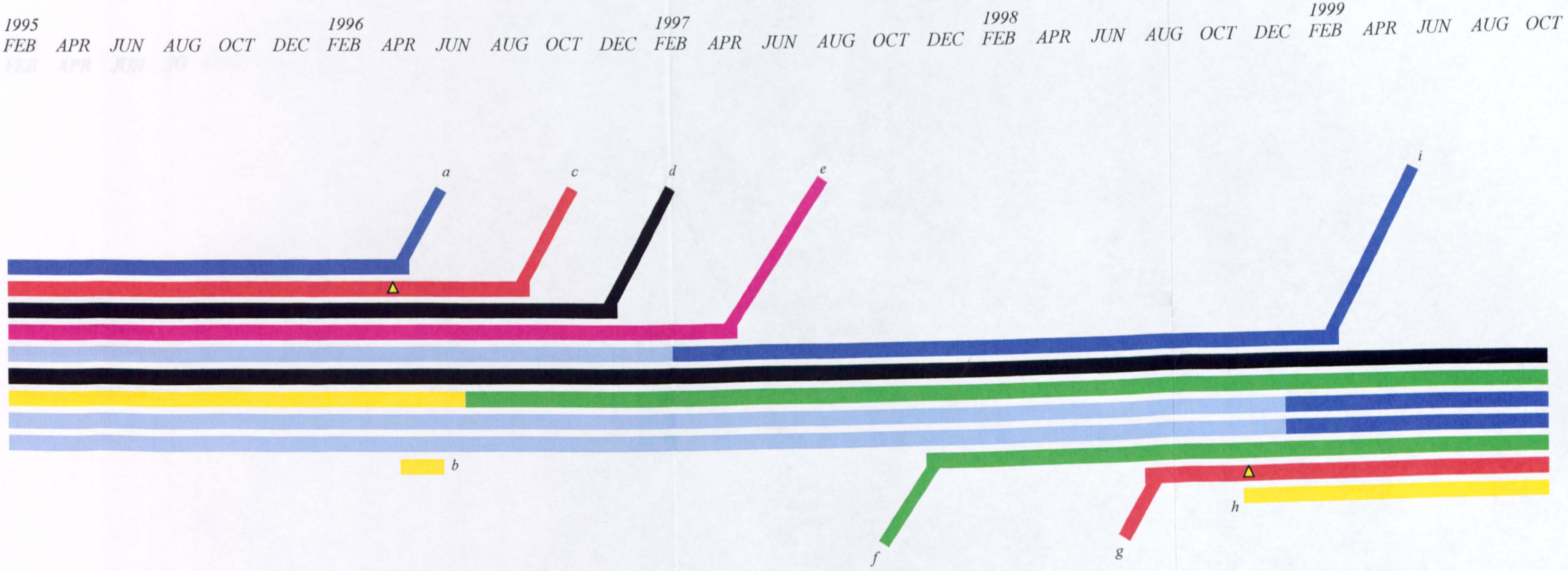
NB. Group first observed June 1997.
There may have been births, deaths or emigrations in this group but they were seen on too few occasions to be certain.
As such, the chart represents primarily the starting and ending composition of the group.

NOO GROUP



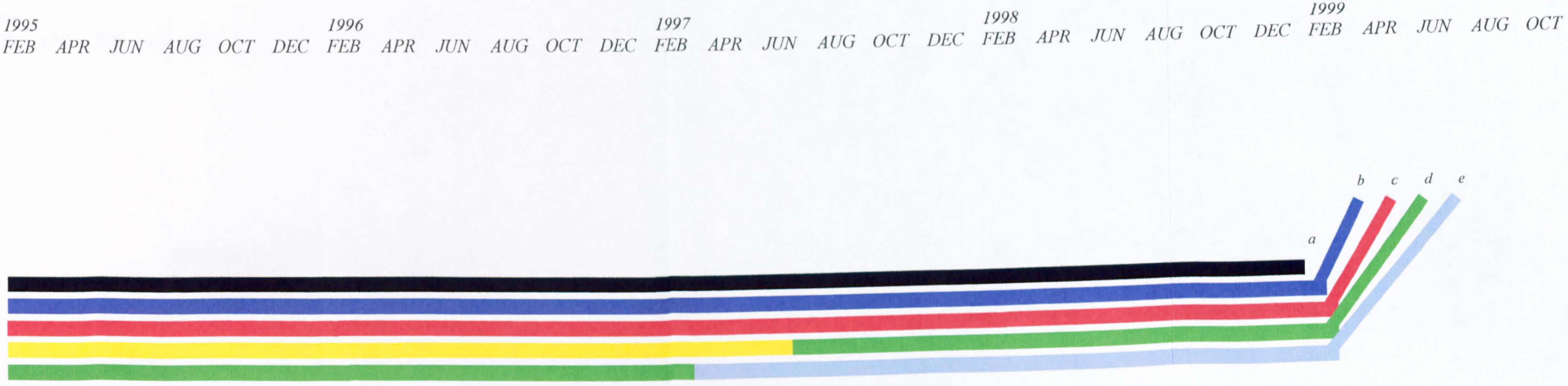
a. Sub-adult female, Cumin, transfers to MAX group.
b. Old adult female, Noodles, disappears from group. Death thought more likely than transfer.
c. Young silverback, Tarragon, emigrates from group to become solitary.
d. Sub-adult male, Sahadouche, joins group with 3 others following the death of their silverback, Bones.
e. Adult female, Martha, joins group with 3 others including her juvenile, following the death of their silverback, Bones.
f. Juvenile, Muffin, joins group with 3 others including her mother, Martha.
g. Blackback, Gretsky, joins group following the death of Bones.
* *d* to *g* all joined NOO at same time. The apparent time gradient is due to line spacing.

TSB GROUP



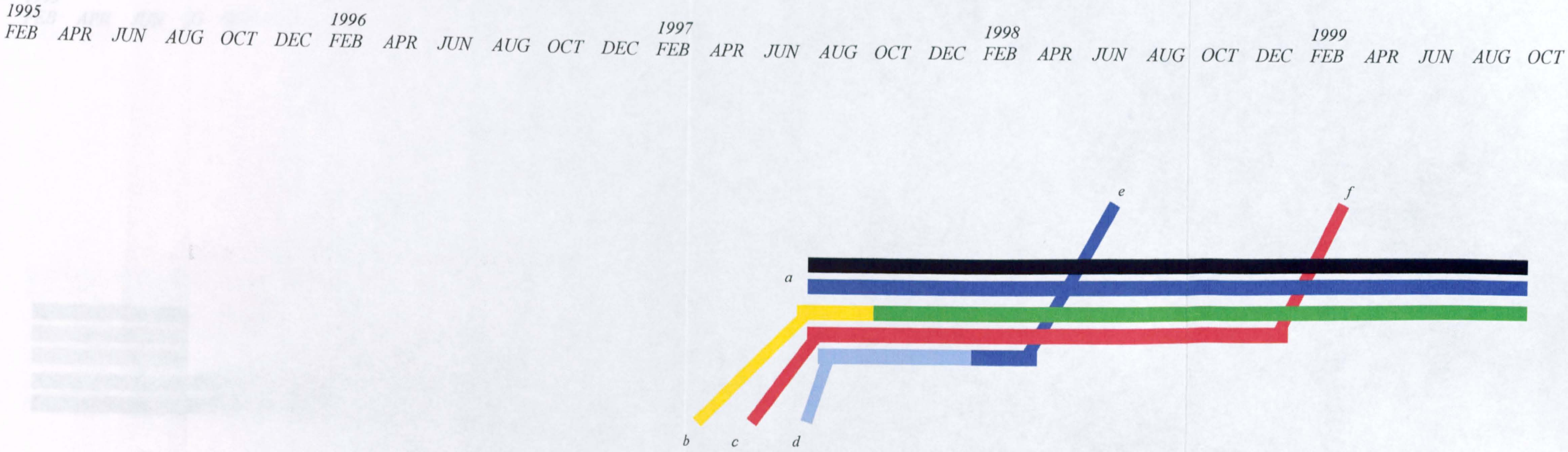
a. Blackback, Frank, becomes solitary.
b. Infant born to AF1. Dies shortly afterwards.
c. AF1, following the death of her newborn infant, disappears from group. Transfer suspected.
d. Young silverback disappears from group. Believed to have recently turned fully adult. Emigration to solitary suspected.
e. Sub-adult female, Misha transfers from group. Destination unknown.
f. Juvenile, Moses, joins group alone. Origin unknown.
g. Misha, the sub-adult emigrant returns to the group as an adult female. Gives birth to Moss 5 months later.
h. Infant, Moss, born to Misha.
i. Blackback, Red Stripe disappears from group. Emigration to solitary suspected.

BON GROUP



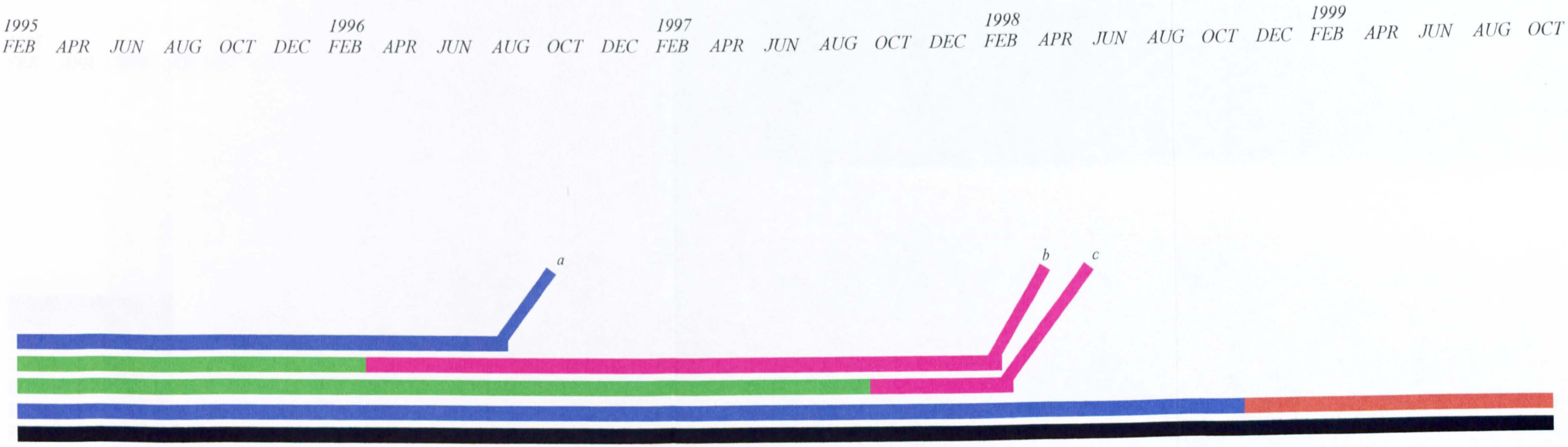
a. Silverback, Bones, disappears. Very likely to have died.
b. Blackback, Gretsky, joins NOO group with three other group members following the death of the group's silverback, Bones.
c. Adult female, Martha, joins NOO. The transfer of these four individuals effectively ends the tenure of BON group as an independent unit.
d. Juvenile, Muffin, joins NOO group with her mother, Martha.
e. Sub-adult male, Sahadouche, joins NOO group.

MOS GROUP



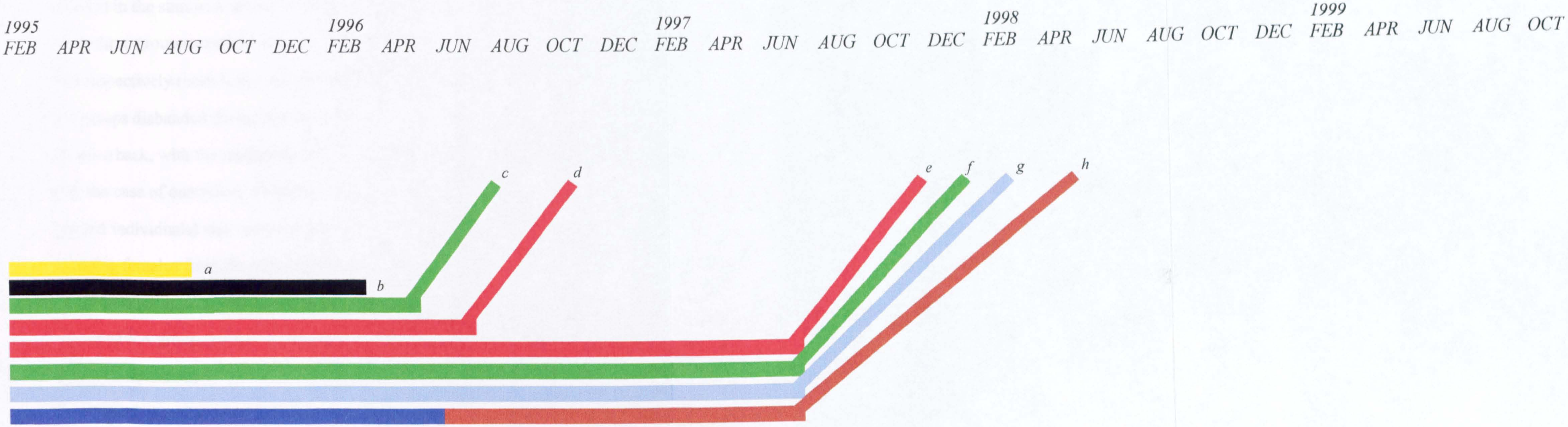
a. Silverback, Mosombo and blackback, Homer, seen for the first time following the immigration of the remains of FFF group.
b. Margo's infant, Iook, joins Mosombo and Homer with his mother.
c. Adult female, Margo, with her infant and a sub-adult, joins Mosombo and Homer, essentially bringing about the collapse of FFF group.
d. Sub-adult, Dougal, joins group with Margo and Iook after collapse of FFF.
e. Sub-adult, Dougal, disappears. Emigration likely.
f. Adult female, Margo, disappears, leaving her infant in the group. May have died, but transfer thought more likely.

TRA GROUP



a. Blackback/young silverback disappears from group. Emigration to solitary suspected.
b. Sub-adult female, Holly disappears from group at same time as young sub-adult female, Paris. Transfer suspected.
c. Young sub-adult female, Paris disappears from group at same time as sub-adult female, Holly. Transfer suspected.

FFF GROUP



a. Infant of adult female 'fff' dead.
b. Silverback missing, presumed dead.
c. Juvenile missing. Dead or transfered.
d. Adult female, 'fff', transfers out of group. Is seen once with solitary silverback, Vince, then joins MAX Group.
e. Adult female Margo, with her juvenile and a sub-adult male transfer to MOS group. This effectively terminates the existence of the group as an independent entity.
f. Juvenile, Iook, transfers into MOS group with his mother Margo and sub-adult male, Dougal.
g. Sub-adult male, Dougal, transfers into MOS group, with adult female Margo and juvenile, Iook.
h. Young silverback, Dylan, who has been becoming peripheral for 21 months becomes fully solitary following the joining of MOS group by the other remaining group members.

Table 4.10 summarises changes in group size for 12 groups at Mbeli, between January 1997 and October 1999 (the histories of two groups were deemed too imprecise to be included in the summary table). Five groups grew in size (range of increases = 17% to 86%), three groups remained the same size, and two groups reduced in size by 40% and 50% respectively (both being without adult females by the end of study). The remaining two groups disbanded during the study period. Both these cases were due to the death of the silverback, with the remaining individuals joining other groups within the population, or in the case of one young silverback, becoming solitary. The greatest increase in group size (+6 individuals) was recorded in MAX group. The silverback of this group began acquiring females from the Mbeli population as a solitary male in August and September 1996. This group was not, however, the largest in the population. This distinction was held by DWA group, with 14 individuals. This group, while experiencing births and emigrations, showed no gross change in size over the period. The four groups that experienced gross losses of individuals were the four smallest groups at the beginning of the period, while those making the greatest gains were medium sized to begin with.

The over-riding impression obtained by an examination of the summary table, and even more so the flowcharts, is one of great range and variation in group size, composition and history. A systematic approach to categorising groups within this range may hold a key to interpreting much of the variation between groups and even populations, and has potentially far-reaching implications for the interpretation of census methodologies and other population data.

Table 4.10 Summary of changes in group size during study period (January 1997 - November 1999).

Gp. ID.	Months of data	Start size	Births	Deaths	Immigrations	Emigrations	End size	End status No. indivs.	End status % change	Comment
MAX	24	7	4	0	2	0	13	+6	+86	gp. amassed by solitary SB
SNO	34	6	4	2 (inf)	1	0	9	+3	+50	-
DUK	34	9	2	0	0	0	11	+2	+22	-
NOO	34	7	0	1 (af)	4	1	9	+2	+29	joined by BON indivs.
TSB	34	6	1	0	2	2	7	+1	+17	-
CLI	34	7	0	0	0	0	7	nc	nc	-
OB1	34	11	2	1 (inf)	0	1	11	nc	nc	-
DWA	26	14	3	1 (inf)	0	2	14	nc	nc	-
MOS	29	5	0	?	0	1+1?	3	-2	-40	all males at end of study
TRA	34	4	0	0	0	2	2	-2	-50	all males at end of study
FFF	7	4	0	0	0	4	0	-4	-100	gp. disbanded
BON	25	5	0	1 (sb)	0	4	0	-5	-100	gp. disbanded
Total	-	85	16	6	9	17+1?	86	-	-	-

nc: No change in group size.

Group Type

Though infrequently commented upon, the idea that groups can be classified into types is not new. Past attempts at classification have focused on describing an 'ageing cycle' for gorilla groups. Harcourt (1978a) recognised groups as either newly formed or established. Newly formed groups contained a single silverback, an adult female and possibly a young infant. Established groups contained more than one adult female and at least one infant of over two years of age. Yamagiwa (1987a) took this idea further by suggesting that the stability of social interactions as well as reproductive success should be considered, in-as-much as bonds between individuals may be weak in newly formed groups and stronger in established groups. In summary though, he states that "A group that consists of successful breeders and their mature offspring should be defined as an established group."(pg. 41). Yamagiwa (1987a) also noted that a characteristic of newly formed groups was rapid group growth, both from female immigration and the birth of infants, and a relative lack of change in established groups. These descriptions acknowledge that all groups may not be the same, but it is suggested that the definitions offered may lack precision and fail to offer a full system for categorising the major changes in a group's history. It is safe to say that group type is a largely overlooked phenomenon which is very seldom mentioned in the literature on group size, composition and change, or when interpreting population census results.

Group types at Mbeli and suggestions for a new classification system

Once again, returning to the flow-charts for the Mbeli groups, it can be seen that the three main areas of variation in groups are in the fields of: a) group size, b) group composition, and c) group stability (or 'group change'). Some groups are extremely small and contain only very young offspring. Others are extremely large but still have only young offspring. Some groups contain a range of offspring, but none nearing adulthood, while other groups contain a full range of individuals, sexes and ages. Finally some groups are small but contain few, if any, young offspring but some older offspring. As Yamagiwa (1987a) pointed out, using what we understand of the dispersal patterns of gorilla individuals, the ages of immature individuals can be used as a guide when categorising groups. Figure 4.4

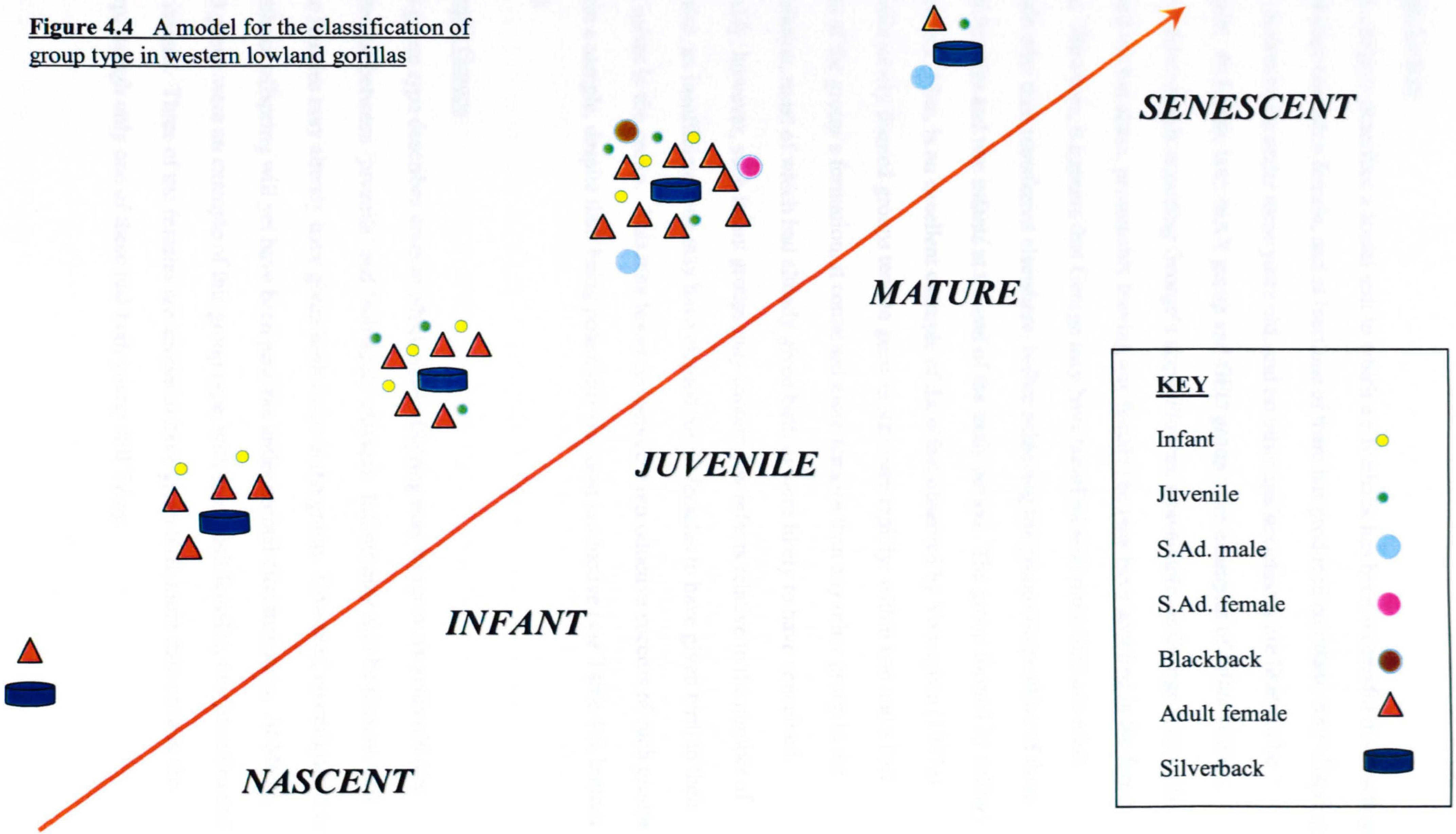
offers a model for the ageing of gorilla groups, based on Mbeli group histories and what is known of western lowland gorilla dispersal patterns.

In place of Yamagiwa and Harcourt's bi-nominal system, this model recognises five stages in what might be termed the 'life-cycle' of a group. It should be borne in mind that some of the group types identified may also be generated through more random demographic events, such as unusual transfer occasions (e.g. unaccompanied juveniles or sub-adults). Furthermore, progress from one group type to another may not always be linear or with the inevitability of reaching the senescent group type after a single period in each type-class. However, the model permits a re-evaluation of what gorilla groups represent, which may be much overdue. It is possible that inclusion of the 'infant' and 'juvenile' group types may divide the ageing process too finely for practical use, and that the sub-division of these young groups is both of less value, and open to greater error than reducing the model to a four stage system (nascent, juvenile, mature, senescent). While acknowledging this, the following model retains these classes in order to demonstrate that such stages may be identifiable in some populations.

Nascent Groups

This group type represents the genesis of most western lowland groups, and is formed when a solitary male acquires a single female. At this stage, no offspring are present, though the female may have conceived. This appears to be a precarious group structure, which may form and collapse several times before breeding commences, possibly as females 'sample' solitary males (Fossey, 1983, Watts, 1990b). This group type was witnessed at Mbeli when solitary silverback, Vince, was joined briefly by adult female, FFF, before she eventually settled in MAX group (Mbeli, long-term records). MAX group itself was likely to have begun in the same way when sub-adult female, Beetle, transferred to join silverback Max, shortly before the group was joined by other immigrants. For a female in such a Nascent Group, feeding competition will be negligible. Silverback attention will be maximised, though this could prove stressful for some females in terms of excessive herding. Solitary males may also represent something of a risk for an adult female as, in the absence of other females and their offspring, a male's worth, both genetic and behavioural, is unproven (*see* Discussion).

Figure 4.4 A model for the classification of group type in western lowland gorillas



Infant Groups

This category describes a social unit in which a silverback has been successful in attracting more than one adult female, and at least one of them has produced an infant. Any offspring will, however, be under three years old, and no other age/sex-classes are likely to be present. At Mbeli, both MAX group and GEO group were examples of Infant Groups. The precise details regarding George's acquisition are unavailable, as George frequently visited the bai alone, presumably leaving any females he may have acquired in the forest edge. However, it appears that George may have travelled with more than one adult female who then transferred elsewhere, before achieving the group composition of three adult females and two infants at the end of the study period. The group formed by solitary silverback, Max, is an excellent example of the effect observed by Yamagiwa (1987a) wherein newly formed groups tend to grow in size very rapidly: within two and a half years of the group's formation, it contained more females than any other group in the population, most of which had already given birth or were likely to have conceived. Notably, however, such Infant groups may contain few infants relative to the number of females, as insufficient time may have elapsed for all females to have given birth to their first infant in the group. This may lower the apparent reproductive success of such groups within a sample, despite their being potentially the most productive (*see* Table 4:5, bottom row).

Juvenile Groups

This group type describes units in which natal offspring may be up to six years old (the borderline between 'juvenile' and 'sub-adult' classes). Infants may also be present, and some females may already have given birth twice in the group. However, no emigration or transfer of offspring will yet have been possible under normal circumstances. At Mbeli, SNO group were an example of this group type, with four adult females, two juveniles and two infants. Three of the females are known to have given birth more than once in the group, though only one of these had both young still living.

Mature Groups

This group type is the equivalent of Yamagiwa's (1987a) 'established group' category, and contains adult females and a range of offspring which may include infants, juveniles, sub-adults, blackbacks and young silverbacks. Diagnostically, problems may arise when the first offspring begin to transfer or emigrate, as groups may temporarily resemble the previous group type (Juvenile) during this stage. The Mature group type was the best represented at Mbeli, with between five and seven groups present (36-50%). This implies that the mature group has a longer duration than the other group types within the population. DUK group are a good example of such a group type, containing offspring from young infants to a 12-13 yr old son.

Senescent Groups

This category describes groups that are nearing the end of their existence. In such groups, the silverback may show signs of advanced age, such as a reduction of muscle mass or difficulty in walking. Senescent groups will have a much reduced or even extinguished reproductive capacity. If females are present at all, they are also likely to be of advanced age. Potential immigrants should recognise such groups as unlikely to offer the long-term stability necessary to successfully rear young, and thus avoid joining them unless as a temporary measure while seeking better prospects. Group size will be small, or medium and groups will lose members faster than new members are born or immigrate.

At Mbeli, TRA group was a good example of a senescent group, from which two sub-adult females emigrated during the study period, leaving only an aged silverback, Travis, and his almost adult son, Stockwell. BON group was led by a clearly aged silverback (Bones) and contained a blackback, a sub-adult male and aged adult female and her juvenile daughter. Bones disappeared during the study, almost certainly having died, at which time the remaining members all joined NOO group. FFF group survived on after the death of their silverback, due to the presence of a young silverback in the group. However, under such circumstances, the group was deemed senescent, and indeed, collapsed when the silverback became fully solitary and the remaining individuals joined MOS group. Prior to this mass transfer, MOS group itself must have contained only aged silverback Mosombo and his almost adult son, Homer. As a senescent group themselves, the transfer of FFF members into MOS can be perceived as a temporary measure. Blackback Dougal emigrated from the group within 10 months of joining and adult female Margo disappeared from the group 19 months after joining.

Table 4.11 revisits the composition of the 14 Mbeli groups and shows total group size, an estimation of silverback age, and the group type classification that best describes each group. NOO and TSB group have been described as mature/senescent as they failed to fit neatly into either category.

Table 4.11 Mbeli Groups listed by group-age status.

Gp.	sb	af	inf	juv	s.ad	bb	ysb	total	sb age	type
MAX	1	8	4		-	-	-	13	p	infant
GEO	1	3	2		-	-	-	6	y/p	infant
SNO	1	4	2	2	-	-	-	9	p	juvenile
OB1	1	4	2	3	1 (1)	-	-	11	p	mature
DWA	1	7	4	2	(2)	-	-	14	p	mature
DUK	1	3	2	1	2	2	-	11	p	mature
CLI	1	3		3	(4)	-	-	7	p	mature
EME	1	6	3	3	2	1	-	16	p	mature
NOO	1	1		1	2 (1)	4	(1)	9	p	mature
TSB	1	1	1	1	1 (1)	2	(3)	7	o	mature/senescent
BON	1	1		1	1	1	-	5	o	senescent
MOS	1	-		1	-	1	-	3	o	senescent
TRA	1	-			(2)	-	1(1)	2	o	senescent
FFF	-	1	1		1	-	1	4	d	senescent

sb age: p - prime (fully developed and in excellent condition) y - young (fully developed, but still young) o - old (reduced muscle mass, increased greying, and possibly reduced mobility) d - deceased (from effects of ageing or killed by predator, other male or accident). Values in parentheses are the number individuals in s.ad and ysb class that were known to have already emigrated from the group.

There is little difference between the group sizes of young group types (Infant and Juvenile) and Mature groups. However the four senescent groups are clearly also the four smallest groups in the population. At the time when these group compositions were recorded, no nascent groups were present, but in a large enough sample, it is predicted that group size will follow an inverse 'U' shaped distribution over time, and thus, group type. The longevity with which each group type is predicted to exist should generate a positive skew in the distribution curve for group types, with mature groups the most frequent, followed by senescent, juvenile and infant, and nascent groups the least frequently encountered type.

Group type is also likely to be strongly implicated in group stability. The flow charts indicate that some groups underwent major changes in size and composition during the period, while others remained almost static. Table 4.12 presents data on group stability first shown in Table 4.10 alongside group type classifications. The least stable groups were the newest and oldest in the sample and the only groups in which the number of individuals was the same at the start and end of the study period were mature groups. With its effects on group size, composition and stability, group type is likely to have considerable implications for the interpretation of census and other population data. These issues will be considered in the Discussion.

Table 4.12 Group type and stability

Group ID	Start size	End size	Percentage change	Group type
MAX	7	13	+86	infant
SNO	6	9	+50	juvenile
NOO	7	9	+29	mature
DUK	9	11	+22	mature
TSB	6	7	+17	mature/senescent
CLI	7	7	nc	mature
OB1	11	11	nc	mature
DWA	14	14	nc	mature
MOS	5	3	-40	senescent
TRA	4	2	-50	senescent
FFF	4	0	-100	senescent
BON	5	0	-100	senescent

Life-history processes

Ideally, demographic analysis of a population will rely on the in-depth examination of population statistics including birth rate, sex ratio at birth, survival rate per sex and age-class, fecundity, life expectancy and reproductive value, through the construction of Age-specific and/or Time specific life-tables. In the context of a three year study, with a small sample size in each age/sex-class, no age differentiation among most adults, and with uncertainty regarding exact dates for certain births and deaths, such an analysis on the data from Mbeli is not currently possible. Furthermore, the fate of older animals that disappear from their groups without re-appearing in other known groups remains ambiguous, making it harder still to generate mortality figures. Given these difficulties, this section is limited simply to reporting certain demographic parameters as a first step towards a comparative analysis with other populations.

Birth rate

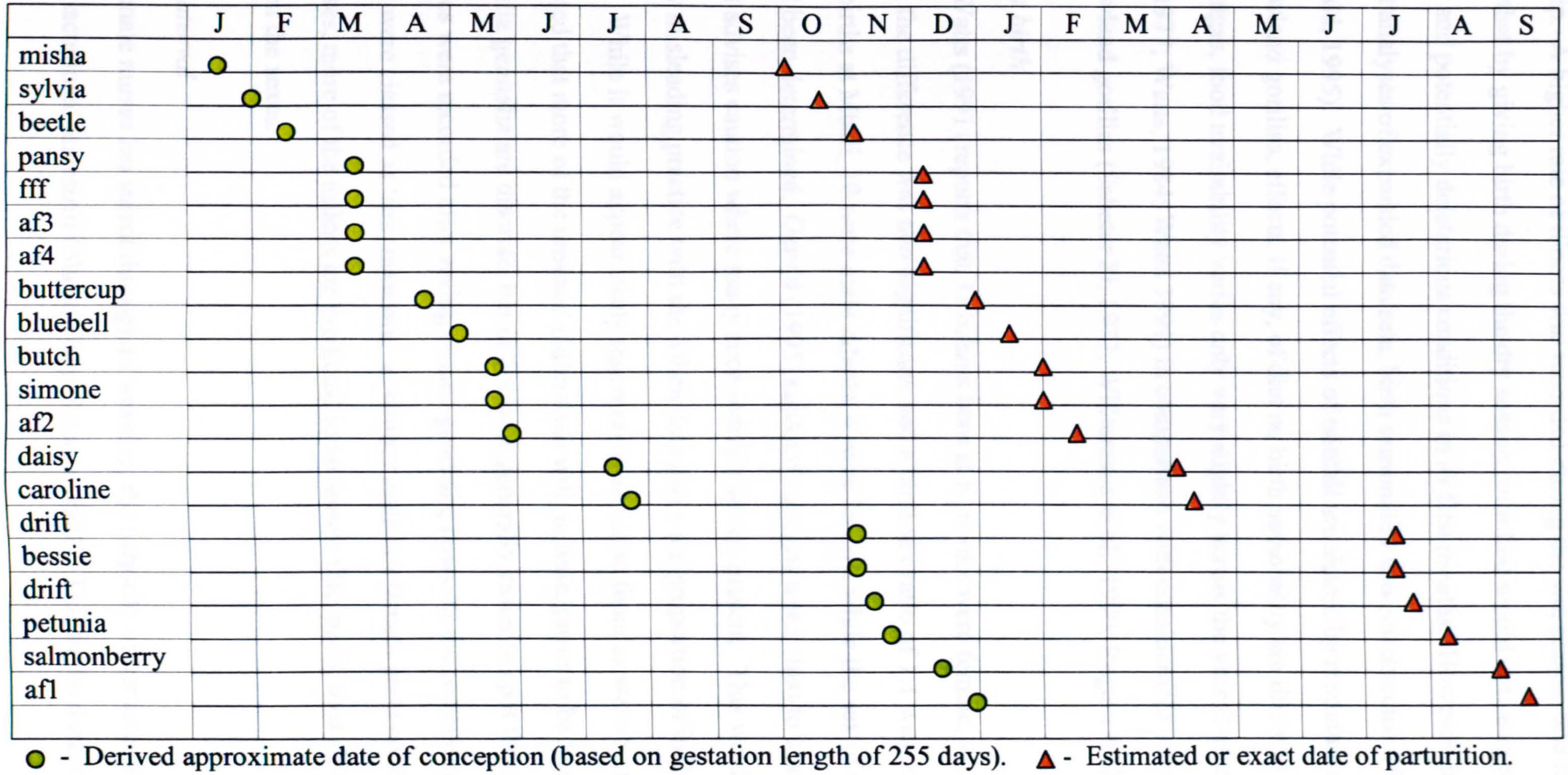
During the 34 months of the study period, 20 infants were born to 19 adult females. Three of these females were known to have given birth for the first time; four gave birth for the first time in the history of the study, but may have done so earlier, and 13 gave birth to what was known to be at least their second infant (for two of these, the birth was at least the third). Only one female gave birth twice during the study period.

Figure 4.5 gives, for each of the 20 births, the date of parturition and the conception date, derived by subtracting the gestation length (255days: Harcourt et al.,1980: Czekala & Robbins, 2001). Study years have been collapsed such that, for instance, all births in December are shown in a single December, regardless of year.

Birth seasonality

There were too few births recorded during the study period for a statistical treatment of birth seasonality. The median number of births per month for the three driest months of the year (the long dry season of Dec, Jan, and Feb – based on five years of data) was 3, whereas the median for the remaining nine wetter months was 1. However, an apparent clumping of births in December was primarily due to three females who all joined a new social group (MAX) at the same time and, being nulliparous, all became pregnant at roughly the same time. With this in mind, neither the distribution of conceptions nor births suggests seasonal effects that might be attributable to food availability, disadvantageous climatic conditions for infant survival, or female reproductive fitness. Even with a larger sample size, significant effects are unlikely to be found, as a female's individual reproductive history (date of menarche, inter-group transfer, fate of preceding infants) and other stochastic events are likely to have greater influence than seasonal variables.

Figure 4.5 Monthly distribution of conception and parturition in 20 adult females



Fossey (1983) suggested that an observed peak in mountain gorilla births in August (during the Karisoke dry season) could be an adaptive response aimed at maximising infant survivorship. A higher rate of illness was recorded during the wet season, and it was postulated that by giving birth during the dry season, an infant would not be exposed to overly wet and potentially deleterious conditions in its first months. However, in subsequent analyses of expanded data sets, birth seasonality was not detected (Watts, 1991: Gerald, 1995). While potential effects of rainfall are shared by mountain and western lowland gorillas, effects, if any, of diet on birth seasonality are likely to differ, as in the Virungas, food availability varies only very slightly across the year (Fossey & Harcourt, 1977; Watts, 1984; Watts 1991) in comparison with considerable variation for western lowland gorillas (Sabater Pi, 1977; Williamson et al., 1990; Rogers et al. 1990).

Sex ratio at birth

Although Watts (1991) reports that 33 infants born at Karisoke were female, while only 26 were male, the difference was non-significant, and a birth sex ratio of 1:1 was recorded. Of the 20 births at Mbeli, 10 were male infants, 4 were female, while the sex of a further 6 had not yet been determined. Gerald (1995) randomly assigns a sex class to unsexed infants, but advises caution where many such individuals are present. This would be a particularly misleading practice with the Mbeli data given the proportion of individuals concerned. While it would appear likely that more males than females were born at Mbeli, it is suggested that more of the unsexed individuals will, in time, prove to be female than male. Gorilla genitalia are discrete, but males were generally easier to spot than females. Four females were recorded after seeing female genitalia, however the remaining six individuals were classed as 'sex unknown' as neither male nor female parts could be seen. In these cases, more of the infants are predicted to be female than male, thus shortening the gap between the sexes.

Interbirth interval

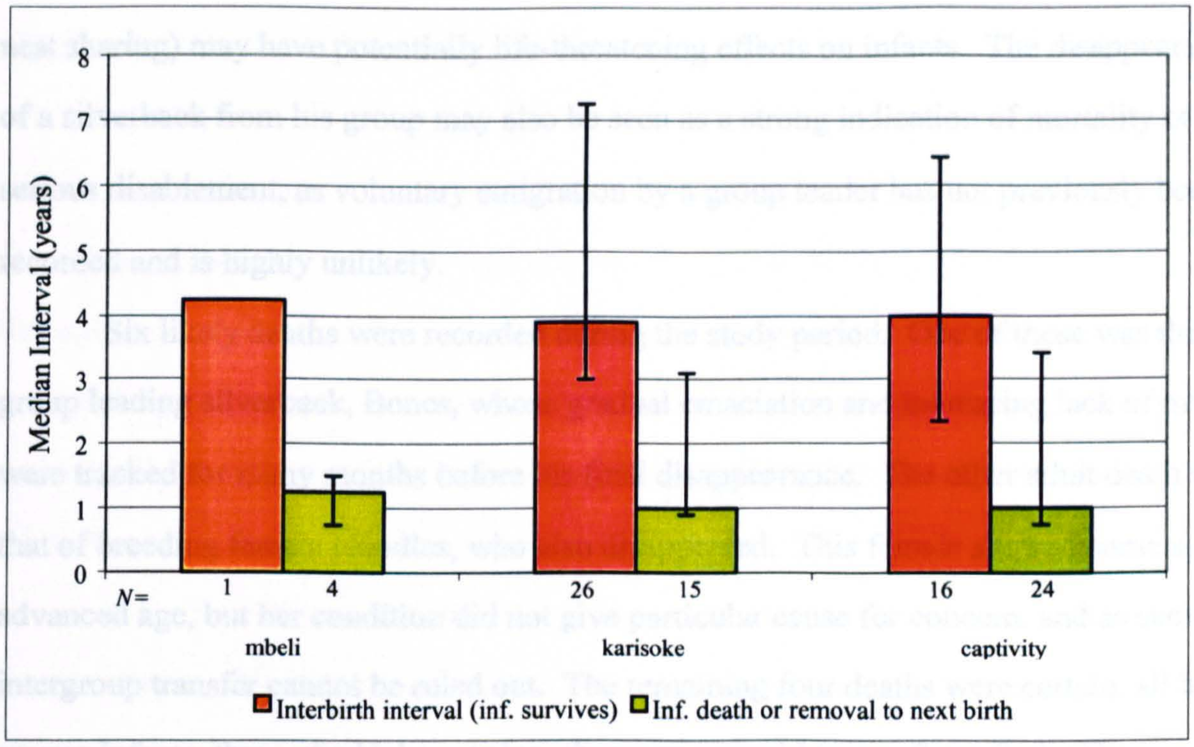
Where a female nurses her infant through to weaning, the majority of her interbirth interval consists of lactational anoestrus (Short, 1976; Stewart, 1988). Due to the duration of the current study and the sample size of adult females, only one 'full-term' interbirth interval could be calculated. Adult female Caroline from SNO group exhibited an interbirth interval of 4 yr,3m. This figure is well within the range of intervals recorded in mountain gorillas and only four months over the median of 3yr,11m (range 3yr – 7yr,3w, *N* = 26) (Watts, 1991).

Interbirth intervals are significantly shorter when the first infant of an interval pair dies before weaning (Stewart et al., 1988). This was found to be the case at Mbeli, where four females who lost infants contributed to a range of interbirth intervals from 10m to 2yr,5m, with a median of 1yr,4m. A further female was excluded from the sample as an intergroup transfer between births extended her interval to 3yr,7m. As interbirth interval following infant death is a function of the age at which an infant dies, for comparative purposes, the interval between the death of the first infant and the birth of the next infant is a more appropriate measure. At Mbeli, the median for this interval was 1yr,3m (range 10m - 1yr,6m, *N* = 5). In mountain gorillas, the median for this interval was 1yr (range 11m – 3yr,1m, *N* = 15) (Watts, 1991).

By subtracting the gestation period of 255 days, and dividing by the average cycle length of 29 days (Stewart, 1988: Czekala & Robbins, 2001), it is possible to estimate that at Mbeli, the median number of potential cycles between the cessation of lactational anoestrus due to the death of an infant, and the conception of the next infant is 6.7 (range 1 – 8, *N* = 5). At Karisoke, the number is estimated at 3 – 4 cycles (range 1 – 20+, *N* = 15). Figure 4.6 summarises interbirth interval data where infants survive or die (or are removed from their mothers) at Mbeli, Karisoke, and in captivity.

When comparing wild populations, intervals at Mbeli are slightly longer than those for mountain gorillas. However the data from Mbeli are currently too few for any ecological or sub-species differences to be confirmed. The general pattern shown in the figure is one of considerable homogeneity.

Figure 4.6 Reproductive intervals for adult females at Mbeli, Karisoke, and in captivity



Karisoke data from Stewart et al. (1988), Watts (1991) and Czekala & Robbins, (2001). Data on captive populations are from Sievert et al. (1991) and are for western lowland gorillas. Error bars show the range of intervals.

Mortality

Individuals leave the population either by emigrating to unknown groups, or by dying within their group. The conditions at Mbeli are such that for many age/sex classes, the fate of disappearing individuals cannot be determined. Females may have transferred, but without evidence of their arrival in another group, this cannot be confirmed. Males suspected of having emigrated may have simply succumbed to illness, or attack by a conspecific or a predator. Even juveniles have been known to transfer into groups without their mothers, so disappearances in this age class may also be ambiguous. With this in mind, caution must be exercised in calculating mortality data. Death can be recorded with greater confidence when observations of an individual's physical state prior to disappearance indicate advanced age or sickness. The disappearance of an infant below approximately two to three years of age, however, can be taken as a fairly safe indication of death, as prior to this age, infants are dependent on their mothers for food, and thus highly unlikely to survive without them (Stewart, 1988). Even if nutritional independence is reached at a younger age in some individuals (e.g. Fossey, 1979) the lack of other care provided by a mother (e.g. carriage during travel, protection from other group members, nest sharing) may have potentially life-threatening effects on infants. The disappearance of a silverback from his group may also be seen as a strong indication of mortality or serious disablement, as voluntary emigration by a group leader has not previously been recorded and is highly unlikely.

Six likely deaths were recorded during the study period. One of these was the group leading silverback, Bones, whose gradual emaciation and increasing lack of mobility were tracked for many months before his final disappearance. The other adult death was that of breeding female Noodles, who also disappeared. This female showed some signs of advanced age, but her condition did not give particular cause for concern, and as such, intergroup transfer cannot be ruled out. The remaining four deaths were certain, all being among infants, three of which were less than one year old (range 2m – 8m). The age of the fourth infant, while less than 36 months, was not known. Of mothers of the dead infants, only one may have been primiparous. Two were known to have successfully raised at least one other infant. Only one of the four infants was recorded as thin and apparently unwell prior to its disappearance.

When deaths in the 23 months of study prior to the start of the current study period are added to the current records (Olejniczak, unpubl. data), 77% of all mortality (10/13) was suffered by infants. The median age at death for eight infants was two months, and 60% of infant deaths took place within the first 6 months (70% within the first year of life). Four of the combined infant deaths affected a single group, SNO. The only other adult death is believed to have been that of the silverback of FFF group, who disappeared in March 1996, leaving breeding females and offspring in his group. Prior to his disappearance, he had appeared in his prime and in good health.

As with births, data on mortality are too few to draw firm conclusions, but the complete lack of records of death from immature individuals over three years of age suggests that survival rates post weaning are extremely high. In mountain gorillas also, the highest mortality rate occurs below six months of age (Gerald, 1995). Sex differences in mortality rates have been found in mountain gorillas, with twice as many females than males dying in the 0-1yr age-class. At the other extreme, four times as many males than females died in the 24-30 age class, although neither of these differences reached significance (Gerald, 1995).

Male and female dispersal

In addition to births and deaths, demographic changes to social groups are brought about through the emigration and transfer of individuals. This section presents data on the overall frequency of inter-unit movements, which age/sex-classes move most frequently, and what the social conditions experienced by an individual pre- and post-emigration can tell us about motive and choice in gorilla social organisation.

In the case of six individuals from two groups, inter-unit movement was due to group collapse. While the destination of these individuals can be examined (as choice may have been involved), the details of the previous group cannot strictly be used when describing emigrations or transfers away from that group as individuals in this situation may not have chosen *per se* to leave their groups. Thus, unless otherwise stated, the figures given are only for individuals leaving groups that remained intact after their departure. The varying numbers of cases in which both the group of origin and destination of individuals is known accounts for the fluctuating *N* in the following summaries.

Overall frequency

Of 122 group-living individuals, 25 (20%) were involved in a total of 28 emigrations from groups between January 1997 and October 1999 (seven transfers are included from mid and late 1996 as they are important to an understanding of subsequent movements). The total population figure, however, includes infants, which are unable to make inter-unit movements unassisted. Movements by infants and juveniles, while in the company of their mothers should not be counted as independent units, but noted only as part of the mother's transfer. However, unaccompanied juveniles have been known to transfer between groups without their mothers, so a straightforward recalculation omitting these age-classes also distorts the figures. In this sample, only one juvenile made such a transfer, and as such, a recalculation omitting juveniles and infants is preferable to including them. It can be argued that silverbacks in single-male groups should also be omitted as they would not be expected to leave a group in which they were dominant.

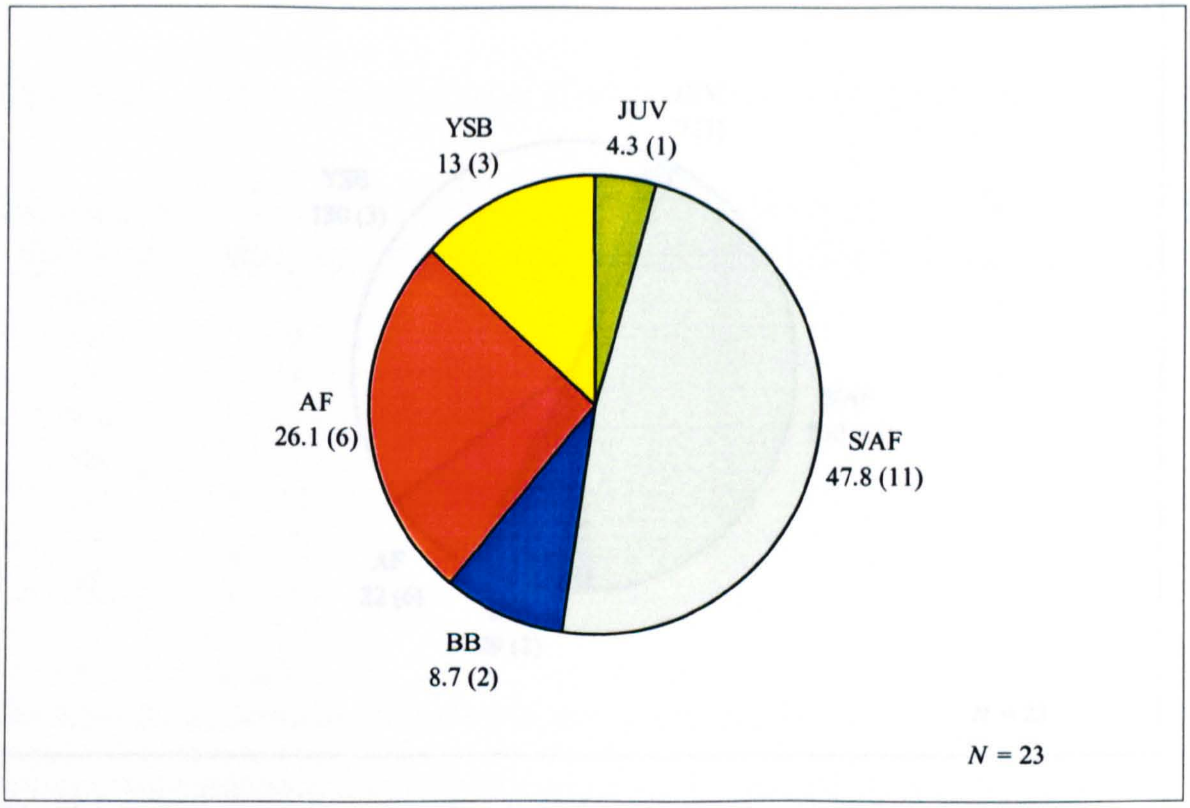
Thus, omitting infants, juveniles, single-male group silverbacks, and group movements following the collapse of a group after the death of its silverback, the frequency of inter-unit movement was 17 individuals out of 51 (33%). Three individuals (all breeding females) moved twice, but all others made only a single movement during the study period.

Frequency among age/sex-classes

In the analyses that follow, infants that transfer with their mothers are omitted, but any juveniles transferring alone are included. Figure 4.7 shows the percentage of emigrating/transferring individuals by age/sex-class. A new category is introduced in this respect; 'sub/adult female' (s/af) describes nulliparous females who are transferring for the first time. All animals in this class appeared to be on the brink of adulthood, and their emigration itself could be seen as confirmation of their maturity (the single younger sub-adult female is pooled with this age-class). For each age/sex-class in Fig. 4.7, the percentage of all emigrants is given, alongside the number of individuals represented (in parentheses).

A considerable dichotomy is evident between males and females, with females accounting for 74% of movements and males, 22%. The remainder represents a single juvenile of unknown sex. Such a sex difference might appear puzzling given that the birth sex ratio favours males over females. However, with such a small sample, the explanation may lie simply in the mass transfer of females from CLI group in 1996; a random sex imbalance in one group swaying results from the rest of the population.

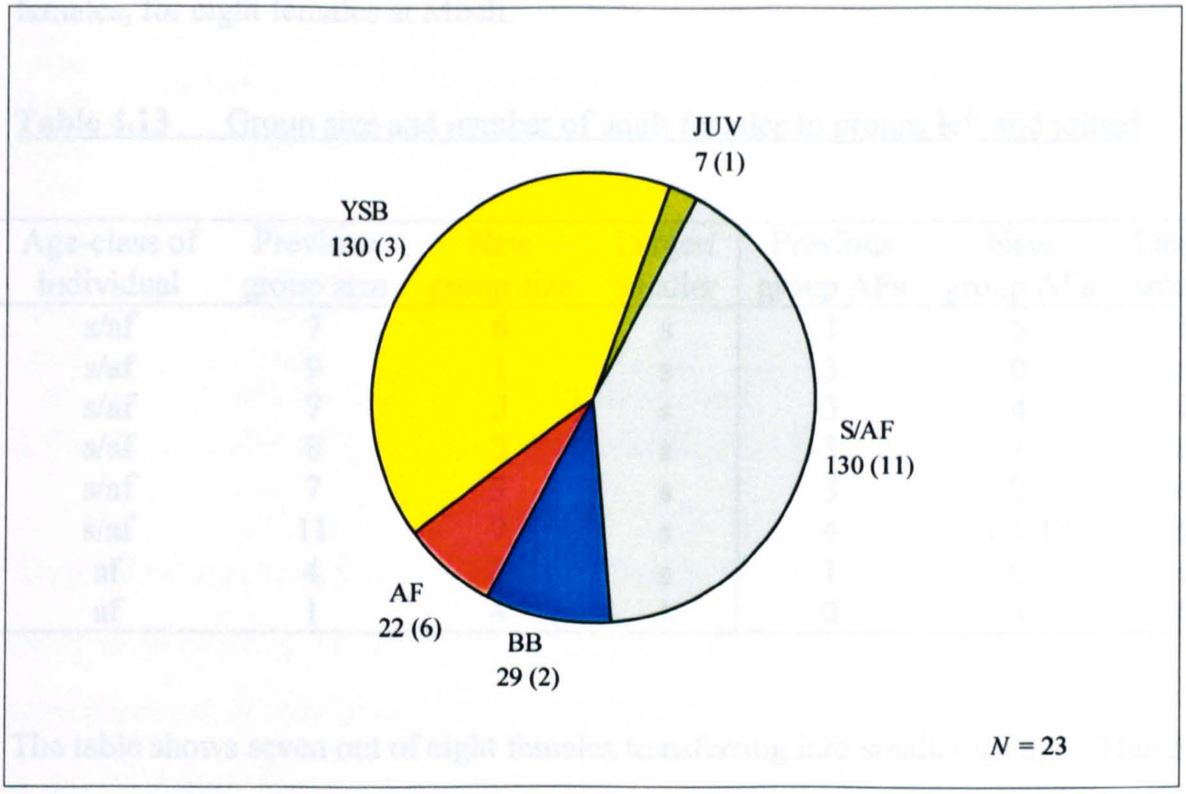
Figure 4.7 Frequency of emigration/transfer by age/sex-class



It should be noted that this chart illustrates the frequencies of transfer and emigration observed, without taking into account the relative numbers of individuals in each age/sex-class in the population. Figure 4.8 however, shows the level of inter-unit movement as an index, calculated by dividing the number of moving individuals in each age/sex class by the total proportion of individuals in that class within the entire population (the age-class of moving individuals was recorded at the time of their emigration, while all others were censused for age/sex class at the mid-point in the study, June 1998).

Figure 4.8 is a more informative representation of the data, in which, with transfer and emigration rates corrected for the number of individuals in the population per age/sex-class, the sexes are more equal. The index shows immatures on the brink of full adulthood (s/af and ysb) leaving their groups at the same rate. However, the proportion of adult females transferring is considerably reduced by the calculation of the index. Further analyses of transfer and emigration require that the sexes be considered separately, as motives, ages, and conditions are likely to differ sharply between males and females.

Figure 4.8 Emigration/transfer Index: proportional to population structure.



Values in parentheses are actual numbers of moving individuals. The other values are the frequency index scores.

Female transfer

Parous adult females transferred less often than sub/adult females transferring for the first time. This is perhaps to be expected, as in the Mbeli population, natal female transfer appears to be a biological imperative (most probably to avoid in-breeding), and secondary transfer an opportunistic optimising of social conditions. Only one true sub-adult female transferred: Paris, who had only recently become sub-adult, appears to have accompanied her elder group-mate and putative half-sister Holly, who transferred out of TRA group on reaching adulthood. Another case of potential joint half-sibling transfer occurred when sub/adult females Lucy and Lobelia disappeared from DWA group at the same time. As already mentioned, four sub/adult females from CLI group all joined the same group (MAX), though their departures appear to have been staggered over a period of 73 days.

Females should attempt to transfer into groups that offer optimum conditions for their survival and reproductive success. Therefore, an examination of the groups that females leave and join may indicate what constitutes an optimum group for female gorillas.

Table 4.13 shows the conditions of transfer in terms of group size and number of adult females, for eight females at Mbeli.

Table 4.13 Group size and number of adult females in groups left and joined

Age-class of individual	Previous group size	New group size	Larger/ smaller	Previous group AFs	New group AFs	Larger/ smaller
s/af	7	6	s	1	5	l
s/af	9	1	s	3	0	s
s/af	7	5	s	3	4	l
s/af	8	2	s	3	1	s
s/af	7	3	s	3	2	s
s/af	11	7	s	4	1 + 1?	s
af	4	1	s	1	0	s
af	1	4	l	0	3	l

The table shows seven out of eight females transferring into smaller groups. This may reflect a real preference among female emigrants for smaller groups. When only the number of adult females per group was considered, the effect was reduced, but still present, with five of eight transferring to groups where competition, either for food or proximity to a silverback may have been less than in their previous group. More data will be required, however, before substantial claims on transfer choice can be made, especially given that four of the s/afs shown in Table 4.13 shared the same original and destination group; an instance where sticking together may have been a stronger motive than any particular qualities of the chosen group.

Table 4.14 shows that when female transfers were examined with reference to group types, seven of the eight females were found to have transferred into a social unit type 'younger' than their previous group (i.e., mature to infant: senescent to solitary male; mature to nascent etc.). As a cautionary note, however, it should be borne in mind that nulliparous s/afs were more likely to be members of mature groups than other group types (*see* Table 4.11). Mature groups have been shown to be larger, in general, than other group types. As there were more non-mature than mature groups, the apparent selection of smaller groups may, in part, have been due to the distribution of group types in the population

Table 4.14 Departed and destination group types for eight transferring females

Age class	Departed group type	Destination unit type	Younger (y) or older (o) unit type
s/af	mature	infant	y
s/af	mature	solitary male	y
s/af	mature	infant	y
s/af	mature	nascent	y
s/af	mature	infant	y
s/af	mature	infant	y
af	senescent	solitary male	y
af	nascent	infant	o

Early Mbeli data hinted that a possible motive for parous female transfer might be the death of an infant (C. Olejniczak, pers. comm.). Three females were noted to have transferred out of their groups at 2.25, 7.75 and 10.5 months following the death of their infant offspring. However, data from the current study period plus records from the two previous years show five other females losing infants, and remaining with their groups throughout the study. Thus, while the death of an infant may prompt particular individuals to transfer, the event cannot be seen as a reliable trigger for transfer. It is possible that the cause of an infant's death may be important in this respect, though data are not available to explore this question.

Three females were known to have transferred out of groups in which they had been observed copulating with the silverback, or were known to be pregnant. Silverback Clive (CLI group) was seen copulating with sub-adult female NSAF, six months before her transfer to MAX group. She gave birth to her first offspring 15 months after her transfer. Sub-adult female, Beetle, was not observed copulating with Clive, but three months after being seen for the first time in MAX group, was observed with what appeared to be the decaying remains of a new- or still-born infant on her back. This offspring must have been conceived while the female was still in CLI group, and it is possible that it was killed in an infanticidal attack by the new silverback, Max.

These reports suggest that at least some of the four sub-adult females that joined Max from CLI group were not born in Clive's group but had transferred into it at some point between weaning and adolescence. Nevertheless, it is interesting to note that Beetle appears to have transferred out of a group while already pregnant. The same may have been true of NSAF though we have no evidence for or against this.

The most unusual transfer event of the study period concerned sub-adult female, Misha. Although her natal origins were not known, as a sub-adult in TSB group (where she had been known since at least February 1995), she was seen copulating with her group silverback, Solomon at the beginning of February 1997. Between the 20th of February, 1997 and the 5th of April 1997, she transferred out of the group. Her whereabouts were unknown, but between the 4th April 1998 and 4th May 1998, she rejoined TSB group (period of absence estimated at 395 days). Then at the beginning of October, 1998, she was seen with a newborn infant, Moss. Assuming that there were no extra-group matings, the interval between Misha's departure and the birth of her first offspring rules out Solomon as the father of the infant. However, Solomon was not observed making any aggressive approaches towards the infant, but rather seemed intrigued and protective of the pair. It seems possible that Solomon and Misha's copulation pre-transfer confused the paternity of her first infant sufficiently to suppress any infanticidal tendencies in Solomon (*see* Discussion).

Transfer following the death of a silverback

Aged group silverback, Bones, is believed to have died towards the end of January 1999, after a long period in which his physical condition was seen to deteriorate. The remaining members of his group, blackback Gretsky, sub-adult male Sahadouche, adult female Martha and her juvenile Muffin, were subsequently seen together twice in the first two weeks of February 1999, but on the 9th March 1999, were all seen visiting the bai with NOO group. During the first few joint visits, the silverback of NOO group, Basil, was clearly ill-at-ease and spent most of his time close to the forest edge, watching the immigrants closely. However, he was not overtly aggressive, and while interactions were recorded between other members, the group merge seemed to be stable and all transferred individuals were still present in the group at the end of the study period.

When the silverback of FFF group disappeared (presumed dead) in February/March 1996, it was feared that the group would split up. However, the presence of blackback/young silverback, Dylan, who was approximately 12 years old at the time may have held the remaining group members (sub-adult male Dougal, adult female Margo and her infant Iook) together. Although Dylan was frequently seen on his own, the group continued to range together without a mature silverback until July 1997 when Dylan was officially classed as solitary. In the same month, Margo, Iook and Dougal were all seen for the first time in a group containing only silverback Mosombo, and his blackback son Homer. Dougal disappeared from the group in May 1998, and Margo either died or transferred in December of the same year. The juvenile Iook remained with the group for the rest of the study period (a further 11 months). He was occasionally seen playing with Homer, and was briefly carried and comforted by him following an injury to the wrist.

Transfer of young immatures

One juvenile, Moses, transferred into TSB group unaccompanied by his mother, despite being only about three years old at the time (details of his previous group are unknown). In the days immediately following his arrival in the group he frequently sought the proximity of the group silverback, Solomon. On several occasions he attempted to ride dorsal on Solomon and on sub-adult male Salaam, especially before crossing streams (*see* Chapter 3), indicating that he may only very recently have lost the services of his own mother for such activities. Both older individuals were tolerant of his proximity, but unhelpful, and Moses only managed to gain assistance in crossing streams by clinging to a handful of hair and being dragged across, before being gently pushed aside. However, fellow juvenile, Bogplant, whose mother had disappeared when he was even younger than Moses, appeared intrigued and pleased with the immigrant and was observed clapping, chest-beating, anal-sniffing and gently touching him. Despite his young age, Moses' health did not appear to suffer from the upheaval of transfer and he adjusted well to living in his new group. The circumstances leading to such a young, unaccompanied transfer are hard to imagine, but may have involved the death of the mother and the subsequent break-up of the natal group.

Male emigration

Eight instances of male emigration by seven individuals were recorded during the study period. Sub-adult male Dougal transferred with an adult female and an infant (see above) into MOS group when FFF group dissolved after the death of the silverback and the increasingly peripheral status of the remaining young silverback, Dylan. A similar transfer was made by sub-adult male Sahadouche as part of the group transfer of BON group individuals into NOO group following the death of silverback, Bones. On that occasion, blackback Gretsky (also of BON group) also transferred directly into NOO group and was still present at the end of the study period. These animals were therefore not choosing to leave their natal group, but electing to remain with them during a block transfer in search of the security of a silverback. As described above, Dougal only remained in his new group for 10 months, before disappearing, despite being only 8 to 9 years old at the time. No overt aggression had been witnessed between Dougal and the existing males in MOS group, although Dougal did appear very nervous in the group, especially in the first few months. It was not known if Dougal became solitary at such an early age, or joined another group. The former seems more likely, as an existing group might not be expected to accept a maturing male without the added incentive of accompanying adult females.

Only two males were confirmed as having emigrated, from what were believed to be their natal groups, into solitary ranging, though three others are believed to have also done so. Confirmed solitary male emigrants were Dylan and Tarragon, both of whom continued to visit the bai after becoming solitary. Dougal, Red Stripe, and DASB were all thought to have gone solitary, but were not seen at the bai again. Figure 4.9 illustrates the process of becoming independent for five young males at Mbeli. The month in which each male made his first solitary visit to the bai (or when the group visited without the male) is given to the left of the chart and the first column corresponds to that month, with each successive column representing months after the initial separation. Every visit, by the group and the male is represented by a square, the colour denoting whether or not the male was independent at that time. (The chart entry for Frank should be read from left to right, and then back to the left again. This is due to space constraints and the length of his peripheral period).

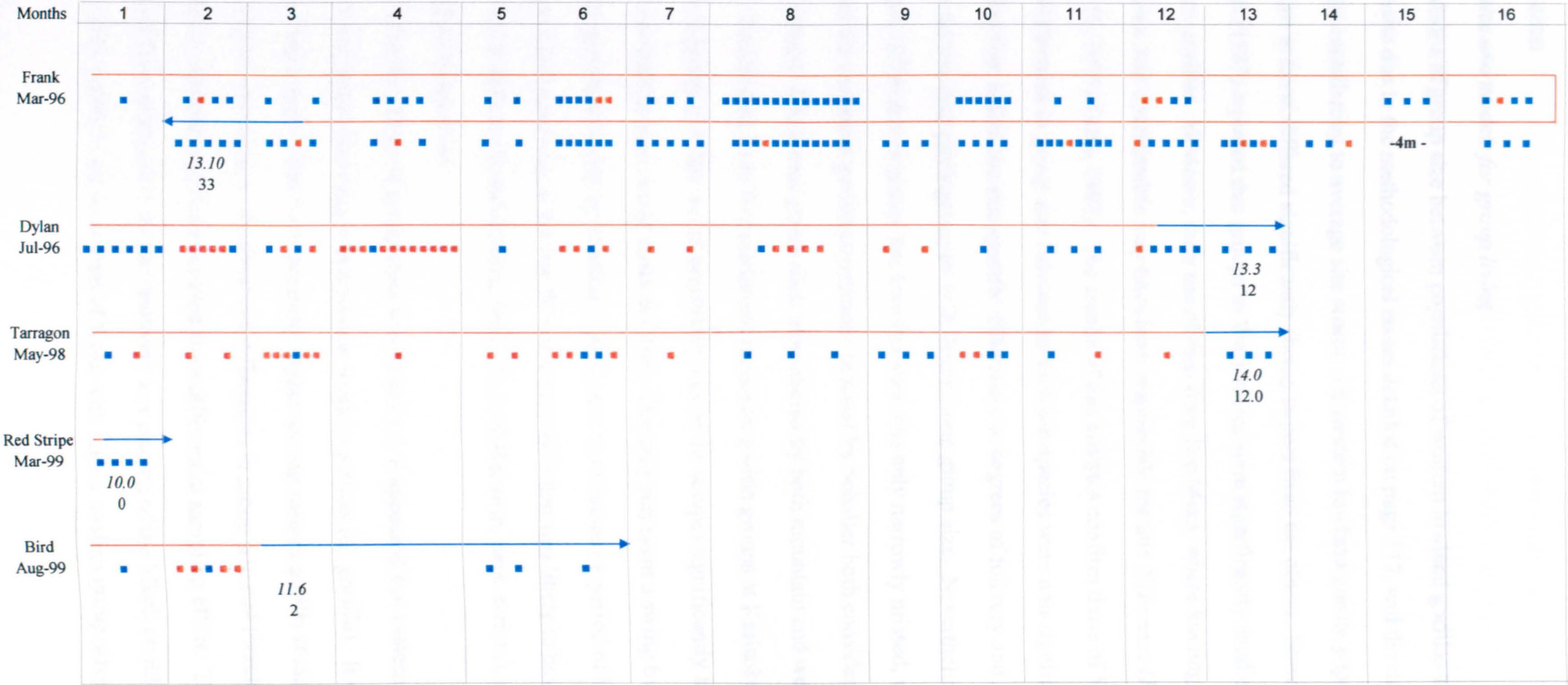
The chart illustrates that among these males, there was considerable variety in the manner of becoming independent. Red Stripe disappeared from TSB group without a period of peripheral ranging. Bird was noted on several occasions prior to his departure from DUK group to feed apart from the group, however, his final departure was also relatively swift. By the end of 1999, DUK group had effectively dissolved, such that Bird would not have had the opportunity to remain peripheral even had he wished to.

Both Dylan and Tarragon separated very gradually, taking approximately one year from the first separation to the final break with the group. This observation is intriguing in the case of Dylan, as his solitary visits to the bai infer that the other members of his group (adult female Margo, infant Iook, and sub-adult male Dougal) were ranging without a silverback during those periods, their dominant silverback having disappeared earlier. Such regular ranging without a silverback has not been recorded before. However, it is possible that during Dylan's solitary visits, the other members of the group were nearby but simply chose not to enter the bai.

By far the longest period of peripheral ranging was by Frank. Although appearing alone on the great majority of visits, he continued to be associated with his group, TSB, on and off for 33 months after his first solitary visit. Frank's many solitary visits do suggest that later visits with his group (during which he usually fed some distance from the group and often arrived or departed alone) may have included chance events where both group and solitary male happened to visit the bai at the same time.

On one occasion, Frank was herded away from his old group. Blackback Red Stripe was the protagonist, but was backed up by the group silverback Solomon, who, though remaining behind Red Stripe, appeared to reinforce the blocking effect. This was the only occasion on which a young male was seen being forced away from his natal group, and no other observations lent support to the hypothesis that natal males are chased from their groups. The social behaviour of emigrants is discussed further in Chapter 5.

Figure 4.9 The process of becoming independent, and the onset of solitary ranging in five Mbeli males



🟦 - male visit to the bai without group, or group visit without male. 🟥 - male visit to the bai with group. Numbers in italics are ages of males in years and months when seperation from group final. The figures below those in italics show the number of months from first to final seperation. 4m - gap in observations of 4 months. ⟶ male permanently ranging alone.
Although the number of visits or the length of time shown after the final 'group' visit appears to vary from male to male, in all cases these individuals were never seen with their groups again.

Discussion

Group size and models for group living

Comparisons of group size between populations of western lowland gorillas are problematic due to the methodological issues detailed on page 117, and the small number of groups contributing to average site scores. Of western lowland gorilla populations, only the groups at Lossi differed significantly (being larger) from the others. Stewart and Harcourt (1987) reported that groups in West Africa were significantly smaller than those of eastern gorillas. However, their use of data from Rio Muni, where hunting and other disturbance was considerable may have been responsible for this difference (Jones & Sabater Pi, 1971; Tutin, 1992). The results of this analysis confirm those of Watts (1996) in that differences in group size between species/sub-species were non-significant, suggesting that individual site-specific differences in degrees of folivory and frugivory are more important than phylogeny *per se* in determining group size. Nevertheless, a significant difference in group size between sites was only narrowly missed, with both Lossi and the mountain gorilla population censused by Schaller both considerably larger than all others. The lowest group sizes were shared by both mountain and western lowland studies. Recent data from five monitored mountain gorilla groups at Karisoke indicate an increase in group size that would potentially render the sample significantly larger than all western lowland groups except those at Lossi. This may represent a swing back towards the larger groups recorded by Schaller (1963) prior to an intensive period of human disturbance and poaching in the late 70's and early 80's that was likely to have lowered group size (Steklis & Gerald-Steklis, 2001; E. A.Williamson, pers. comm.), although other factors may be involved.

When the range of group sizes was examined, it appeared that eastern gorillas (*G. beringei*) had larger size ranges overall than western gorillas (*G. gorilla*). It was noted, however, that sample sizes were generally higher among eastern gorilla studies, raising the spectre that at least some of the observed differences in group size and therefore group composition statistics may have resulted from differential sampling effort. This factor may also be partially responsible for the relatively low placing of the Mbeli population among other western gorilla sites, as several of those with higher median group sizes have extremely small sample sizes. Large groups are more conspicuous than small groups, and their trail (and therefore their nests) easier to find. Furthermore, large groups may be those deliberately selected as the focus for ecotourism/research projects. As such larger groups may be over-represented in small samples.

In the absence of human disturbance, the abundance of terrestrial herbaceous vegetation ('THV') has been cited as the principal factor influencing gorilla densities and ranging (e.g., Goodall, 1977; Vedder, 1984; Tutin & Fernandez, 1985; Fay, 1997; Remis, 1997; Magliocca et al., 1999). No attempt can yet be made to correlate group size with herb availability at Mbeli, but it seems likely that the unusually large groups recorded at Lossi are linked to a super-abundant availability of these foods (Bermejo, 1997). This area centres on the site of an abandoned village and is characterised by an extremely high density of terrestrial herbs (secondary growth) and an unprecedented density of gorillas (up to 11.3/km^2; Bermejo, 1997). Although high gorilla density need not necessarily imply large group size, the presence at Lossi of groups ranging from 18 to 32 individuals suggests that in areas with an abundant and year-round food source, large groups are likely to develop. So what constitutes an optimum group size for gorillas, and which, if any, of the current models for group living best describe Mbeli and the other gorilla populations featured in the analysis?

As mentioned in the introduction, group living has evolved to serve the individual, so any discussion that fails to take into account the varied needs of individuals, or more precisely, of different age and sex classes, is bound to be misleading. Solitary adult males are able to range and feed themselves comfortably without the need of group backup. More data are needed on solitary male mortality levels from predation and conspecific aggression, but at least nutritionally, they appear well able to cope with being alone. In a group setting also, a silverback is dominant over all females, and therefore not susceptible to scramble or contest feeding competition. However, reproductive success in males is limited by access to females, and more particularly, to the number of females a male can attract and the length of time he is able to maintain his group (Robbins, 1995). Therefore, the more females a male can attract, the greater his reproductive output is likely to be. A ceiling to this effect is likely if a male is unable to offer adequate protection to females from infanticidal males or predators. Furthermore, should females wish to transfer out of a group because of this risk, a given male's ability to block such a move should be negatively correlated with female group size. Tolerating the presence of a son into adulthood (causing a shift to a multi-male group) is suggested as a mechanism by which, through coalition support, a silverback may maintain a large group, even at the expense of potentially losing a guaranteed monopoly on paternity (Sicotte, 1993; Robbins, 2001). Group tenure may also be extended by such tolerance, as an elderly silverback's presence may be tolerated in a group after a son has assumed dominance (Robbins, 1995). For maturing mountain gorilla males, remaining in the natal group offers greater reproductive potential than going solitary (Dunbar, 1988; Robbins 1995; Watts 2000). Thus, for young, and older silverbacks, larger groups may be preferred, though maintenance of the largest groups may be limited by the availability of adult or near-adult sons. For adult females, the primary 'engineers' of group structure in gorilla society, the situation may be more complicated. Why do females associate permanently, and what represents the ideal social unit for such individuals?

The 'feeding competition model' (Moore, 1984; Dunbar, 1988) predicts that females will select smaller groups, in which feeding competition is minimised and birth rate subsequently maximised. Watts (1996) points out, however, that in mountain gorillas, females transferred equally as often to groups that were larger than their previous group as they did to those that were smaller. The abundance, distribution, and temporal stability of herb foods available to mountain gorillas ensures that scramble and contest foraging competition are minimal, and females seeking to transfer are unlikely to be greatly influenced by the dietary benefits of joining smaller groups.

Western lowland gorillas are more likely to suffer intra-group feeding competition than mountain gorillas. Firstly, competition may arise from the temporal and spatial discontinuity in fruit availability. Furthermore, access to any given fruiting tree is limited by its 'carrying' capacity for gorillas (Remis, 1999). Competition may also be felt during herb feeding, as in undisturbed forest types, herbs may be scarce and found in smaller patches. Even in forest types of high stem density, such as secondary 'Marantaceae forest', stem densities are considerably lower than those available to mountain gorillas

(Lopé – 1.87 stems/m², Karisoke – 8.81 stems/m²; White et al., 1995). Behavioural consequences of reduced herb density and the variation in fruit availability include an increase in day range, increased group spread, smaller group size, and possibly a reduction in group cohesion (e.g., Tutin et al., 1992; Mitani, 1992; Goldsmith, 1996a; Remis, 1997; *for review* Doran & McNeilage, 2001). At Mbeli, transferring females showed a stronger preference for smaller groups than those at Karisoke, with seven out of eight moving into such groups at transfer.

The great abundance of aquatic herb foods available in Mbeli Bai could be seen to approximate conditions in the Virungas. However, there may be constraints on the intake of these plants (*see* Chapter 3), and the distribution of bais within a given group's range may greatly limit the overall contribution of this food source in the diet. The low median group size recorded at Mbeli, even in comparison to Lopé, where no bais are found, suggests that the dietary effects of bai-use on group size may be negligible.

Watts (1990, 1996) points out that group size correlates negatively (albeit non-significantly) with infant survival rate to 1yr old, and suggests that this undermines support for the 'predator protection model' for group living. The model (van Schaik, 1983; Dunbar, 1988) predicts that although birth rate is negatively correlated to group size, the anti-predation effects of larger group membership ensure that infant survival is improved.

While predation risk (Stewart & Harcourt, 1987) may have had an influence on the evolution of group structure in gorillas, its direct effect on group size may be slight. Only leopards (*Panthera pardus*) are capable of predatory attacks on gorillas, but while evidence of such attacks exists (Baumgartel, 1961, Tobias, 1961; Dart, 1961; reviewed in Schaller, 1963; Fay et al., 1995), confirmed gorilla kills by leopard are rare. Leopards in African tropical forests exploit a broad prey-base (Hart et al., 1996; Hoppe-Dominik, 1984) containing many species whose capture would present considerably less risk of injury than attacking a group of gorillas. Young, elderly or sick solitary gorillas are likely to be at increased risk however, and it is possible that certain individual leopards favour gorillas as prey (Kingdon, 1997), but it is suggested that leopards, at most, pose a marginal threat to most gorillas. The gorilla's status as the largest of the primates may in itself have been partially in response to predation pressure incurred by exploiting a more terrestrial niche, and Dunbar (1988) suggests that for an animal the size of a gorilla, even relatively small group sizes may be adequate to ensure efficient predator detection advantages. A positive correlation between group size and predator protection is only likely to be felt, however, through the dilution effect and not improved detection. Gorillas lack the visual acuity necessary to spot a stalking leopard after dark, and have no aural specialization (Schaller, 1963; Dixson, 1981). Furthermore, the diurnal lifestyle of the gorilla means that much of the night may be spent asleep.

Finally, if predator protection itself were the primary influence on grouping patterns, females might be expected to remain together following the death of their silverback until 'adopted' by a solitary silverback, rather than dispersing to join other groups (Watts, 1989, 1996). So for both eastern and western gorillas, while protection from predation cannot be eliminated as an ecological benefit to grouping (Doran & McNeilage, 2001) it would not appear to be the primary cause of grouping or variations in group size and composition.

The 'male protection' model (Dunbar, 1988; Wrangham, 1979, 1982, 1987; Watts, 1996, 1989) gives infanticide risk as the primary cause of current male/female grouping patterns. Females require the presence of the father of their offspring, or possibly his kin, to protect them from infanticidal attacks on their offspring by extra-group males wishing to trigger a resumption of sexual cycling through the cessation of suckling (caused by the death of an infant). As most infanticide occurs following the death of a group silverback, the presence of a silverback within a group may be adequate to deter attacks (Sicotte, 2001), but the uneven distribution of females to silverbacks in all gorilla populations attests to female choice of males, suggesting that some males may be better protectors than others. However it remains unclear how anti-infanticidal qualities might be assessed by females. Male qualities for protecting against infanticide and predation may be similar, thus a good male will benefit a female in both circumstances (Watts, 1996).

The male protection model predicts that small groups are likely to reflect the presence of a poor quality male and thus have lower reproductive success, but that large groups will suffer lower birth rates as a result of feeding competition (Dunbar, 1988). Therefore medium sized groups are predicted to be optimum within this theory. However, an effect probably over-riding the influence of feeding competition in mountain gorillas is that whereby greater protection from infanticide is gained in larger, multi-male groups, due to the coalition forming behaviour of the two or more silverbacks. Indeed, such groups are known to contain more females than single male groups and infants are less likely to die from infanticidal attacks (Robbins, 1995). In addition to coalition support, infanticide risk is reduced upon the death of a dominant silverback in a multi-male group, as the group is more likely to remain together under the leadership of a previously subordinate male (Robbins, 1995).

At Mbeli, only one possible case of infanticide was recorded (MAX group) following the transfer of a pregnant female to another group. On another occasion, primiparous female, Misha, transferred back into her previous (and possibly natal) group while pregnant with the offspring of another male, but the infant was accepted. In mountain gorillas, no females have been recorded to transfer while pregnant and give birth in the new group (Watts, 1990a), though Watts (1989) suggests that paternal behaviour following such an event could possibly be induced by a female through copulating with a new male prior to the birth of the infant. In the case of Misha, it appears that copulating prior to conceiving in another group may have saved her offspring from infanticide once she had returned to her original group.

Following the death of their silverback, the remaining members of FFF group ranged with only a young male (Dylan, a 12-13yr old who may have been the son of the remaining female) for over a year prior to joining a new mature silverback. In this instance the single female in the group may have been aware of the danger to her offspring and waited until he was older before risking a transfer to an unrelated male (the infant was 1yr,6m old at the time of the SB's death, and 2yrs,10m when joining the new group). During this period, the group was harassed by solitary silverback, Vince (pers. obs.). In response to Vince's repeated aggressive approaches toward the female (Margo) and her infant, the young silverback Dylan, retreated from the interaction, leaving a sub-adult male (Dougal) to repeatedly reposition himself between Vince and Margo. This buffering by a younger individual (who exhibited intensive displacement feeding throughout the interaction) seemed to effectively dissuade Vince from continuing his attack. It can be hypothesised that Dylan's disinclination to involve himself was due to a perception of the greater probability of his sustaining serious injury than was likely for the sub-adult.

Four and a half months after the death of the FFF silverback, another of the group's adult females left the group (her infant had died a year earlier). She eventually joined MAX group three months later, but in the interim, was seen on one occasion travelling with solitary silverback, Vince. This observation supports the prediction arising from the infanticide protection model suggested by Watts (1996), that females may transfer temporarily to solitary males in order to sample their suitability as permanent protectors. The mass transfer of members of BON group into NOO group following silverback Bones' death did not provoke an attack on the group female's offspring, though at over four years of age, its death would not have been required for a resumption of cycling in the mother.

The evidence of infanticide and its avoidance from Mbeli therefore add support to the value of the male protection/infanticide model for gorilla grouping patterns. The risk of predation appears negligible for mountain gorillas and only slightly greater for western lowland gorillas, suggesting that this of itself is unlikely to contribute significantly to current grouping patterns. However, elements of the feeding competition model appear important in constraining group size in all populations without a super-abundant and temporally stable food source.

A puzzling enigma remains, however. In the Virungas, abundant herbs allow large groups to form and be maintained. In the absence of major predation pressure, the most likely benefit of such groups is improved protection from infanticide, possibly resulting in part from the dilution effect, but mainly due to the presence of two or more silverbacks. However, at Lossi, where abundant herbs also permit the development of large groups, the largest groups in the population remain single male (M. Bermejo, pers. comm.). Within the grouping models described, females in such groups should be subject both to increased feeding competition (with concomitant lowering of reproductive success) *and* a reduction in protection from infanticide due to there being only one male protector for many females, and little chance of group survival through the assumption of leadership by an adult son on the death of the silverback. The existence of such groups at Lossi raises questions regarding the reasons for the development of multi-male groups at Karisoke and the extent to which mountain gorilla social structure has been affected by humans. It also begs the question of why large groups might develop in western lowland gorillas.

Where the costs of feeding competition are low, a possible mechanism for the formation of large groups in western lowland gorillas is the selection by females of groups already containing several females with healthy infants. Such groups may act as an advertisement of both a silverback's fertility and his ability to deter infanticidal males and possibly predators. A larger group may, in a sense, represent an 'honest handicap' to a male in the sight of a potential immigrant female. Conversely, joining a solitary silverback or a very small group may constitute entering into a genetic and behavioural unknown and could prove more costly in the long-term than any slight reduction in reproductive success through competition in a larger group. In this model, females would continue to be attracted to large groups until some behavioural or ecological variable created a ceiling (Weatherhead & Robertson, 1979). However, the point made by Sibly (1983), that groups of optimum size are inherently unstable, should be borne in mind. He predicts that the largest groups in a population may contain up to twice as many individuals as are optimum for survival and/or reproduction.

Group composition and type: multi-male groups and solitary males

All groups in the Mbeli population contained only one fully mature silverback. Prior to this study period, a group with two silvered males was observed, one of which left the group at the end of 1996. Photographic records suggest that this individual may have been approximately 15 years old at the time of his departure, and as such, we are unable to say with any confidence that he was other than a standard natal emigrant, departing at the upper limit of the normal range for the species. This example may underpin much of the conflicting information regarding multi-male groups both for *G. g. gorilla* and *G. b. beringei.*

Maya Bai (Magliocca et al., 1999) and Mbeli together describe 45 western lowland groups where silverback numbers are known. None of these groups contained more than one fully adult silverback. Given the proposed benefits of multi-male groups (Sicotte, 1993; Robbins, 1995; Watts, 1989, 2000), these figures are surprising. Multi-male groups have been recorded at several western lowland gorilla study sites (Lopé - Tutin et al., 1992; Ndoki - Mitani et al., 1993; Bai Hokou – Goldsmith, 1996c; Remis, 1997), in eastern lowland gorillas (Yamagiwa et al., 1993; Yamagiwa, 1996), and most frequently among mountain gorillas, where approximately 40% of groups contained more than one silverback (Weber & Vedder, 1983).

While differences between these populations may be real, some of the variation may be due to imprecise definitions and compromising methodology. As already noted, the number of silverbacks per group is likely to be over-estimated by nest counts in western lowland gorillas. A confounding issue concerns how multi-male groups are defined. In analyses of mountain gorilla groups through nest counts and observation, Weber and Vedder (1983) are correct to define silverbacks as males of 12 years and above, as from 12 to 13 years on, the dung diameter of such individuals may be indistinguishable from that of older males (pers. obs.; Yamagiwa, 2001; Williamson, pers. comm.). However, this age-classification should only be used to limit error in nest counts. To include males between 12 and 15 years into the 'adult silverback' category when considering group composition and male dispersal patterns conceptually 'short-circuits' the natural process of male dispersal. Data on male emigration age for western lowland gorillas are not available, however the range of estimated emigration ages for five Mbeli males was 10 to 14 years (pers. obs.), and for mountain gorillas 12 to 15 years (mean 13.5, SD 1.195, N=9: Robbins, 1995). The presence of males within these age ranges in their natal group should not necessarily be taken as a reflection of an individual's strategy for optimising breeding opportunities (as against becoming solitary). Several authors have noted that groups may alternate between single- and multi-male status as males mature and emigrate from their natal groups (Yamagiwa, 1987a; Robbins, 1995), and certainly, the presence of such individuals may facilitate multi-male group benefits such as male coalitions in acquiring or defending females and their offspring. However, it should be borne in mind that such 'age-graded' groups (Eisenburg, 1972) are temporary phenomena, the existence of which is entirely dependent upon the presence of immature males in a group. While such young males may be fertile and in some circumstances may even sire offspring, it is proposed here that in relation to social structure, groups be referred to as 'single-male' until such time as natal males reach 15 years. This would not preclude the use of other terms for labelling groups containing older adolescent males when examining, for instance, inter-group interactions, but it would permit a more precise approach when considering group structure and mating systems.

To illustrate this point, a census of Mbeli group structure within six months of the end of the study period, taking males 12 years and above as adult silverbacks, would have returned a figure of 25% multi-male groups for the population (3/12). There would be no reason to believe, however, that any of these males had made decisions based on their chances of breeding within or outside their natal groups. Indeed, data suggest that all would have become solitary before reaching 15 years of age. Many of the groups described as 'multi-male' at other western lowland gorilla study sites may be of this nature, and as such, could be seen as misnomers.

Nevertheless, data from the Virunga population do show both higher numbers of 'true' multi-male groups, and a greater propensity for young silverbacks to remain in their natal groups for longer before emigrating. Weber and Vedder (1983), using 1978 census data from the Virungas (not including Mt. Mikeno), found 37% of groups to be multi-male (7/19), although the maximum number of silverbacks per group was two. While current and detailed comparative data are unavailable, the number of silverbacks per group (including males 12yrs and above) in the Rwandan sector of the Virungas appears to have increased (despite an overall reduction in the number of multi-male groups between 1987 and 1989; Watts, 2000). At the time of writing, in one group (Shinda's), six silverbacks are currently present. Both Shinda's and Pablo's groups currently contain 14 year-old subordinate silverbacks who, despite frequent and severe attacks from the dominant silverback, remain in their natal group rather than becoming solitary (Williamson, pers. comm.).

In contrast to both Mbeli and Maya, the ratio of solitary males to group individuals at Karisoke is extremely high, showing that there are relatively few such individuals in the population. There is very little evidence that males at Mbeli are coerced into leaving their natal groups. Rather, emigration appears to be voluntary. Smaller group sizes, imposed by feeding competition, may offer fewer breeding opportunities to young males, and this combined with the well-described effect of breeding preference for unfamiliar mates may be sufficient to provoke emigration. Ubiquitous food resources in the Virungas permit large groups to be maintained, offering more breeding opportunities to young males. Crucially however, large groups do not appear to offer the same inducement for males to remain with the natal group at Lossi.

Males in mountain gorilla groups are thought to gain more reproductive opportunities by remaining in their natal group than by becoming solitary (Robbins, 1995; Watts, 2000). It is not yet possible to model male strategy at Mbeli, but it would appear that while some breeding opportunities and the potential to inherit leadership may be available to subordinate males in natal groups, the possible rewards of the solitary search for females may be much higher for any given individual. It is true that some males may never acquire females (solitary silverbacks Bear and Vince have remained alone since the start of the study), but others have been extraordinarily successful (solitary Max acquired eight breeding females within approximately two years). However, the question remains; does the level of multi-male grouping observed in the Virungas represent a response to varying social and demographic conditions in a basically stable demographic- and habitat-type, or does it represent a more recent response to demographic pressures imposed by human disturbance, or as Robbins (2001, p48) puts it, "making the best of a bad job"?

One hypothesis for the apparent rise in multi-male groups and a disinclination toward emigration by males in the Virungas may be that demographic pressures have made life as a solitary silverback increasingly stressful, hazardous, and/or unrewarding in terms of female acquisition. Up to ten lone males currently roam the Karisoke study area, and are known to be violently attacked whenever they encounter a group (Williamson, pers. comm.). Population growth (due to improved anti-poaching measures (Harcourt & Fossey, 1981; Vedder & Weber, 1983; Steklis & Gerald-Steklis, 2001), immigration from less well-protected areas, and possibly a reduction in available ranges (due to human encroachment) may be creating higher than usual densities of gorillas in some areas of the Park. Raised levels of aggression both between intra-group males and between group and solitary silverbacks (Williamson et al., 2001) further attest that the level of multi-male groups may be a reaction to recent demographic forces, rather than a reflection of an optimal 'undisturbed' dispersal system. Watts (2000) points out, however, that while population density can influence male dispersal strategies, in yellow baboons (*Papio cynocephalus*) males are less likely to emigrate from groups in low population density areas (Alberts & Altmann, 1995a).

A mechanism for the increase in multi-male groups at Karisoke may involve a 'feed-back' effect on other groups. Coalition support in groups containing two silverbacks may increase their likelihood of success both at female herding and acquisition. Conversely, a group silverback unable to rely on such support may be more likely to lose females and encounter more difficulty in acquiring them. Creating conditions such that maturing males delay their emigration (tolerance of proximity and limited breeding access to females?) may be the only means available to some silverbacks for maintaining viable groups. In this way, a virtual 'arms race' can be envisioned in which increasing numbers of silverbacks are required for a group to remain competitive. This hypothesis for multi-male group formation has been commented on by Robbins (2001), but has received scant attention. Whether constant population pressures have brought about the current demographic profile of the Karisoke population or whether a 'feed-back' effect of multi-male grouping could have been initiated by a particular event in the population's recent past (e.g., the killing of males by poachers in the late 70's and early 80's) is a matter for debate. The lack of true multi-male groups at Mbeli and Maya however, suggests that at least for some western lowland gorilla populations, the presence in the same group of two or more fully adult silverbacks is not part of the normal dispersal pattern.

All-male groups

Yamagiwa (1987b) suggests that increased levels of agonism in the population may have led to the formation of two all-male groups at Karisoke. This alone seems unlikely as inter-unit agonism is now at a higher level than previously recorded (Williamson et al., 2001), and there are currently believed to be no all-male groups in the population (Williamson, pers. comm.).

None of the groups identified at Mbeli have been 'all-male'. Some groups have contained only male individuals as a result of female emigration or death, however a clear distinction should be made between groups containing only males, and what are sometimes termed 'bachelor groups'. In order to maintain the functional context of these terms, it is suggested that only groups containing no adult females, which have received male immigration at a stage when no adult or sub-adult females were present in the group, should be classed as all-male or bachelor groups.

Though data are not available to test such a hypothesis, the lack of all-male groups at Mbeli may be another indication, in addition to the lack of multi-male groups, that in undisturbed habitat types, or those with higher levels of feeding competition, adult males consistently avoid proximity with each other, whether related or not. The complete lack of evidence for bachelor groups in western lowland gorillas, and the rarity and instability of the Karisoke all-male groups (only two groups have been well described, most members emigrated on reaching maturity, and both groups eventually collapsed) should, despite early encouragement (Harcourt, 1988; Johnstone-Scott, 1988), serve as a warning to managers of captive gorillas that the creation of such groups as a means of housing 'surplus' males socially, may not prove to be a long-term solution (Parnell, 2000a).

Group stability

Mbeli is not the most suitable site at which to address the question of whether groups split temporarily into foraging and/or nesting sub-groups, as proximity to the bai may act as an impetus for re-grouping, making such observations unlikely. Despite over 700 group visits to the bai, only one group has shown any evidence of such sub-grouping (Olejniczak, unpubl. data) but this ended following the emigration of one of the group's silverbacks (an individual that may have only recently attained full maturity). Despite several groups containing near-adult sons, no other evidence of sub-grouping was recorded. This contrasts with Mitani's (1992) suggestion that sub-grouping might be responsible for small gorilla group sizes in the Ndoki forest contiguous with Mbeli Bai, and data from Remis (1997) and Goldsmith (1996) supporting sub-grouping and a generally looser grouping structure at Bai Hokou (65km north of Mbeli). Mitani's data were preliminary and later results from Nishihara (1994) show larger groups for that area. The Bai Hokou data are more puzzling. Gorillas in this area sleep on bare ground more frequently than any other population yet recorded (47% of nests: Remis, 1993) and as such, a greater degree of inaccuracy in nest counts is to be expected, making interpretation difficult. However, data for some groups are also obtained from observation and repeated follows of the same sub-group. Differences in food availability are the most intuitive cause for such discrepancies between sites (Remis, 1997), but more detailed habitat descriptions, and more solid proof of sub-grouping are required.

However, evidence of temporary group merger was recorded during the Mbeli study. On several occasions, a known group entered the bai with one or two other known groups, and following a period of interaction or peaceful feeding in the same zone, exited together without re-forming into their usual group structures. On one such occasion, three groups entered the bai together, fed and interacted, then shortly before dusk, exited together. Early the following morning, all three groups re-entered the bai, with members still completely merged. A subsequent night-nest count, while inconclusive, did not rule out the three groups having nested together. Similar merged evening exits and morning re-entries were subsequently observed in another two groups.

Group type

Of all the factors described in this chapter as possible influences on group size and population structure, none have previously received so little attention in the literature, relative to their potential importance, as 'group type'. Census results themselves only present a static picture of a population. It is therefore easy to imagine groups themselves as the static, finished result of a social evolutionary process fashioned by ecological pressures. However, social structure, while potentially stable, is constructed of essentially fluid processes.

Despite early attempts by Harcourt (1978a) and later Yamagiwa (1987a), few authors appear to have considered group type as a concept, let alone approached it as a significant social variable when interpreting census results. With a naturally occurring group type distribution present in every gorilla population, it is unfortunate that examinations of group size, composition, and dispersal strategies commonly treat all social units as equal commodities when expressing descriptive statistics. It may be singularly unhelpful, for instance, to consider rates of female transfer according to group size. While small groups may be found to be targeted for transfer by many females, such groups may be very new (nascent or infant) groups, or older (senescent) groups. The implications of joining one or other group, from a social viewpoint, could not be more different. As a further example, reporting on the incidence of multi-male groups in a population would be a meaningless exercise unless mature or senescent group types were proportionally represented in a sample, as these are the only two group types in which such a condition can normally be found.

Unfortunately, at many study sites, the number of groups accessible is simply too small for an adequate sampling of the distribution of group types in a population. Furthermore, a rigorous examination of the variation in groups within each group type, under the five-stage system described in this chapter, and with the ratio of group types found at Mbeli, could require up to 190 groups. Clearly, this is quite unattainable. However, the Mbeli system is not offered as one that will meet all practical and theoretical conditions; rather it is provided as a model with which to approach group structure in a manner more sensitive to the actual conditions under which gorillas live.

Summary of findings

- Of seven western lowland gorilla studies, only one data set showed a median weaned group size smaller than that at Mbeli. However, small groups are liable to be overlooked in nest census counts, especially where sample size is low.

- There was a significant difference between western lowland gorilla group sizes; the difference being due to the large groups at Lossi. Across all species/sub-species, a significant difference in group size was only narrowly missed, with a western lowland and a mountain gorilla population showing the largest groups. The smallest groups were also recorded among both species.

- A significant correlation was found between sample size and group size range, suggesting that some of the difference in maximum group size between western and eastern gorillas may be influenced by sampling effort.

- The number of infants and juveniles per group did not correlate significantly with either group size, nor the number of adult females per group, suggesting that the effects of feeding competition were not sufficient to influence reproductive rate. However small sample sizes, stochastic life-history variables and group type may influence reproductive rate more than group size.

- Of three western lowland populations, the median proportion of adult females per group was highest at Mbeli. Of eight populations from both species, only Kahuzi-Biega had more females per group than Mbeli, though overall, differences failed to reach significance. A highly significant difference between the median proportion of young immatures (infants and juveniles) per group across all sub-species was found, with Schaller's 1963 groups from the Virungas implicated as having the highest.

- Of five western lowland gorilla studies, the ratio of young immatures to adult females was lowest at Mbeli, however census results from the Virungas in the mid to late seventies, and results from Kahuzi-Biega, showed a lower ratio.

- No all-male (bachelor) groups were present at Mbeli.

- At Mbeli, all immature males emigrated from their natal group at or shortly before reaching adulthood. Thus, no multi-male groups were recorded in the population. Differences in the incidence of such groups may to a degree result from methodological and conceptual issues. At Mbeli the dispersal of all natal males is probably due to a natural intolerance of silverbacks to each other's proximity, and a ceiling on group size imposed by feeding competition that may permit extra females, but does not facilitate more than one male. It is also hypothesised that human disturbance and/or population density factors may have created conditions in the Virungas where solitary ranging is deleterious to male reproductive potential, and multi-male grouping necessary for the acquisition and maintenance of females and the protection of their young offspring.

- It is suggested that when considering parameters such as group size, composition, stability and dispersal, the issue of group type has been neglected. Groups are shown to vary greatly over time, and such variation should be considered when interpreting census results, especially where sample sizes are small.

- Reproductive intervals were found to be roughly equivalent to those in mountain gorillas and in captivity. There was no evidence of birth seasonality at Mbeli.

- Almost 80% of gorilla mortality was suffered by infants, and 60% of infant deaths were within the first six months of life.

- Excluding dominant silverbacks, infants, juveniles, and those immigrating after group collapse, almost 33% of the population transferred or emigrated during the study period. Proportionally, rates of male and female emigration were similar. No individuals were recorded breeding in their natal group.

- 88% of transferring females immigrated into groups that were smaller and of a younger group type than their previous group. However large groups were present in the population and received female immigration. The number of young immatures per adult female did not correlate significantly with group size or the number of adult females per group. Once again, group type may be implicated in apparent transfer choices as, by default, natal emigrants are most likely to be present in larger, 'mature' groups.

- Two groups suffered the death of their dominant silverback. In both cases, remaining group members stayed together and eventually joined other groups together (including blackback males).

- Findings were not inconsistent with infanticide being an important influencing factor in grouping patterns and transfer decisions.

Chapter 5

Intra-group Adult Interactions

Introduction

It is generally accepted that animals live in groups and exhibit particular traits in social structure as a response to the requirements of predation avoidance and food acquisition (Pulliam & Caraco, 1984). In turn gregarious living inevitably incurs costs to the individual through competition for resources (Janson, 1988). Variation in the ecological conditions present in any habitat create variation in the adaptive responses in and between individuals for coping with competition, which shape and vary the nature of the evolving social system (e.g., Crook, 1970; Clutton-Brock & Harvey, 1977). These responses involve an interplay between cooperation and conflict (Crook, 1970); a balance with imperatives, motives, and outcomes that differ considerably with the age, sex, and reproductive condition of the individuals making up the group (e.g., Walters, 1987; Smuts, 1987). Females are generally affected more than males by ecological variables such as food availability, due to higher levels of parental investment in offspring and overall slower reproductive rates (Trivers, 1972; Bradbury & Vehrencamp, 1977). For males, the principal limitation on reproductive success is access to females (e.g., Wrangham, 1980). Thus while females are generally thought to be organised with respect to feeding resources, males are organised around female distribution patterns. The nature of interactions between group members is the most immediate signpost to an understanding of how selection pressures originating from environmental conditions have shaped the social system at work within a species or population.

In contrast to mountain gorilla inter-unit interactions, intra-group behaviour has been well described. Reasons for this dichotomy include: a) that inter-unit interactions are rare and hard to observe in a forest environment, and b) for inter-unit interactions to be unbiased, researchers should either be hidden, or habituation of both interacting units should be at an equal level. By contrast, one well habituated group can provide many hundreds of hours of detailed behavioural observation (N.B. Most records of intra-group behaviour in mountain gorillas come from a limited number of groups [e.g., Harcourt, 1979a, 1979b; Watts, 1991, 1992]). Most social data from eastern lowland gorillas is also of this nature (Yamagiwa, 1986a; Yamagiwa & Kahekwa, 2001). Eastern lowland gorillas are influenced by ecological variables similar to those encountered by both mountain gorillas and by western lowland gorillas. As such, the influence of ecological variables, and especially diet, on social structure is harder to interpret. Mountain gorillas, with their abundant and seasonally constant diet of terrestrial herbs (Schaller, 1963; Fossey & Harcourt, 1977; Watts, 1984) offer a more contrasting example against which to examine the effects of diet and other ecological variables on western lowland gorilla social structure.

While the social behaviour of immatures has implications for adult life, this chapter confines itself primarily with adult interactions. Some data on immatures are, however, included in the general analyses at the start of the result section, and preliminary data on the intra-group relationships of immatures at Mbeli are also available elsewhere (Nowell, 2001).

In gorilla groups, adults are group silverbacks, and adult females (≥8yrs) with or without offspring. Young silverback and blackback males are thought to be capable of siring offspring in mountain gorilla groups (Robbins, 1999), and the presence of such young males (especially young silverbacks) within a group is reported to confer reproductive benefits to females, who are less likely to suffer infanticide should a dominant silverback die (Harcourt & Stewart, 1981; Fossey, 1982; Stewart & Harcourt, 1987; Watts, 1990a). Therefore the presence of such males in a group is likely to a have more immediate effect on demographic and behavioural variables than younger immatures. As such, data on older immature males is included in the following analyses.

The quality of female relationships in primate groups is largely a function of the availability of food (e.g., Sterck et al., 1997). Without strategies to maximise their foraging success, females in groups where within-group contest competition for food is high are likely to suffer fitness costs. In such groups, strict dominance hierarchies are likely to form, reflecting the potential for gains to be made in contest competition over resources. Within dominance hierarchies, cooperation can be expected between relatives (kin selection) leading to indirect fitness gains, and direct fitness benefits can be secured through cooperation between non-relatives (Periera, 1989; Chapais, 1992). The increased reliance of females on cooperation and coalition-forming with other females results in the costs of emigration being raised: females dispersing from their natal group will enter groups at or near the bottom of the dominance hierarchy, with no-kin support or investment in non-kin reciprocal support relationships. Such potential costs of transfer promote female philopatry (Sterck et al., 1997).

Where within-group contest competition is low, the costs of establishing and maintaining dominance hierarchies and contesting resources outweigh the potential gains from increased fitness. In such situations, females have little need of agonistic support and dominance hierarchies are weak or absent. As a result, the costs of dispersal are greatly reduced and females may transfer without the support of kin (transfer may be selected to avoid scramble competition and inbreeding). In Wrangham's (1980) model, groups of this nature were classed as 'non-female bonded'. Sterck et al. (1997) in a re-evaluation of the basic ecological model, label this social type-class 'Dispersal-Egalitarian'. Species showing similar traits include Thomas Langurs (*Presbytis thomasi*: Sterck, 1997), hamadryas baboons (*Papio hamadryas*: Abbeglen, 1984), and patas monkeys (*Erythrocebus patas*: Isbell & Pruetz, 1998). Female relationships differ within some species, due to variations in food availability. Such intra-species variation is noted in grey langurs (*Semnopithecus entellus*), in which dominance hierarchies are established in areas of less abundant food where the monopoly of resources is possible, but not in habitats where the distribution of food is such that within-group contest competition is minimal (Koenig et al., 1998). The existence of such intra-species variation raises interesting questions regarding relationships among gorilla females, in which the mountain and western lowland species live in very different habitats.

Mountain gorillas fit well into the 'Dispersal-Egalitarian' class of the model proposed by Sterck et al. (1997). The abundance and lack of seasonality of their food plants creates conditions where the benefits of competing over food are low, thus reducing any advantage that might be gained from dominance hierarchies, which are accordingly weak or absent (Harcourt, 1979a; Watts, 1985, 1994, 1996). It follows then, that transfer costs are low, and although some females may reside for some time in groups containing relatives, many transfer several times and live in groups without kin other than offspring (Watts, 1990, 1996). Harcourt, (1979a) reports that females were involved in few agonistic interactions, and most received more agonism from the silverback than they did from other females. Watts (1997) however shows that although some females receive little agonistic support from other females, some do, and at rates comparable to species including most cercopithecines (in which female philopatry is present). Aggression among females was most frequent during feeding, but rarely led to individuals losing out in access to food (Watts, 1994b): little evidence of reconciliation between females has been observed. Harcourt, (1979a) reports few affiliative interactions between females, with most relationships best characterised as showing 'tolerance'. Watts (1994a) notes that female relatives were more tolerant in their female-female interactions than non-relatives, and also that they groomed more, and more often with other females than those without female relatives in the group. In general though, most female relationships were neutral, showed bi-directionality, or showed temporal variation suggesting they may have been of limited long-term value (Watts, 2001).

Early findings suggested that resident females were not aggressive to female immigrants (Stewart & Harcourt, 1987). This might be expected given that the conditions leading to low transfer costs should also allow for tolerance of new group members. However, Watts (1991b) reported frequent harassment of immigrant females in one large group of mountain gorillas, following the immigration of a large number of new females. The unusual reaction of the resident females in this case was explained by their high degree of relatedness, the number of immigrants involved, and the inability of the two silverbacks to control such behaviour (Watts, 1991b). While an already large group receiving large-scale immigration may provoke important levels of within-group feeding competition, it has been suggested that another resource contested by female mountain gorillas is access to the silverback (Watts, 1994b) who provides protection from predators, potentially infanticidal males, and possibly indirect protection from other group individuals.

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Female relationships in mountain gorillas are not merely a product of the influences of food availability and the freedom to transfer. Males exert a strong controlling influence on female behaviour and relationships. Silverbacks are known to intervene to stop female-female aggression, and mostly do so without showing preference for either opponent, although breaking up a fight could be seen to somewhat give support to the original target of the aggression (Watts, 1997). Such 'Control Interventions' (de Waal, 1982) further negate any potential benefits of female dominance within groups. Male interventions were also noted during the harassment of new immigrants by resident females, although it was notable that in the group studied by Watts (1992) in which an older and a younger silverback were present, the elder male only intervened in support of older residents, while the younger male intervened in situations in which immigrants may have gained support, thus possibly forming bonds with them and reducing their likelihood of transferring again. As a consequence of this, immigrant females spent more time in proximity to the young silverback (Watts, 1992).

Outside of male interventions in female agonism, most male-female agonism involved displays that appeared to advertise the silverback's fighting ability or 'agonistic prowess', and provoked submission and reassurance-seeking behaviour among females (Watts, 1992). Other agonism was connected with silverback displacements of females from feeding sites, and was typically achieved by approach only, occasionally with the addition of cough-grunting (cough-grunts by silverbacks were mostly made during feeding). Finally, the 'herding' or agonistic manoeuvring of females during intergroup encounters is a characteristic behaviour of mountain gorilla silverbacks, which is apparently aimed at preventing emigration, and is mostly observed in multi-silverback groups (Sicotte, 1993).

Western lowland gorillas

As already described, the diet of the western lowland gorilla is very different to that of the mountain gorillas. Fruit is eaten whenever available, and most habitats support a less abundant supply of herb foods than is present in the Virungas. Several effects of this variation in food type and availability have been proposed, and are discussed by Doran &

McNeilage (2001). Within-group scramble competition is predicted to limit group size (Malenky et al., 1994), as are associated limits to group spread (Doran & McNeilage, 2001). This study (Chapter 4) shows that group size does not differ significantly between western and mountain gorillas, although there is a suggestion that maximum group size may be limited by herb density (Lossi and the Virungas having the largest groups on record). Group size did differ significantly within western lowland gorillas, however; once again, super abundant herbs at Lossi were implicated in facilitating the creation of the largest groups. Average day range of western lowland gorillas is over twice that of mountain gorillas, and home range size is at least twice as large (Doran & McNeilage, 2001), although foraging for fruit is thought to be the causal agent for this rather than extended searching for sparsely distributed herb foods. In addition to reduced herb density, the greater utilisation of fruit by western lowland gorillas may lead to increased intra-group contest competition, both through the more patchy distribution of fruit trees, and the limited number of feeding sites within a given tree (e.g., Remis, 1999).

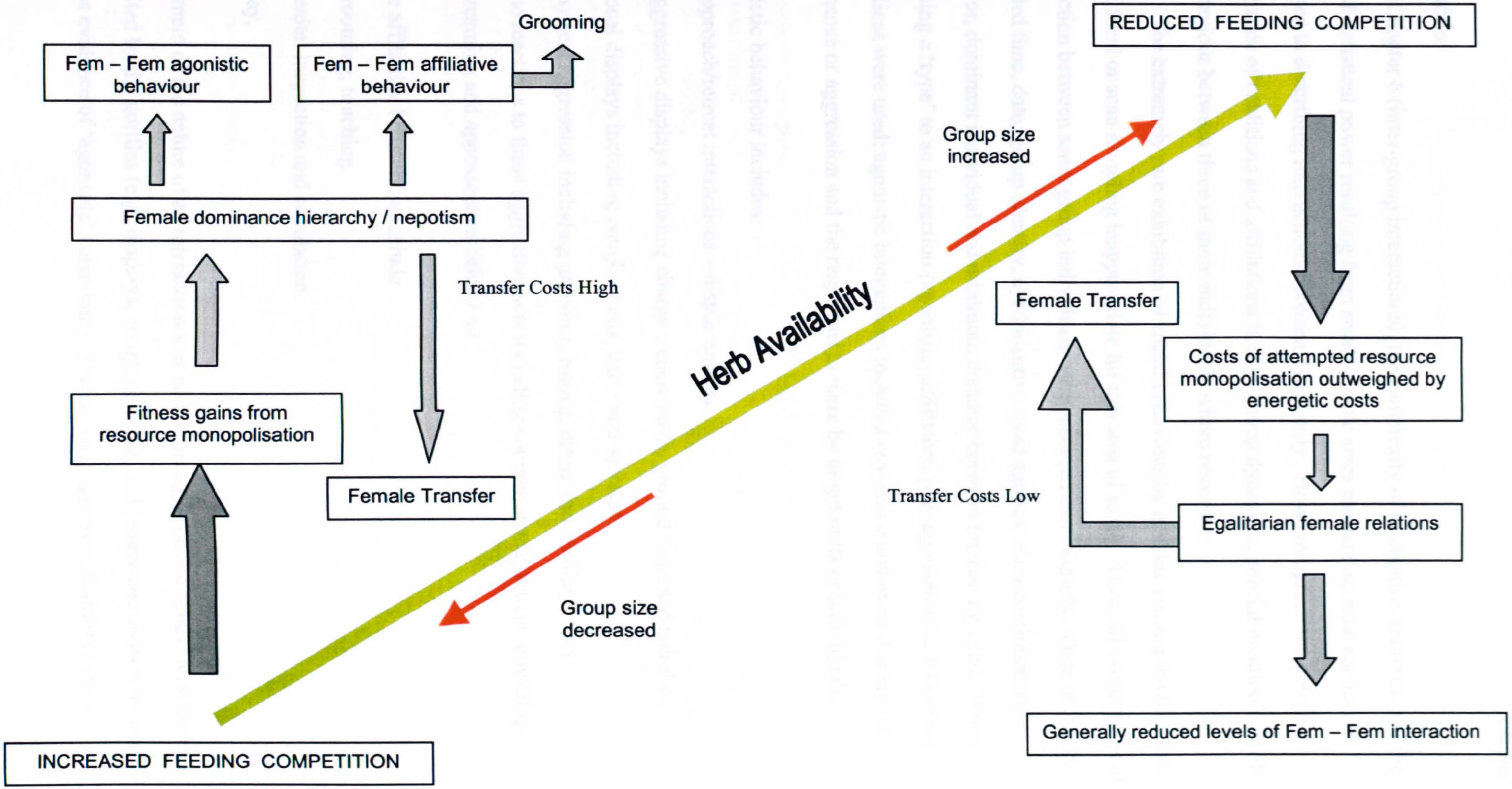
No study has yet examined the extent to which intra-group relationships might vary in the western lowland gorilla. Reports on intra-group social behaviour in the species are essentially non-existent due to a lack of habituated subjects, though it has been established that female transfer and male emigration does occur (Tutin, 1996; this study – Chapter 4). The following hypothesis and predictions should thus guide an examination of the data from Mbeli:

Should less abundantly distributed herb resources and patchily distributed fruit foods incur fitness costs on females through the influence of contest competition, the value of a dominance hierarchy and female philopatry may be increased.

In comparison to food plants in mountain gorilla habitat, herb foods are less abundant in the forest surrounding Mbeli, as they are in the habitats of most western lowland gorillas. Although an accompanying rise in feeding competition has not been shown conclusively, there is evidence (above) to suggest that this is a potential outcome. If these conditions are of sufficient magnitude (although it is not yet possible to quantify 'sufficient'), then female relations can be predicted to betray this in following ways: a) agonistic interactions may be more frequent than in mountain gorillas and show stable uni-directionality in outcome; feeding displacements may be common, as may agonistic support interactions; b) females should show increased levels of affiliative behaviours such as grooming, as a means of maintaining and strengthening bonds and alliances; such behaviours should be most frequent among any relatives present, but also extend to non-relatives; c) females should show intolerance towards female immigrants, especially in larger groups. Figure 5.1 summarises some of the hypothesised effects of herb availability on female relationships (without the influence of male behaviour). At this stage, access to fruit resources in not included, but can be generally thought to act, if at all, in agreement with the model (i.e., fruit may be considered a limited and potentially monopolisable resource likely to increase competition). The green arrow represents the central 'axis' of the model, with the flow items on the right being the result of higher herb availability and thus reduced feeding competition, and the items on the left being the result of reduced availability and increased competition.

There are several problems that may confuse the examination of these predictions at Mbeli. Firstly, the abundance of aquatic herbs in the bai may mask competition effects present when feeding on terrestrial herbs. Although the likelihood of this is high, the fundamental nature of female relations should nevertheless be visible due to the large number of hours of observation amassed. Secondly, whatever the apparent gains to be made through the establishment of a dominance hierarchy, silverback intervention in female conflicts, if present, may suppress the exhibition of related behaviours. Finally, effects on social relationships within the group may be minimised by the adjustment of group-size and/or group-spread while feeding.

Figure 5.1 Predicted effects of variation in food availability with regard to female relationships in gorillas



Methods

As in Chapter 6 (inter-group interactions), the complexity of interaction analyses, and the lack of statistical power resulting from small sample sizes means that most results are confined to describing interactions between dyads only. However, given the potential importance of coalitions and affiliations in intra-group dynamics, special mention is made of behaviour between three or more individuals where necessary.

The extremely rare exhibition of social behaviour by gorillas visiting the bai made use of focal or scan sampling inappropriate for this area of study. Thus, all occurrences of interaction between same-group individuals were recorded continuously. Data recorded included time, date, group identity, dyad identity, dyad age/sex-class combination, initiator, dominant individual and minimum distance between interacting dyad. When assigning a 'type' to an interaction (agonistic, affiliative, play agonistic) the following guidelines were used: agonistic interactions included any active and overt displays of dominance or aggression and the responses to these by target units or individuals.

Agonistic behaviour includes:

- Approach/retreat interactions – displacements.
- Aggressive displays including charges, chest-beats, ground slaps and splashes.
- Vocal displays including cough-grunts, barks and screams.
- Physical aggression including grabbing, hitting, biting and holding down.
- The reactions to these aggressive acts including counter-attack, retreat, cowering, screaming and appeasement behaviour.

Active affiliative behaviours include:

- Grooming, touching.
- Genital inspection and copulation.
- Play.

Judgement of the nature of an interaction was based primarily on the behavioural elements exhibited by the gorillas (e.g., displays, cough grunting, and lunges and slaps were largely seen as evidence of 'agonistic' behaviour). It was noted, however, that these same elements were frequently used by immatures during bouts of play. In other words, the nature of an interaction is not merely a function of the elements employed, but is also context dependent.

Play was easy to detect in juvenile gorillas, being the predominant social behaviour not connected to the mother. Play bouts frequently included chasing, chest-beating and wrestling, and were identifyable as play by their long duration, the regular, equitable swapping of roles, exhibition of a 'play-face' and the lack of any screaming or attempts to rejoin the mother. Under such circumstances, it was appropriate to record such behaviour as 'affiliative'. Greater difficulty was encountered when labelling the interactions of older immatures, and in particular, blackback males. Central to this issue is the notion that play behaviour serves to equip the developing individual with the skills needed for real situations later in life. As an individual nears adulthood, the line between playful 'practice' of adult behaviours, and genuine adult behaviour may become blurred. At Mbeli, dyadic interactions between blackbacks and other older immature males looked considerably more serious than the play exhibited by juveniles, and yet it seemed that on some such occasions, the males were boisterously 'showing off' to their contemporaries, rather than engaging them in serious aggression. Such an anthropomorphic judgement is intrinsically open to error, and yet it seemed reasonable to identify a sub-set of such 'play agonism' interactions from the data on agonism, such that the examination of both agonism and affiliation is not derailed by ambiguous records.

In order to score the intensity of agonistic (and play agonistic) interactions, a four point intensity scale was employed and each interaction scored within it:

1. Distant displays, or approach-retreat displacements without vocalisations or display.
2. Displays at less than 30 meters. Vocal or display displacements.
3. Mild contact aggression: slaps, grabs, pushes etc. Unlikely to cause injury.
4. Severe contact aggression: biting, hitting etc. Likely to cause injury.

When comparing frequency of interaction for different age/sex-class combinations from different groups, it was first necessary to account for the potential for interaction based on: a) the time the group was under observation during the study period, and b) the number of possible dyads in the group. For inter-unit interactions (Chapter 6), the complexity of calculating the time available for any two individuals in separate groups to interact influenced the decision to use instead, the number of *visits* any two given units spent in simultaneous bai-use. This was acceptable on the grounds that only one interaction by any given individual was usually recorded on any one given visit, and visit length was considered a relatively minor influence on the frequency of interaction. Data for intra-group interactions show a considerable number of cases where the same individual interacts more than once during a single visit. This, and the greater ease with which 'time available' could be calculated, permitted the consideration of 'interactions per hour of potential-dyad time' as the unit of measure. For each of the dyad combinations of age/sex-classes 'adult female', 'silverback' and 'blackback' (for the purposes of this analysis, this includes young silverbacks still in their natal group), the total number of dyad-minutes under bai observation was calculated. For instance, in CLI group, three adult females (af) were present throughout the study period, permitting expression of intra-group behaviour between them in three dyads: the group spent a total of 10750 minutes (converted to 179.2 hours) in the clearing, thus the total time 'available' for af-af interactions within the group was 179.2 multiplied by 3, equalling 537.5 hours. By contrast, only one female was present in MOS group, and as such, no af-af interactions were possible. The actual number of dyadic interactions per age/sex-class combination from each group was then divided by the value calculated for dyad-time. Finally, the resulting index values were multiplied by 100 for ease of presentation.

Despite roughly 1681 hours of data collection, so few intra-group interactions were recorded for each adult sex-class combination, that it is almost impossible to examine the data with a strict adherence to statistical independence. Partly as a consequence of this, relative frequencies of behaviour cannot be used in comparisons with data from mountain gorillas. As such, the emphasis placed on the results that follow, must rest firmly on a presence/absence approach (were key behaviours witnessed or not?), and a qualitative, contextual description of the nature of such interactions. While less compelling than a complete statistical analysis, this method may be sufficient to signpost the basic principals at work in within-group relationships, and suggest areas for future study.

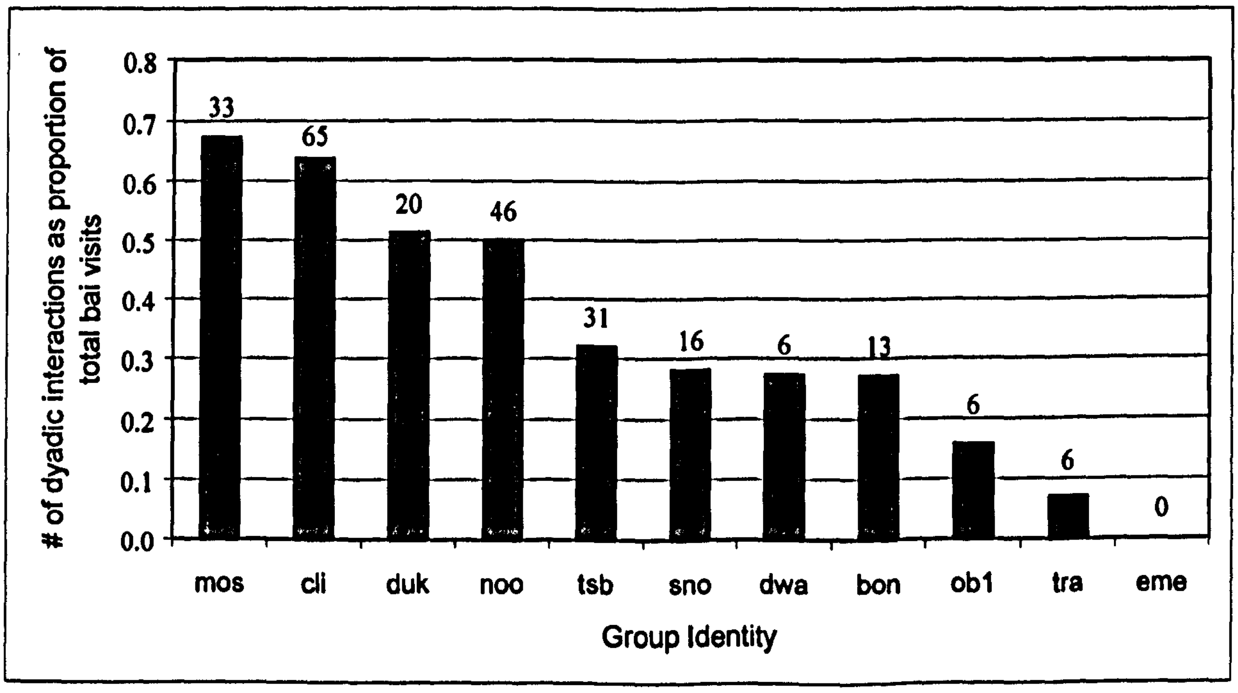
(N.B. Throughout the text, where dyad types are denoted by abbreviations (e.g., af-sb), no directionality in initiation or dominance is implied by the order of the symbols, which for consistency, are listed alphabetically.)

Results

Frequency and group variation

In total, 244 independent dyadic interactions (all age/sex-classes including immatures) were recorded between members of 11 social groups. The number of interactions recorded per group varied widely, and interactions per group were found to correlate positively with the number of visits made to the bai (Spearman Rank Correlation; $r_s = 0.771$, N = 11, $P = 0.006$). Given this bias, Figure 5.2 expresses the number of dyadic interactions per group as proportions of the total number of bai visits made by each group.

Figure 5.2 Frequency of intra-group dyadic interactions per group



Values above columns are the actual number of dyadic interactions per group. Group 'Geo' are omitted due to the extremely inconsistent number of individuals both in the group and in entering the bai.

In order to explore the observed variation further, the variables 'total group size', and the 'proportion of immatures in each group' were tested for correlation with the frequency of dyadic interaction per group expressed as a proportion of total visits. Total group size is an obvious potential factor given the prediction that the more individuals present, the greater the chances for expression of the behaviour. The proportion of immatures is examined as such individuals can be predicted to interact at particularly high rates due to the incidence of play behaviour (use of this variable inevitably examines the effect of adult proportion simultaneously, depending on the direction of any correlation found). Neither variable showed a significant relationship (group size-interaction frequency: $r_s = -0.276$, $N = 11$, $P = 0.412$: immature proportion - interaction frequency: $r_s = -0.132$, $N = 11$, $P = 0.699$). This result poses interesting questions regarding the personality of individuals within such groups as CLI and MOS, as opposed to groups like OB1. The latter contained more individuals than either of the former groups and an equivalent or slightly higher proportion of immature group members, and yet exhibited a much reduced proportion of intra-group dyadic interaction. In the case of EME group, only having made nine visits to the bai may in itself have greatly reduced the chances of intra-group interaction being witnessed. However, even the removal of this group from the analysis does not alter the overall outcome of the above tests.

The number of visits made may have other effects: an unfamiliarity with the bai could be a potential inhibitor of normal frequencies of behaviour. With only nine visits, EME group may have been particularly shy or vigilant, thus precluding other behaviours. Yet no significant correlation was found between the number of visits per group and the corrected interaction frequency proportion ($r_s = 0.509$, $N = 11$, $P = 0.110$).

General nature of interactions

Before embarking on a more detailed break-down of interactions by age/sex-class, some general characteristics of intra-group interaction can be presented. Table 5.1 shows the frequency of interactions of different 'types' for all individuals and groups. In the two left-hand columns, all agonistic behaviour-patterns clearly not within a play context are pooled. In the right-hand columns, agonism scores are adjusted and consequently reduced by the establishment of a 'play-agonism' category for interactions where, for the contextual reasons discussed in the Methods, the behaviour witnessed did not appear to be genuinely agonistic, but was more akin to high-spirits or teasing.

Table 5.1 Interaction-type for all dyads, including and excluding play-agonism

Interaction-type	No. of interactions	%	No. of interactions (incl. play agonism).	%
Agonistic	131	53.5	118	48.5
Affiliative	104	43	104	43
Unknown	9	3.5	9	3.5
Play-agonistic	-	-	13	5
TOTAL	244		244	

Table 5.2 compares the percentages expressed in the right-hand column of Table 5.1 with those from the analysis of inter-unit dyadic interaction types (Chapter 6, pg. 286).

Table 5.2 Comparison of intra- and inter-unit interaction-type proportions

Interaction-type	% of intra-group total interactions	% of inter-unit total interactions
Agonistic	48.5	60
Affiliative	43	24
Unknown	3.5	(Other) 2
Play-agonistic	5	14
N =	244	208

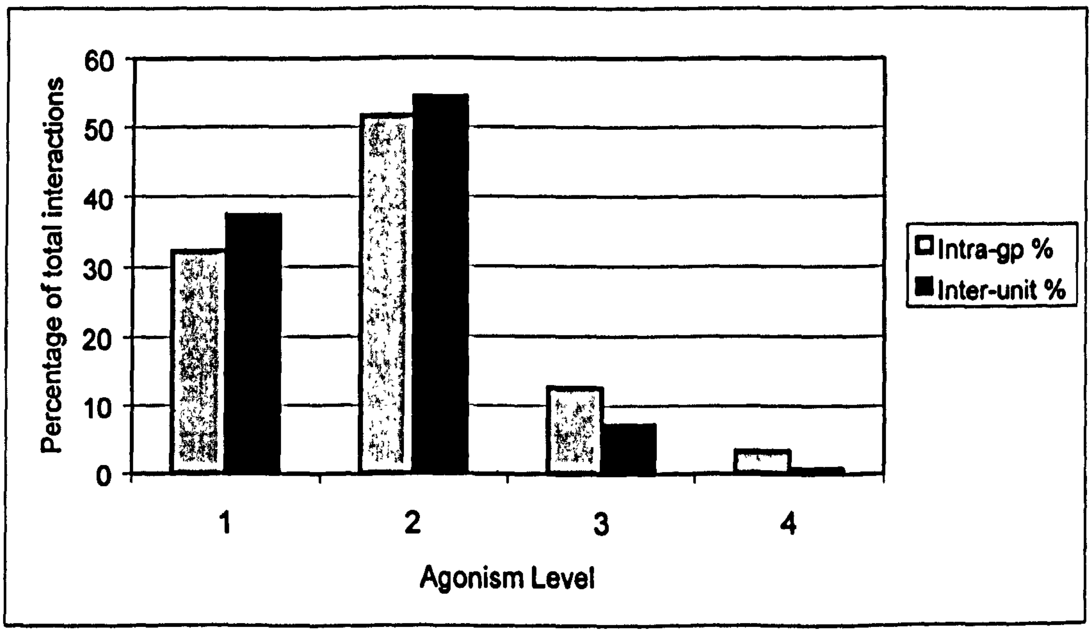
Table 5.2 indicates that intra-group interactions are in general less agonistic and more affiliative than those between individuals of different units. Play-agonism is over twice as frequent during inter-unit interactions than during intra-group encounters. Further analysis of interaction-type within age/sex-classes is required to explain these differences.

The mean minimum intra-dyad distance during interaction (including zero scores where contact was made [mother-offspring interactions excluded]) was 1.7m (SD = 1.9, N = 227). Using medians, minimum intra-dyad distance was compared between intra-group and inter-unit pairs (medians were 1.0m and 4.0m respectively), and the difference in medians found to be highly significant (Mann-Whitney *U*-test: $U = 11234$ [$z = -7.402$], N1 = 227, N2 = 172, $P < 0.001$).

Figure 5.3 compares agonism level scores from agonistic intra- and inter-unit dyads, using the intensity scores given in the Methods (1 = Distant displays; simple approach/retreat interactions without display or vocalisation; 2 = Close-range non-contact interaction with vocal and/or physical display; 3 = Interaction with contact unlikely to cause injury; 4 = Severe contact aggression liable to cause injury).

The chart shows that non-contact agonism is shown by the majority of dyads, with close displays more common than distant displays and simple approach/retreat displacements. Frequency of agonism level scores (expressed as percentages of the total number of agonistic interactions) are similar for both intra- and inter-unit dyads.

Figure 5.3 Agonism level during dyadic agonistic interactions: intra-group and inter-unit comparison

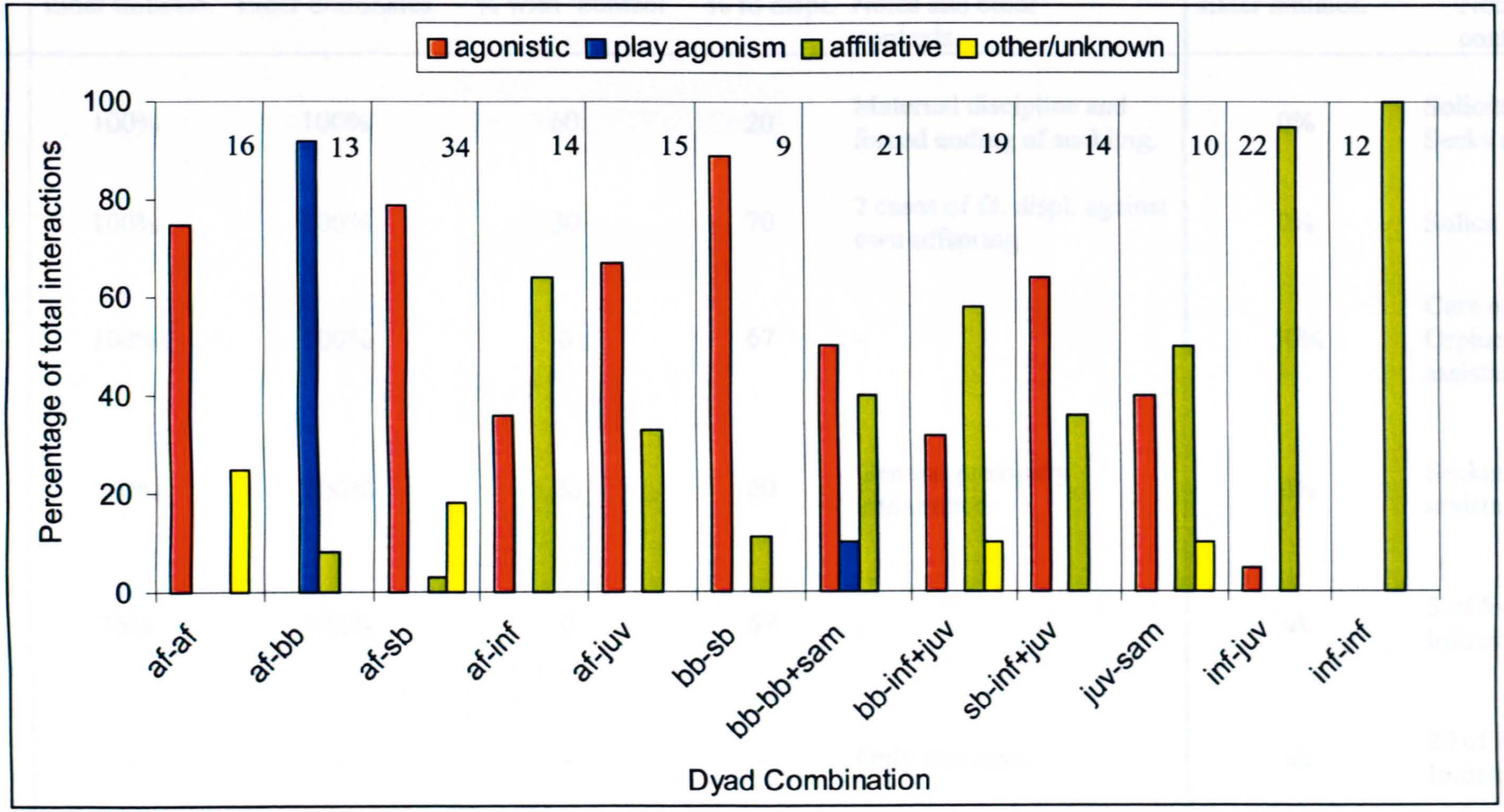


Severe contact aggression is rare in both situations, but mild contact was almost twice as common in the intra-group context. Potentially injurious contact was only witnessed once during inter-unit encounters and three times during intra-group interactions.

Summary of all interactions by age/sex-class

Figure 5.4 gives the percentage of each dyad type's total intra-group interactions that were either agonistic, affiliative, play-agonistic, or other/unknown. Most dyad types are represented, though notable exceptions are dyads involving sub-adult females and sub-adults of unknown sex. Too few interactions were recorded involving these individuals and the lack of precision regarding their sex make analysis of little value. Small sample sizes also prompted the collapsing of infant and juvenile classes, and blackback and sub-adult male classes in certain combinations. Table 5.3 gives additional data on these interactions. Adult interactions, which form the main focus of this chapter, are described separately in the following section.

Figure 5.4 General context of dyadic intra-group interactions for most age/sex-class combinations



Values next to columns are the numbers of actual interactions represented.

Table 5.3 Summary data on non-adult-adult intra-group interactions at Mbeli

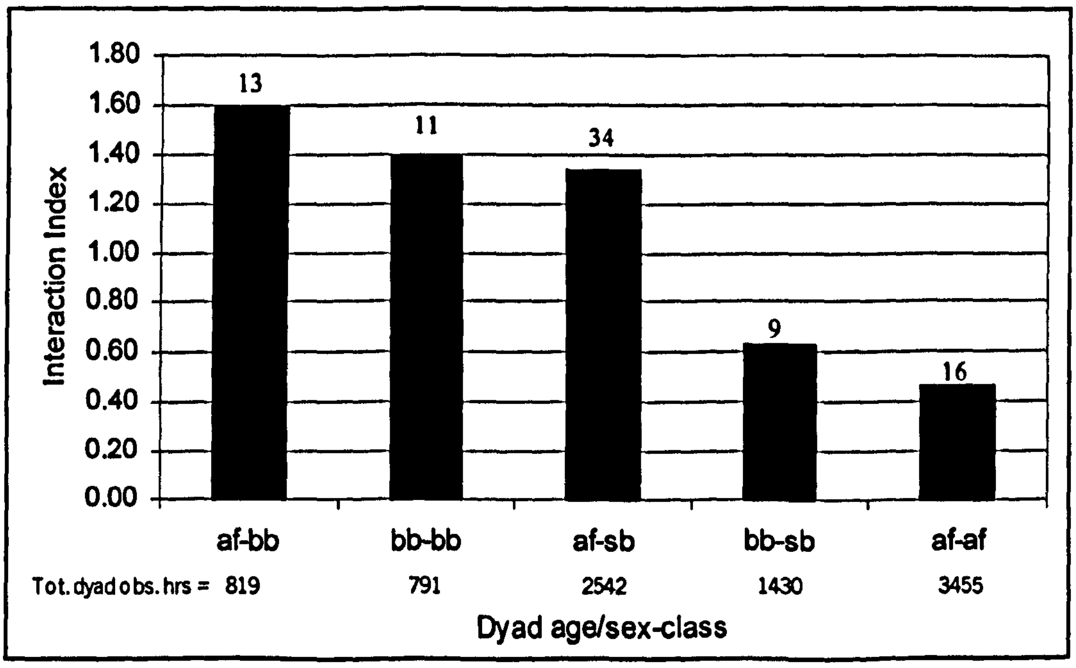
Dyad type	AGONISTIC INTERACTIONS					AFFILIATIVE INTERACTIONS	
	Elder initiates.	Elder dominates.	% with 'contact'	% fd displ.	Notes and other contexts.	Elder initiates.	Notes and other, contexts.
af-inf	100%	100%	60	20	Maternal discipline and forced ending of suckling.	0%	Solicits suckling. Seeks assistance.
af-juv	100%	100%	30	70	2 cases of fd. displ. against own offspring.	0%	Solicit assistance.
bb-inf/juv	100%	100%	0	67	-	50%	Care of injured juv. Orphan seeks assistance. 64% play.
sb-inf/juv	100%	100%	20	60	General proximity intolerance.	0%	Seeking contact, assistance or play.
juv-sam	75%	100%	0	67	-	uk	5 of 6 cases play. Initiator unclear.
inf-juv	-	-	-	-	Only one case.	uk	20 of 21 cases play. Initiator unclear.
inf-inf	-	-	-	-	-	uk	All cases play.

fd. displ: feeding displacements. Sample sizes available in Figure 6.3.

Silverback, adult female, and blackback interactions

Figure 5.5 shows the interaction index (*see* Methods) for each adult age/sex-class combination. The nature and direction of the interactions represented by the columns in the chart are discussed in detail in the following section. Notably, however, blackbacks and females were the most 'interactive' combination (almost all such interactions being initiated by males). For the relatively few dyad-hours possible for blackback-blackback combinations, their actual rate of interaction was quite high, followed by interactions between silverbacks and adult females (which were the most numerous in absolute terms). The rarest interactions were between silverbacks and blackbacks, and especially between adult females and adult females, who had the highest potential rate of interaction (based on number of dyad hours), but a relatively low absolute number.

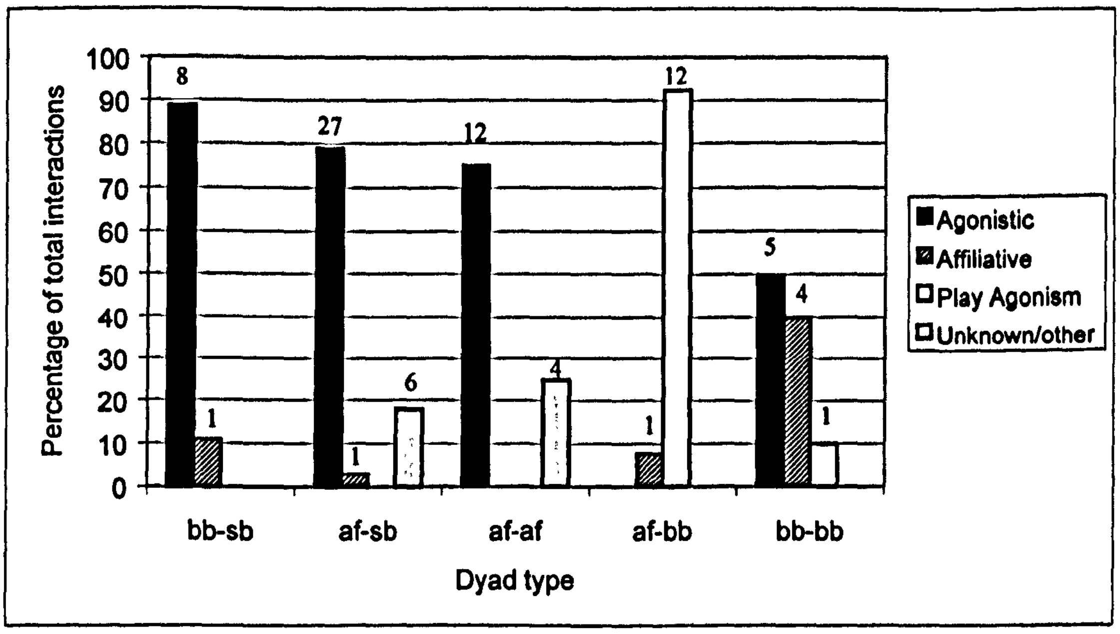
Figure 5.5 Interaction index scores for each age/sex-class dyad.



Values above columns are the number of interactions taking place: values below columns are the total number of dyad-hours of observation conducted on the given age/sex combination.

In Figure 5.6, the interaction type for each dyad combination is shown as a percentage of their total interactions. Despite the low number of interactions represented, agonistic interactions clearly dominate. In af-bb interactions, play agonism is the predominant type. Interactions between blackback males showed the highest level of affiliation relative to agonism.

Figure 5.6 Interaction type per age/sex-class dyad as a percentage of total interactions



Values above columns are the number of interactions taking place.

Table 5.4 gives the number and percentage of the agonistic interactions shown in Figure 5.6 that included contact aggression (level 3 – mild contact; level 4 – severe contact, capable of causing injury). Sample sizes are extremely low, but it is likely that the high rate of contact aggression among adult females and between females and silverbacks is a genuine reflection of greater seriousness of these interactions.

Table 5.4 Frequency of contact aggression per age/sex combination

Dyad type	Number of interactions	Freq. agon level 3.	Freq. agon level 4.	Tot. contact aggression	Percentage of total.
af-af	12	2	1	3	25
af-sb	27	3	3	6	22
bb-bb	5	1	0	1	20
af-bb	12	1	0	1	8
bb-sb	8	0	0	0	0

Blackback – Blackback interactions

Only two groups at Mbeli had the potential for blackback-blackback interactions; NOO and TSB. In TSB group, the eldest blackback (bb) disappeared from the group at the same time as two sub-adult males became bb. Therefore no interactions were possible between blackbacks of different ages. The eldest bb did interact with one of the sub-adult males before they turned to bb, however. Over the course of one week, five independent interactions were recorded on separate days between the elder Redstripe and the younger Salaam (another similar interaction took place some months later). All were agonistic; four were initiated by Redstripe, and in all five, the elder male was dominant. Three were displacements (two directly connected to feeding location), and two appeared to be general intolerance of proximity. However these are all likely to be proximal explanations; the concentration of agonism between these individuals over a relatively short period may be evidence of a systematic imposition of Redstripe's dominance over Salaam. The attacks were unprovoked and most involved aggressive approaches with cough grunting. One occasion of particular note is described in Appendix A5.1. This example raises the question of whether an older male may seek to intimidate a subordinate younger half-sibling to such an extent as to prompt his premature emigration from the group. This could be envisaged as beneficial were there any evidence that natal males take over leadership of their group as the silverback becomes old or infirm. However, this did not appear to be the case at Mbeli.

Only one example of affiliative interaction between older immature males was observed in TSB group. Isaak, who was still a sub-adult at the time of the encounter, ran to aid Redstripe after the latter suffered a particularly aggressive attack from a solitary male. The two group members then charged the solitary male together causing him to retreat. Such support intervention or coalition forming may benefit the younger aid-giver either through increasing his chances of receiving similar aid in future, or possibly in decreasing the likelihood of agonistic attacks such as those suffered by Salaam (above).

Following the block-emigration of adult female Margo, her juvenile Iook, and blackback/sub-adult male Dougal from the collapsing FFF group to the silverback and bb/ysb of MOS group, no agonistic interactions were observed between the Dougal and the new bb/ysb. However, Dougal disappeared from the group (probably having emigrated) only 10 months after the group merge at a time when his estimated age was a mere 8.3 years. This is approximately four years earlier than we would expect natal emigration to begin in males. Whilst his having died cannot be ruled out, it seems reasonable to suggest that as an older male, his residency in a group already containing a non-kin bb/ysb, was a sub-optimal situation for him, both in terms of receiving silverback protection during inter-group encounters, and possibly due to aggression from the bb/ysb.

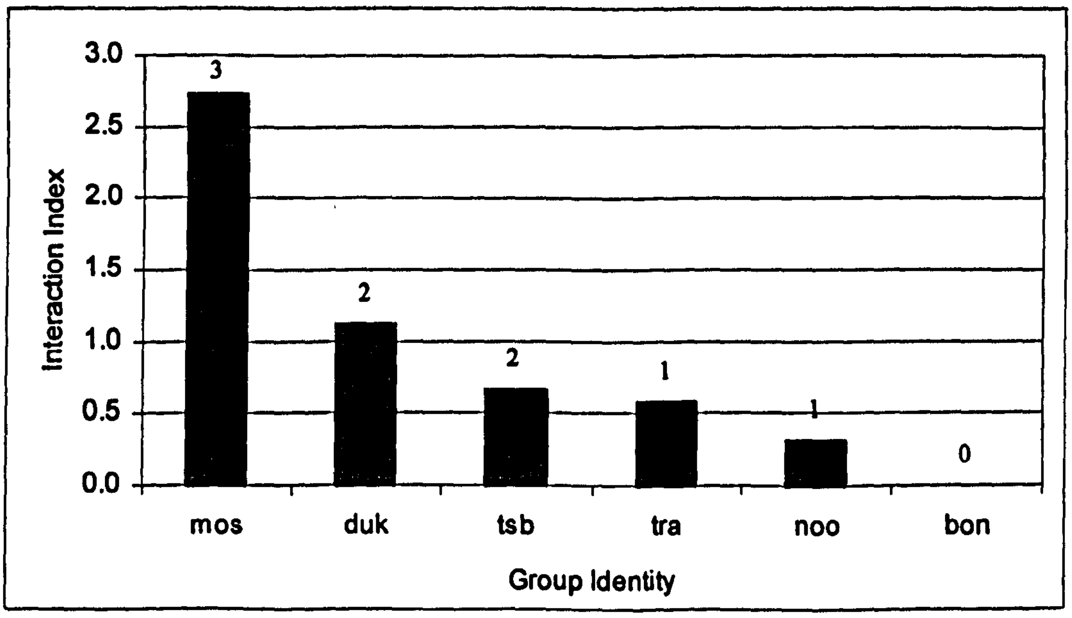
The only other case of an older male transferring to a new group was that surrounding the collapse of BON group, due to the disappearance (almost certainly death) of the group's aged silverback. After two bai-visits without their silverback the remaining members (af, older bb, juv, younger bb) all joined NOO group. Although the merge can be described as generally calm, within the first three months, five agonistic interactions between blackbacks were observed. Four of these involved the eldest of the blackbacks, Gretsky, who was one of the immigrating ex-BON members, and in three of these, he was the dominant individual (in the fourth case, silverback Basil sat between the displaying males, effectively bringing their exchange to an end). These interactions were characterised by cough-grunting and approaches, either in feeding displacement, general proximity intolerance, or in one case, when Gretsky intervened to assist Martha (an adult female who transferred with him), who was being harassed by a younger blackback from NOO group. In this case, Gretsky overpowered the younger male and held him down for several seconds. These interactions suggest that despite immigrating from another group, Gretsky set about asserting dominance over the younger natal blackbacks and sub-adult males of NOO group almost as soon as he arrived in the group. Perhaps surprisingly (with the possible exception of the blocking example above), no attempts at intervention weighted towards the natal males were made by the group silverback Basil, despite the potential loss to his own genetic success due to costs of harassment and lower dominance suffered by his male offspring. By contrast, the younger immigrant male (approximately eight years old) was only once targeted with agonism by an original member of NOO group, but was involved in three affiliative play interactions with his new group-mates.

In total, 11 interactions between blackbacks were witnessed: six were agonistic, one was play agonism, and four were affiliative play interactions. If the age-class is stretched to include encounters between blackbacks and sub-adult males (6-8yrs old), a further 11 interactions were recorded. Nine of these were agonistic (in all of which, the elder gorilla 'won' the encounter), and two were affiliative. Although few data are available, there is evidence to suggest that immature males at Mbeli do occasionally compete with each other for positions of dominance within a group. However, given that all males eventually emigrated from their natal groups, such dominance as may have been gained could only be temporary and affect little more than access to easily monopolised feeding resources (unless half-brothers consider each other future competition for females following emigration to solitary status).

Blackback – Silverback interactions

Figure 5.7 displays the interaction index for all six groups in which blackbacks were present. Considerable variation is evident, with at one extreme, BON group, where no interactions were recorded, and at the other, MOS group, where the blackback and silverback interacted at over twice the frequency of the nearest other group.

Figure 5.7 Interaction index for blackback-silverback intra-group interactions



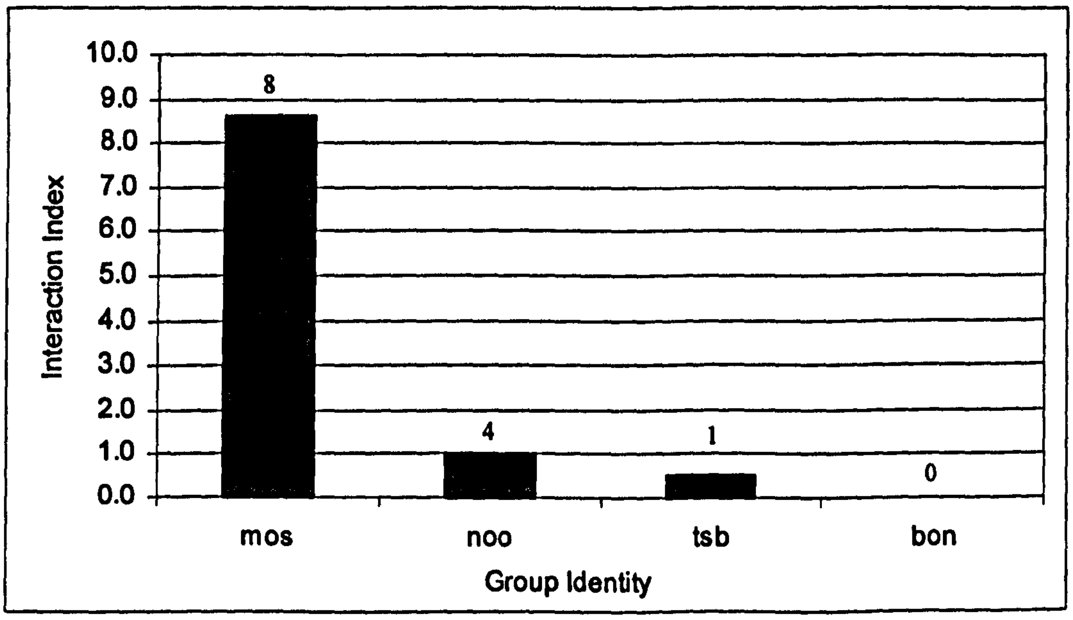
Values above columns are actual numbers of interactions per group per combination-type.

However, only nine interactions contribute to this distribution, so little can be explained by the data. Eight of the nine interactions were agonistic, and all of these were initiated by the silverback, who was dominant in every encounter. The context of seven of the eight agonistic interactions, was feeding displacement, and in the other case, general proximity intolerance. Displacements were achieved by simple approach, combined in five cases with cough-grunts (*see* Appendix A5.2). Median aggression level was two. Only one possible example of affiliative interaction between sb and bb was recorded (a coalition defence of a sub-adult male from an aggressive attack by a solitary male – Appendix A5.3).

Blackback - Adult Female interactions

Interactions of such dyads produced the highest interaction index score of the five combination classes. Thirteen interactions took place between blackbacks and adult females in 819 dyad hours of observation; a sample size that is once again too small to deal with at a level independent of bias from the effects of individual gorillas. Only four groups for whom sufficient observation time was achieved had compositions permitting these interactions, and as Figure 5.8 shows, interactions took place in three. Only a single female and blackback were present in each group, further limiting the possibility of independent analysis.

Figure 5.8 Interaction index for blackback-adult female intra-group interactions



Values above columns are actual numbers of bb-af interactions per group.

In all but one of the thirteen cases, the initiator was the blackback. Type and context were difficult to assess in most interactions: outwardly, all but one of the interactions by blackbacks on adult females were agonistic. All consisted of charges, frequently accompanied by chest beats or ground-slap/splash displays. On only one occasion was physical contact made; a powerful push from behind. Although containing agonistic elements, all of these interactions were scored as 'play agonism', for the following reasons;

1) the demeanour of the males was relatively playful, and most resembled 'teasing'; 2) in all but two such cases, the female ignored the male's behaviour and continued feeding; 3) in no cases did blackback 'agonism' ever provoke intervention by the silverback (this last point might not be appropriate were immature male agonism to reinforce silverback behaviour aimed at preventing females from emigrating). The only intervention witnessed in the context of blackbacks and adult females was by elder blackback Gretsky, in defence of Martha, an adult female with whom he had emigrated into NOO group. The initial agonism was initiated by younger blackback Parsley, a natal resident of NOO group (*see* Appendix A5.4).

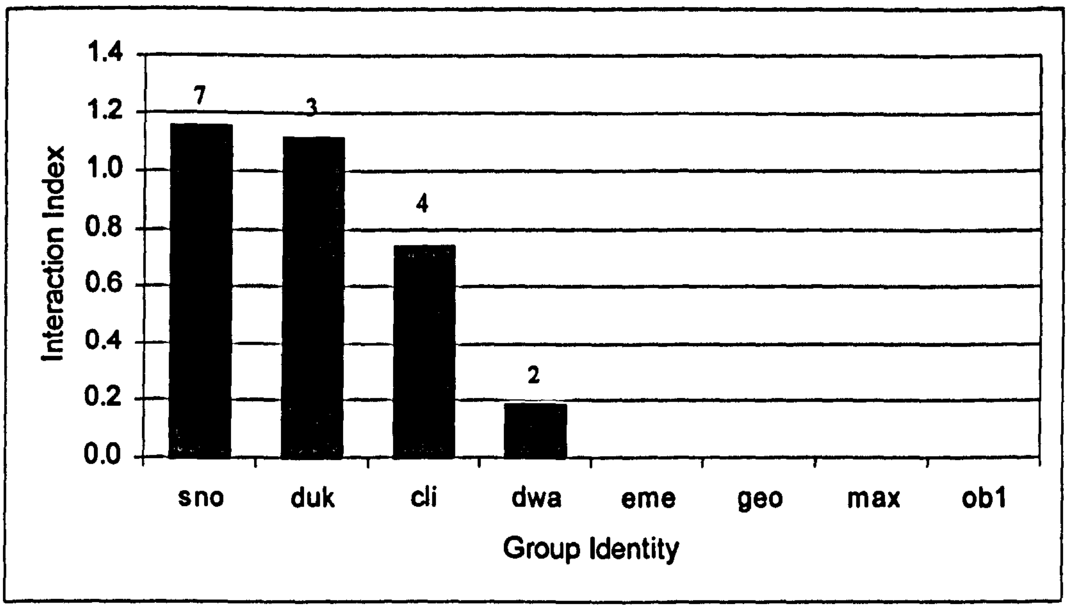
BON group, where no interactions took place, was a 'mature' or 'established' group, with an elderly silverback, his putative blackback son, a sub-adult male, the adult female Martha, and her juvenile son Muffin. No interactions between blackbacks and adult females took place in NOO group at a time when the only adult female was an elderly long term resident of the group. However, as mentioned earlier, upon the death of BON group silverback, the remaining members of his group joined NOO group, and it was only at this time that bb-af interactions took place within the group, initiated by the resident males and directed at the immigrant female. The same pattern may have applied to the interactions observed in MOS group (the unit showing the disproportionately high relative frequency of bb-af interactions in Figure 5.8). The target of all interactions in the group was the recent immigrant Margo, who with her juvenile son, joined the group which at the time consisted only of a silverback and his putative son (bb). During the brief time her previous group was observed with a putative natal blackback, no interactions between them were observed. On joining MOS group, however, she became a focus of attention for the group's resident blackback. This individual, Homer, appeared perhaps more than most gorillas, to have a generally 'pleasant' and playful personality, and his approaches to Margo appeared particularly light-hearted. On one occasion, although Homer's behaviour involved a display run past Margo, they were later seen following one another and feeding in close proximity. Homer was noted, furthermore, as the only male of his age-class to play affiliatively with a juvenile (Martha's son), and once even appeared to comfort him when he had suffered a temporary injury. The single overtly 'affiliative' interaction represented by the data was between Homer and Margo, and involved Homer prodding Margo's ano-gential region then sniffing his fingers. He then sniffed at her shoulders before standing directly in front of her and staring hard at her face for several seconds. She did not react in any visible way, and merely sat to feed. The group silverback made no moves to intervene in any of Homer's approaches towards the new female.

In a final example of bb-af interactions, TSB group bb Isaak had been sitting watching the group's only adult female nursing her newborn infant ventrally. After two minutes, the two got up to move away and Isaak charged past them chest-beating. The female raised one arm up in defence, but the interaction ended there and both then resumed feeding some way apart. The group silverback did not react to the exchange. The female in question had been a member of the group as a sub-adult female, but had emigrated and been absent for over a year. The interaction took place some months after her return to the group.

Adult female – Adult female interactions

In total, 3455 dyad-hours of observation were amassed on females; the highest in the study. Yet only 16 actual interactions were witnessed, thus producing the lowest interaction index score of the five dyad classes. Figure 5.9 shows the distribution of index scores across Mbeli groups containing more than one adult female. Interactions were noted in only four of the eight groups in which they were possible, however of the four not showing interactions, GEO and MAX groups together only contributed 99 dyad hours, and EME group only 235 to the total. Only thirteen individuals are involved in the 16 interactions observed, forming 10 independent dyads.

Figure 5.9 Interaction index for adult female-adult female intra-group interactions



Values above columns are actual numbers of af-af interactions per group.

Female agonism

Of the 16 interactions witnessed, 12 were agonistic. The median agonism-level was two, but the distribution contained two examples of mild contact aggression, and one of severe aggression. No examples of play-agonism or exuberance were recorded between females. In CLI group, all four interactions were agonistic, and in three of these, the context could best be described as 'proximity intolerance', where one individual struck out or displayed as another approached. In one of these cases, a female lunged at another as the three females present exited the bai in close proximity, and in another, a female was prevented from descending a *Nauclea* tree by another seated on a lower branch. Twice, the higher female was repelled by the cough-grunts and lunges of the lower individual, who refused to let the other pass. The silverback descended the tree shortly afterwards and passed both females without incident. Three of the interactions were against adult female Winona, two being by Jodie, and one by Jewel (the only other females present in the group). One interaction was broken up by the silverback (*see* af-sb interactions), but in all three, Winona was the original targeted individual.

Of the two agonistic interactions in DUK group, the same two individuals were involved; each initiated one incident, and in both cases the initiator was dominant in the interaction. One case concerned proximity intolerance during feeding, and in the other, a female lunged at the other who happened to be nearby when rough play had caused her offspring to shriek, thus possibly confusing the mother as to the origin of the juvenile's distress. In DWA group, the same female was responsible for both agonistic interactions, though against different partners. One case involved a feeding displacement and the other, proximity intolerance in a small tree (though as above, not apparently linked directly to feeding competition).

Reactions to new immigrant females by resident females

Although female transfer was seen several times during the course of the study (*see* Chapter 4), and no females were known to have bred in their natal group, opportunities to observe the treatment of immigrants were very scarce. Adult female Jodie and a sub-adult 'natal transfer' female joined CLI group in 1996, before the current study. The sub-adult subsequently emigrated again but Jodie remained in the group and bred. Two females joined MAX group when resident females were present during the study, but the group was not seen again. The only group with female residents that received female immigration during the course of the study was SNO group. This group showed the highest female-female interaction index, and the highest actual number of such interactions.

Adult female Drift joined the group in April 1997, which then contained three other female residents. Her origins were unknown, and it could not be said with certainty if she was nulliparous or not, however she gave birth in July 1998, and following the death of that infant in September 1998, did so again in July 1999. All seven af-af dyadic interactions in the group were directed at Drift. Three interactions were hard to classify. On two occasions on different days, Salmonberry, a resident adult female with dependent offspring, sought proximity to Drift. This was during the first month following the birth of her 'first' infant, and the purpose of the approaches appeared to be inspection of the new-born. On both occasions, Drift turned her back on Salmonberry and physically blocked her from seeing or approaching her ventral infant. The same blocking action was seen by a female in DUK group, within two months of giving birth, as another adult female tried to approach her and the infant three times. Finally the curious female sat six metres from the pair and was 'permitted' to observe the infant from that distance.

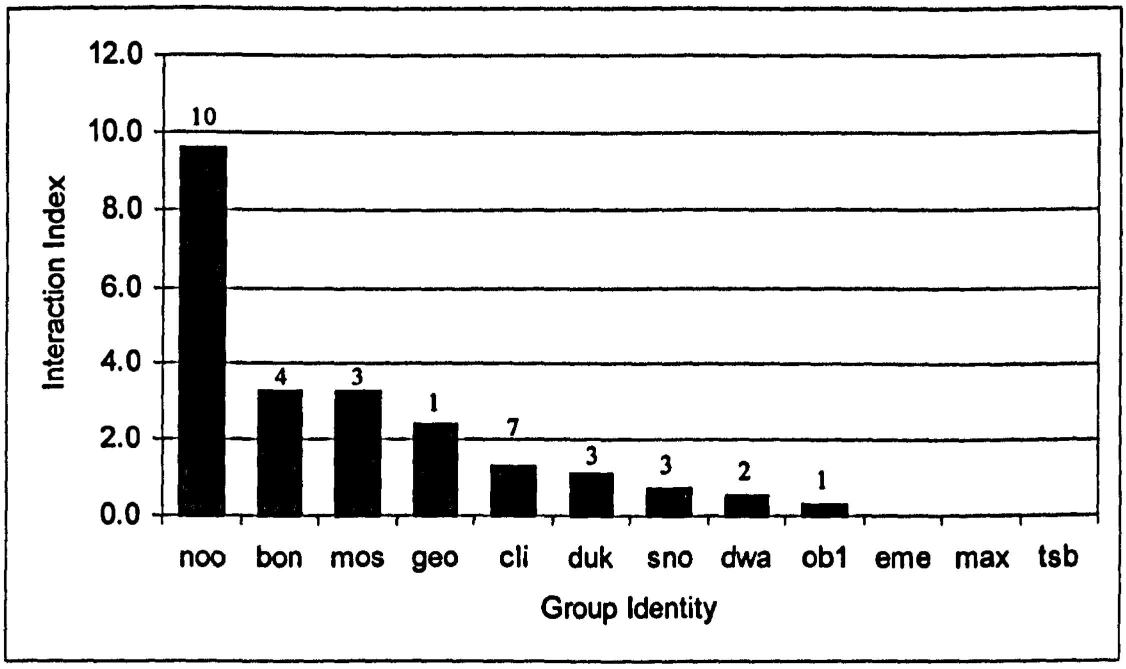
The other four female-female interactions in SNO group were all agonistic and appeared to fit within the context 'harassment of immigrant females by resident females'. None of the agonistic approaches recorded were provoked by actions on the part of Drift, and did not lead to feeding displacement. One female became stiff-limbed and tight-lipped in display as she walked passed Drift. The displays of female Salmonberry were more aggressive; on two occasions she approached Drift in a stiff-limbed walk, and chest-beated several times, and on a third, charged and chest beated. These acts of aggression were temporally well spaced, but all took place prior to the birth of Drift's first infant in the group. Drift did not react to any of the displays, and none provoked silverback intervention. Interestingly, on one of these occasions, immediately following the chest beat and charge of Salmonberry, the third female of the group, who had never been involved in the agonistic displays, calmly approached and stood next to Drift. Were this akin to a gesture of affiliative support, it would rank as the only case of female affiliative behaviour recorded at Mbeli.

No cases of female-female grooming were observed and females were never seen to form coalitions or intervene in conflicts in support of one or other opponent. Contest competition for food was not evident among females in the bai; none of the 16 interactions involved feeding displacements. Although contact aggression was seen between females, only two interactions led to 'fights', only one of which appeared to be severe (*see* Appendix A5.5).

Adult female-silverback interactions

Interactions between adults of opposite sex were by far the most numerous of the adult data set, although proportionally, they ranked after interactions among blackbacks and between blackbacks and adult females. Thirty five interactions were recorded in 2542 dyad-hours. Nine groups contributed to the data, though as Figure 5.10 illustrates, unevenly. NOO group exhibited the most interactions and had a much higher interaction index than all other groups. Only three of the groups with potential for af-sb interactions did not exhibit them, although of these, EME group only made nine visits (94 dyad-hours), and MAX group only made two visits (26 dyad-hours).

Figure 5.10 Interaction index for adult female-silverback interactions



Values above columns are actual numbers of af-sb interactions per group.

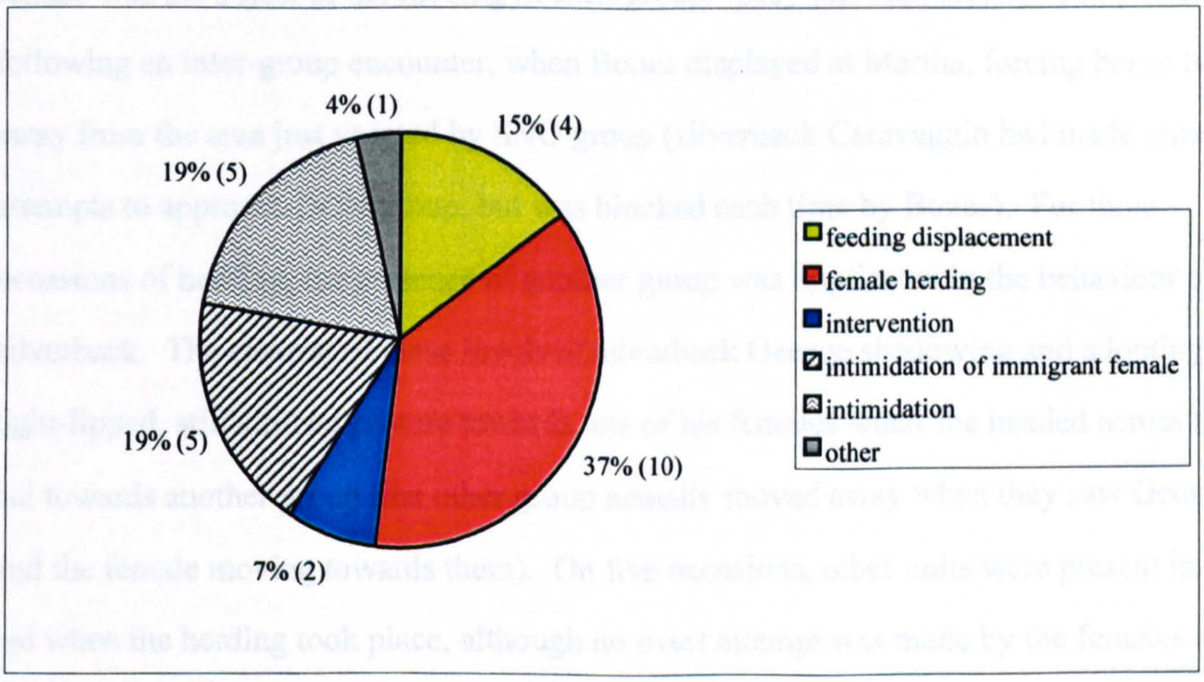
Twenty-eight of 34 (82%) interactions were agonistic, one had a sexual context, one was affiliative, and the context of four was indiscernible. Only three of the 34 interactions were initiated by adult females. In one, a new immigrant female (Martha) sought the proximity of silverback Basil and stared at him intently, before moving off and resuming feeding (context given as 'unknown'). In the second case, female Jodie ran in front of silverback Clive and sexually presented to him, with her back slightly lowered (possibly indicating a submissive act rather than a sexual solicitation). Clive, after a hesitation, then slapped her on the back with one palm, after which she moved away and fed. The final case was the only evidence of affiliative behaviour between the sexes, and involved adult female Martha prior to her immigration to NOO group. Her then silverback, the aged Bones, had spent an entire visit lying on his back without feeding. Towards the end of the visit Margo approached and sat very close to him for several minutes, waiting until he eventually sat up. She then calmly exited the bai with the old silverback walking behind her. Even in this instance, an affiliative context may be questioned.

Silverback – adult female agonism: herding, intervention, and intimidation

The median level of agonism displayed was two, though a high rate of contact aggression was recorded (25% of agonistic records), including three cases of mild aggression and three of severe, level four aggression. No agonistic interactions were initiated by females. In three interactions, no clear sign of submission was evident, but in all others (89%), the silverback was clearly dominant. Figure 5.11 shows the 27 agonistic interactions between silverbacks and females by context. Percentages are given and values in parentheses give the actual number of interactions witnessed.

In only four of 27 agonistic interactions (15%) was feeding displacement judged to be the primary motive of aggression. A simple walking approach seemed sufficient to accomplish a displacement, but males also used a tight-lip expression and cough-grunts. Females were never seen to defend a contested feeding patch against a silverback.

Figure 5.11 Context of agonistic interactions between silverbacks and adult females



Interventions

Interventions, in which a silverback breaks up a conflict between two females, were witnessed twice at Mbeli. This seems low, but it should be remembered that most female agonism was fleeting, and only one serious fight was witnessed in the whole study period; thus intervention was not often required. In the first case, an adult female in DWA group charged and grabbed at a sub-adult female in the group. In this instance, the silverback did not react immediately. Although the females did not pursue their interaction and resumed feeding, the silverback approached them after several minutes and ran chest-beating in-between them. Following this, both females exited the bai. A similar delayed silverback reaction occurred over 15 minutes after infant Wendy from CLI group threw a screaming tantrum, forcing her mother to run to comfort her. Silverback Clive eventually charged with a chest-beat and a ground slap between the pair (three metres from each). The rarity of such male behaviour strongly suggested that in both cases, despite the delay, group 'discipline' was being dispensed. The least ambiguous example of silverback intervention occurred during a serious fight between adult females Jodie and Winona from CLI group, field notes from which are appear in Appendix A5.5.

Herding and intimidation

Ten cases of female herding by silverbacks were witnessed in six groups, and only one female was the object of the herding in each group. Only one case clearly took place following an inter-group encounter, when Bones displayed at Martha, forcing her to head away from the area just vacated by SNO group (silverback Caravaggio had made repeated attempts to approach BON group, but was blocked each time by Bones). For three occasions of herding, the presence of another group was implicated in the behaviour of the silverback. The clearest of these involved silverback George shadowing and adopting a tight-lipped, stiff-limbed posture towards one of his females when she headed across the bai towards another group (the other group actually moved away when they saw George and the female moving towards them). On five occasions, other units were present in the bai when the herding took place, although no overt attempt was made by the females to approach them. Finally, on three occasions females were herded when no other groups were in the bai, but the females had moved away from the centre of their groups. A typical example of this behaviour is given in Appendix A5.6.

Five of the ten examples of herding took place between silverback Basil and the only adult female in NOO group, Martha, within the first 8 months following her immigration into the group from BON group. On separate occasions, Basil used combinations of charging, ground slaps, facial expressions, chest-beat, hitting, and staring, while physically blocking any attempt by Martha to move further from the centre of the group. On most of these occasions, Martha's behaviour was extremely submissive, being frequently cowed, sometimes visibly shaking, and wrapping an arm defensively across her chest. Images of two such occasions can be seen on pages 46 and 368. Two occasions lasted less than a minute, one lasted eight minutes, and two were protracted herding 'campaigns' lasting almost 30 minutes each.

These examples were judged as 'herding' due to the blocking effect of the silverback's behaviour on female movement. Allied to these were five observation of what was judged 'intimidation of new female'. In these cases, the silverbacks actions did not appear to be aimed at altering female direction of travel, but were simply agonistic behaviours targeted at immigrant females. Basil performed two of these on Martha, charging, and using postural and facial displays that caused her to adopt a more submissive posture and maintain close proximity to him. The other three cases concern the behaviour of silverback Caravaggio towards his recent immigrant female, Drift. One case involved a minor facial and postural display and approach, while the other two involved serious repeated charges and vicious blows while Drift prostrated herself, cowering and screaming. Following one attack, Drift immediately followed the silverback for some metres. All three attacks took place within the first four months after Drift's arrival in the group (April 1997); a period that also coincided with agonistic displays from some of the resident females. Following the observer's absence from the site for three months from August to November 1997, Drift was next seen with a well-healed but major wound down her forehead and over her brow-ridge. While Caravaggio cannot be confirmed as the cause of the wound, his previous behaviour, and the small chance of another female being permitted to attack her in such a way, makes him the likely suspect. Like the more extreme examples of herding, these attacks on immigrant females had the effect of terrorising them into submission.

The final five cases of agonism by silverbacks against their females are labelled simply 'intimidation'. In these cases, the targets of aggression were not new immigrants to the group, and herding was not involved. In three cases in CLI group, one in DWA and one in BON, silverbacks displayed or hit out at females for no apparent reason. Twice the females were feeding quietly, and on the other occasions, the group had only recently entered the bai. The reaction of the females was submissive in three cases, and neutral in two. It is hypothesised that herding, intimidation of new immigrants, and intimidation are all examples of a homogenous behavioural pattern in silverbacks.

Discussion

As a general observation, intra-group interactions were very infrequent, especially among adult group members. This is unquestionably due to the pre-eminence of feeding behaviour among most individuals when in the bai. One class relatively freed of these constraints were juveniles and infants, several of whom played for extended periods while their parents fed. The greater confidence in interaction shown by young immatures in an intra-group context is reflected in the fact that affiliative interaction was almost twice as common in this setting than in inter-unit interactions, largely due to the behaviour of playful immatures. Nevertheless, considerable variation in the frequency of intra-group interaction was observed, with neither group size, or the number of immatures apparent as variables exerting a significant effect on interaction frequency. This focuses the attention more upon the characters of individual gorillas within these groups as the origin of such variation. The infants and juveniles of CLI group played on the majority of their bai visits, whereas those in other groups (e.g., OB1) seldom did. 'Character' was not measured as a variable in this thesis, but was subjectively judged to have been an important factor in influencing interaction frequencies. Long-term monitoring may reveal whether the characteristics of other group members during development can influence the sociality of individuals on reaching adulthood.

Of adult and near-adult interactions, blackbacks are a difficult group to characterise. On the one hand, they may, like all other non-silverback members of the group, be susceptible to costs from contest competition over food, and thus be expected to exhibit behaviours consistent with this. At the same time, however, hormonal changes (e.g., Stoinski et al., 2002) elicit a predilection for behaviours based upon competition for females. As shown in Chapter 4, no males remained in their natal groups into full adulthood during the course of the study. As such, interactions occurring within the group were unlikely to have any direct impact on the individual's reproductive potential, thus potentially modifying motivational states.

When interacting with other blackbacks, there was some evidence of the assertion of dominance, and older (larger) individuals were always dominant in all agonistic exchanges where a 'winner' was discernible. Of particular note were the attempts of a recent immigrant blackback to assert dominance over resident, but younger males; a strategy that appeared to be successful, provoking little intervening response from the group silverback. Affiliative interactions were also noted: all blackbacks in the same group will, with the exception of rare cases of male immigration, have been group-mates and probably play-mates from infancy. Blackbacks accordingly demonstrate an unusual mix of assertive, aggressive behaviour, and more juvenile patterns of playfulness towards one another.

Blackback interactions with adult females were almost all initiated by the male. The majority appeared to be play agonistic in the sense of their having little long-term purpose, being roundly ignored by the female targets, lacking certain elements of true agonism, and failing to arouse intervention by the silverback. All cases of such behaviour at Mbeli involved resident males and immigrant females. As such, silverbacks may have been more tolerant of blackback 'harassment' if it reinforced their attempts to keep immigrants from secondary transfer. However, the lack of response by females to blackback displays did not suggest that they were effective in this capacity.

Interactions between blackbacks and silverbacks contained no element of playfulness. Although very few in number, most were feeding displacements, all of which were initiated and won by the silverback. Despite an apparent feeding context, such behaviours might be viewed as symptoms of a general antagonism by silverbacks towards their maturing sons. Were this so, however, such behaviour would be predicted to take place more frequently and not be confined to one context (feeding patches). As discussed in Chapter 4, evidence from mountain gorillas suggests that the benefits of multi-male groups may extend to all adult males within the group, and adult females (Robbins, 1995, 1999; Watts, 2000). Silverback relationships with maturing males at Mbeli seemed generally ambivalent, with little to suggest that the presence of such males was considered beneficial or detrimental to the dominant male. It can be argued that a lack of systematic aggression against young males is in itself evidence of silverbacks encouraging young males to remain in the natal group. That all males emigrated without silverback encouragement suggests, however, that in this population at least, young males recognise more opportunity for acquiring breeding access to females through becoming solitary. This in turn raises questions regarding the demographic and motivational states of blackback and young silverback mountain gorillas.

Female-female relationships

It is primarily among the relationships of adult females that variations in social system resulting from ecological pressures are likely to be observed. It remains difficult to quantitatively compare food availability between areas so radically different in species composition and form as the slopes of the Virunga volcanoes and the lowland forests of Congo and Gabon. However, it is undisputed that fruit plays a negligible role in mountain gorilla diets while being important in those of western lowland gorillas. Herbs have also been shown to be abundantly and densely distributed in the Virungas, but more patchily and thinly so for most western lowland gorillas (Doran & McNeilage, 2001). Thus at least qualitatively, there appears reason to predict that variation in female dispersal patterns and intra-group relationships might exist. This data-set cannot, unfortunately, provide much illumination with regard to comparisons of the frequency of different types of female-female behaviour between mountain gorillas and the Mbeli population, due to the prohibitively small sample size gathered at Mbeli. However, the size of the sample itself can possibly offer clues to female social structure, as can a consideration of the *types* of behaviour witnessed, regardless of frequency.

In a sense, such an exploration is already partially answered by the finding in Chapter 4 that female transfer appears ubiquitous in the population. Were feeding resources sufficiently patchy and restricted as to be regularly monopolised by given females, the evolution of a 'female-bonded' philopatric system would be predicted, and female transfer become too costly as a consequence. Nevertheless, some species have been shown to fit less well into the ecological model (Sterck et al., 1997), and consideration of other predicted effects of contestable feeding resources is of interest.

Firstly, female interaction at Mbeli appears to have occurred at a low frequency. Watts (1997) conducted 1969 focal hours on females from 'Group 5' and 'Beetsme's' group at Karisoke, and recorded 253 conflicts between females. At Mbeli, 3455 dyad-hours of observation produced a mere 16 interactions of any kind. This apparently huge difference raises the question of the effect on behaviour of the bai habitat. If herb foods are patchily distributed in the forest, then it might be imagined that the feeding associated with a sudden emergence into a zone of abundant herbs might mask otherwise normal behaviours. This is an inevitable danger of all behavioural study at bais, and one that is hard to quantify. However, it is suggested that were a strict dominance hierarchy in effect among the females of the Mbeli population, some evidence of this would still be betrayed during long-term study. Thus even if frequencies themselves are affected, such behaviours as are witnessed should still be influenced by, and relate to, the basic social organisation of the population.

Twelve of 16 female-female interactions were agonistic, and none of the observed examples of agonism involved feeding displacements or clear indication that any particular resource (e.g., food or proximity to the silverback) was contested. In one group, a female was targeted with aggression on three independent occasions, by one or other of the groups other females. Each time, she became the submissive partner in the exchange, raising the possibility that some form of dominance structure was present. However, on the only occasion that this aggression was serious, a support intervention by the silverback punished the aggressor, thereby negating the attack and balancing relations within the group. In one other pair of females, one partner was dominant during one interaction and submissive during the next. Most aggression therefore did not appear to be part of a set social structure such as a dominance hierarchy. In context, low level intolerance and minor, temporary antagonism seemed the cause of most interactions. Silverback control or support intervention was infrequent, due probably to the low frequency of serious fights among females, but was clearly present as a sanction against any attempts by a female to gain advantage at serious cost to another. An exception may have been the examples of agonism shown by females in SNO group against a new immigrant female. This was the only group already containing females to receive such immigration, and was notably the unit with the highest interaction index for female-female agonism (all cases of which involved harassment of the immigrant). If these were genuine attempts to coerce the female into leaving the group, thus lowering competition, it may be important to note that the silverback did nothing to prevent such aggression. Indeed, the silverback was himself apparently involved in something of a campaign of intimidation against the female. Watts (1991b) links harassment of immigrants by resident females in one group at Karisoke to the large number of females immigrating at one time, and to the already large size of the group into which they transferred. Although no statistical exploration of this is possible at Mbeli, the group in which harassment was noted was of a 'juvenile' group type and contained only 3 adult females, each with a dependent offspring. No evidence of coalition forming by females was observed at Mbeli.

Female philopatry predicts not only the presence of structured agonistic interactions, but also evidence of the formation and maintenance of affiliative bonds between females (e.g., Wrangham, 1980). This leads to a consideration of one of the more puzzling aspects of intra-group relationships at Mbeli compared to those at Karisoke.

The grooming problem

Many reports attest to the ubiquity of grooming as a common intra-group behaviour in mountain gorillas. Most grooming is between mothers and offspring, but it also extends, in reducing frequency, to maternal relatives, paternal relatives, and unrelated individuals. Juveniles groom each other and also groom the group silverback; adult females are known to groom silverbacks and adolescent males sometimes groom other adult females (Schaller, 1963; Harcourt, 1979a, 1979b; Stewart, 1981; Fossey, 1983; Fletcher, 1994; Watts & Pusey, 1993; Watts, 1994). Grooming almost certainly serves a social purpose in terms of reinforcing such bonds as exist between individuals, but is ultimately related to the removal of ecto-parasites, dry skin flakes, and vegetation (particularly the food plant *Gallium ruwenzoriensis*, which is covered in tiny hooks, making it particularly adherent to dense hair [Williamson, pers. comm.]).

At Mbeli, grooming was exceptionally rare, and was not recorded at all in the pilot stages of the study (Fay, 1997). During the current study, grooming was never seen in an inter-group context. Within groups, on one occasion a juvenile was seen to pluck an item from his paternal younger sibling's body with his lips, and on another occasion, the infant did the same to the juvenile. These, however, were unconvincing as examples of the more generally accepted grooming patterns. On six occasions, adult females were observed to groom their infants or young juveniles, using the lips and fingers. The only area of the body targeted in these cases was the head, with the area surrounding the eyes receiving particular attention on three occasions, with the females ingesting whatever debris or exudate they obtained (only once did an infants eyes appear to be inflamed or infected prior to the grooming). Infants and young juveniles groomed their mothers on five occasions. One coincided with an infant receiving grooming from his mother, but the other four cases were all linked to solicitous behaviour by the juvenile/infant. In each of these cases, the offspring noticeably stopped whatever activity preceded the grooming and appeared to assume a submissive, almost obsequious attitude. Movements became slow and cautious and grooming of the seated mother usually began with the offspring standing bipedal behind her and picking at her back, then gradually edging round to her side and from there trying to gain access to her ventrum and presumably, nipples, from beneath one or other arm. One such occasion led to a suckling bout, but in each other case, no reward of any kind was forthcoming. These instances may be seen as examples of behavioural responses on the part of offspring to reduced access to suckling and maternal care with weaning. Adults were observed to self-groom injuries or skin conditions, but no evidence of social grooming other than the two cases described above was recorded in anything other than mother/infant (and young juvenile) dyads.

As with so many issues relating to gorilla behaviour in bais, it is necessary to consider whether the environment itself, or the behaviour of the gorillas while in it, may have masked behaviours more common in the forest. Indisputably, the primary activity of all weaned gorillas in the bai is feeding, and feeding behaviour usually begins as soon as groups arrive, and only terminates shortly before they depart. However, with gorillas clearly visible for almost 1700 hours, it is almost unimaginable that no evidence of other grooming would have been seen, were it a standard behaviour in the population.

A brief census of some captive groups of western lowland gorillas perhaps surprisingly suggests that relatively low levels of grooming may be a species trait. At Columbus Zoo, Apenheul, Amsterdam Zoo, Toronto Zoo, Howletts, and Port Lympne, grooming was rare and almost always confined to mothers and young offspring (E. Armstrong; R. van der Beek; G. van der Kroon; V. Phellan; P. Halliday; all pers. comm.). At Melbourne Zoo also, most grooming was between mothers and infants and very rarely between adults (H.Wenk, pers. comm.).

Some evidence for coalition forming and differentiated female agonism and affiliation exists among mountain gorillas, though this is primarily due to degrees of relatedness: consequently grooming patterns also primarily reflect relatedness (e.g., Watts, 2001). Group members at Mbeli appear to be less related (so far, male and female emigration appear systematic), and this may have contributed to reduced levels of grooming. However, this is only among adult individuals, leaving considerable scope for grooming between older immature offspring and their mothers or the group silverback. Could it be that the presence of *Gallium* at Karisoke, with no equivalent at Mbeli, could create variation in the proclivity to groom? With the gorilla as a non-female-bonded species, it is possible that the physical imperative of grooming is divorced from the social to a greater degree, such that populations with a higher rate of contact with parasites, skin conditions, or clinging plants might groom at higher rates.

However, perhaps the most compelling proximal suggestion for the apparent differences in grooming patterns and rates relates to rest periods. Most groups at Karisoke are known to feed for the first few hours of the morning, and then enjoy leisurely rest periods straddling the mid-day period (Harcourt, 1978; Fossey, 1983). It has been observed that most intra-group social behaviours take place at these times, when group members typically sit close to one another, sometimes dozing, digesting their meals, playing with offspring and siblings, and grooming. There are still too few data on the activity patterns of western lowland gorillas to say for sure if such rest periods are a regular feature of group life. The patchy distribution of food resources that force western gorillas to travel further per day than mountain gorillas might, however, be predicted to leave them less time for such group relaxation sessions, and thus suppress the frequency of grooming in the species. Clearly, however, more data are required before such discussion can make further progress.

Silverback-adult female interactions

These were the most numerous adult intra-group interactions witnessed. The prevalence of such interactions was strongly skewed towards a group in which the herding of an immigrant female made up most of the records, but most groups in the population showed some evidence of silverback-female interaction. Females only initiated three out of 34 interactions, and of the 82 percent of interactions that were agonistic, all were initiated by males (as in mountain gorillas – Harcourt, 1979b). Females were never dominant over silverbacks in agonistic encounters.

As mentioned in the Introduction, while females are thought to be distributed around food or protection resources, male distribution is geared first and foremost to access to females. It is perhaps not surprising therefore to find that feeding displacement was not a major purpose in interactions. Where other group members may have attempted to oust others from feeding position, the silverback will probably have taken possession of the best locations by default, with other individuals spacing themselves so as never to pose any spatial competition to him. In general, male aggression towards females appeared to be either random or directed at new immigrants. In fact, it was probably never random. In 75% of herding cases, other groups were present in the bai, though only one followed an actual intergroup encounter in which another male approached the group. In 67% of cases the group was either alone in the bai, or the other group present was distant. The function of herding is relatively well understood with regard to physically preventing a female from emigrating, but data from Mbeli suggest that in addition to this effect, herding is part of a general dynamic of agonism and intimidation by silverbacks, aimed at preventing secondary female transfer. The violent behaviour of silverback Caravaggio towards recent immigrant Drift initially came as something of a surprise. An anthropomorphic sensibility predicted that silverbacks might behave affiliatively towards new females and also prevent any intimidation from resident females. While silverback intervention in female conflicts was witnessed as an effective strategy for limiting the expression of female dominance (during a fight) in CLI group, it was not evident in the group to which Drift transferred. Indeed, on several occasions, Caravaggio attacked Drift violently; a behaviour that might be predicted to actually provoke female transfer. In mountain gorillas (Harcourt, 1979b; Watts, 1992), female responses to silverback aggression often involve submissive behaviours, or the temporary following the male. This was also seen in the case of Drift and Caravaggio and between Basil and Martha. On the first occasion that previously solitary silverback Max was seen with recently immigrated females (MAX group) their behaviour was relaxed and affiliative towards individuals from other groups prior to his arrival in the bai, but switched to being extremely nervous and submissive as soon as he entered the bai and approached them.

Non-herding intimidation of immigrant females by silverbacks was also noted as a context of aggression between the sexes, with the remainder of cases being the intimidation of resident females without apparent motive. Harcourt (1979b) suggests that the timing of many silverback-female displays at Karisoke may indicate that such agonism functions merely to attract female attention prior to moving off after rest periods. This was not evident in any sense at Mbeli, where females frequently left the bai well before the silverback had finished feeding. Watts (1992) suggests that such apparently unprovoked cases of agonism towards females function to advertise "male agonistic prowess". He argues that this may be necessary when females exercise considerable mate choice, and may preferentially transfer to males offering the best infanticide-protection services. While it cannot be disputed that sexual dimorphism in the species and the range of secondary sexual characteristics displayed by silverbacks probably influence transfer decisions among females (*see* Appendix 7), 'advertising' these features once a female has made that decision is unlikely to be necessary. The aggressive behavior of the Mbeli silverbacks towards newly immigrated females, and at reduced levels towards longer-term resident females suggests that these males maintain a background level of actual intimidation aimed at dispelling any thoughts of attempted emigration among females. That such intimidation is most frequent and extreme against new immigrants suggests that such females may be engaged in 'sampling' groups, or at least may be more likely to transfer again sooner rather than later should conditions not be ideal. It is suggested therefore that at least until such time as females are settled in a group, or have the added impetus of offspring to prevent them from secondary transfer, males create a climate of intimidation and fear as their prime means of preventing females from exercising further mate-choice.

Summary

Intra-group social behaviour was not expressed at a high frequency at Mbeli. Overall, this may in some large part be attributable to the fact that most bai-time is spent feeding. Sample sizes were consequently prohibitively low for a full comparative analysis with the mountain gorillas of Karisoke; a process that, given the differences in the primary activity of the gorillas during data collection, may have been fundamentally flawed in any case. At Karisoke, most intra-group social behaviour takes place during rest periods, while at Mbeli, all data collection was confined to times when gorillas were feeding in a super-abundant feeding patch.

Behavioural elements were identified as present in both sites, however. No compelling evidence for strict female dominance hierarchies was found, suggesting that any effects of increased contest competition resulting from less evenly distributed food resources did not have a profound influence of the social structure of the population. Indeed, if anything, female mountain gorillas offered more evidence of linearity in relationships, although more data are needed from western lowland groups habituated in the forest to confirm or dispute this observation. Mbeli females were agonistic towards one another, but not primarily in the context of competition for identifiable resources, whether food or proximity to the silverback. In the only group capable of providing data, females acted agonistically towards an immigrant female. Only one major intervention in female conflict was seen, during which the losing female gained support. Frequency of intervention was probably low due to the rarity of fights between females, but other evidence suggested that silverbacks do fulfil a policing role within the group and are likely to minimise any advantages females may attempt to acquire by gaining dominance rank over other females.

Affiliative behaviour was all but absent among adults, and with the exception of the mother/infant dyad, grooming was not observed. Grooming may be a considerably less prominent aspect of western lowland gorilla behaviour than in mountain gorillas. Food availability, with its concomitant effects on activity budgets and the establishment of communal rest periods, possibly combined with the frequency with which the two species require the physical process of grooming may explain some of this variation. No other evidence suggested that affiliative bonding was a feature of female-female relationships, thus making the likelihood of coalition forming very slim.

Adult male-female relationships were characterised by male agonism and female submission. Silverbacks herded and intimidated immigrant females more than resident females, but it is suggested that the incidence of secondary transfer is limited by displays of male aggression.

Chapter 6

Inter-unit Interaction

Introduction

Among the few general predictions of how primate groups are likely to interact with each other, the degree of territoriality of a group, population, or species is probably the most frequently cited. Typically, groups able to fulfil their nutritional requirements within a small area will have correspondingly small home ranges. Such groups may be able to detect the presence of other groups, making active defence of the resources within the range a possibility (Clutton-Brock and Harvey, 1977b; Mitani and Rodman, 1979; Lowen and Dunbar, 1994) and are said to be 'territorial'. In such cases, groups are more likely to be dominant in interactions with intruding groups while within their own territory. Species considered territorial under this definition have included ring-tailed lemurs (Kopfler and Jolly, 1970), dusky titis (Robinson, 1981b), vervet monkeys (Cheney, 1987), and diana monkeys (Hill, 1994). Many such species use 'loud calls' to advertise their presence and demarcate their territory.

In groups for whom food resources are more patchily distributed, home-range size is likely to be larger, making active defence of the area untenable (Brown, 1964). In these cases, home-ranges may overlap extensively, and agonistic inter-group interactions are generally less likely; e.g. baboons (Anderson, 1981), grey-cheeked mangabeys (Waser, 1976). However, variation exists, and some species still engage in agonistic resource defence despite appearing non-territorial, e.g. howler monkeys (Seckulic 1982a), and guereza colobus (von Hippel, 1996). In many of these cases, the resource being defended is not the entire home-range, but a rich feeding patch or even a particular fruiting tree. Such effects are more likely to be expressed through female grouping patterns than male. The principal limit to female reproductive success is food, and Wrangham (1980) proposed that the degree of intergroup feeding competition determines the degree to which populations are female-bonded and females partake in inter-group aggression. By contrast, the primary limitation to male reproductive success is access to mates (Trivers, 1972), and males are known to actively initiate and participate in inter-group encounters both to acquire females and to protect their breeding access to those already in their groups. Distinctions between the motives for apparently 'territorial' behaviour may be ambiguous (e.g., blue monkeys - Lawes and Henzi, 1995) and may vary within the same species according to ecological variables.

In contrast to intra-group behaviour, inter-group interaction is an understudied subject area in primatology (Cheney, 1987). Researchers frequently have considerable trouble in simply habituating a single research group sufficiently for unaffected behaviour to be recorded. If such habituation does not, however, extend to a range of neighbouring groups, then the recording of inter-group activity is unlikely, as other groups flee the presence of observers. Even should interactions take place, it may be hard to feel with confidence that the behaviour of either habituated or non-habituated group was unaffected by the presence of an observer. Making hidden observations of interactions may occasionally be possible, but in most forest types, dense vegetation forces an approach to a distance where detection by one or other group is almost inevitable.

As highlighted in this chapter, further difficulties may be encountered with regard to defining when an interaction has or has not occurred. Proximity thresholds that may constitute an encounter may vary not only between species, but also within the same species depending on different habitat types. Such issues plague the study of interaction and make both a within and cross-species comparative approach to the subject problematic.

Gorillas are generally considered to inhabit home-ranges that can not be 'economically defended' (Brown 1964), in that the distribution of food resources ensures a home-range size too large to be 'policed' with the intensity necessary to detect and expel intruders. As such, gorillas can be regarded as 'non-territorial', and live within a social system that permits extensive home-range overlap. Such overlap is due, in the case of mountain gorillas, to the relatively uniform distribution and quality of food resources, and in more frugivorous populations, to the seasonal extension of the home-range to exploit particular fruiting tree species (Casimir and Butenandt, 1973; Fossey and Harcourt, 1977; Tutin, 1987; Watts, 1987; Yamagiwa et al., 1987; Remis, 1994). Despite lower levels of food resource defence, some contest competition over access to particularly rich food patches, including single fruiting trees may nevertheless occur, and for w.l. gorillas at Lopé, appeared to be the cause of the majority of inter-unit encounters (Tutin, 1996). However, competition over feeding resources should not be a major cause of inter-group interaction for mountain gorillas (Wrangham, 1980). Most serious agonistic interaction between mountain gorilla units is related to the acquisition of breeding females. Adult male gorillas compete vigorously in attracting new females, and those already with groups also aggressively prevent other males from attracting females away from them; both by herding females away from the foreign male, or by displaying and sometimes attacking the competitor (Harcourt, 1978a; Yamagiwa, 1986; Sicotte, 1993). The degree to which this is also true in w.l. gorillas has not yet been established due to the difficulties of habituation already mentioned.

Chapter 4 demonstrated that the Mbeli gorilla population has an essentially single silverback social system, within which all males emigrate to solitary status from their natal group, and all females transfer from their natal group into other groups or to a solitary male. An implication of this is that females in such groups are unlikely to be 'female bonded' (Wrangham, 1980) and that a lack of female philopatry (Chapter 5) substantially lowers the cost of female transfer. Evidence from the Karisoke population of mountain gorillas shows that females seldom if ever range alone, and that transfers are always directly from one unit to another (Harcourt et al., 1976, Harcourt, 1978a). While it is impossible to say as much with certainty about the Mbeli gorillas, the absence of observations of solitary females visiting the bai suggests that a similar system is in operation.

The implications of this are important. Essentially, the only apparent method for initial group formation is through inter-unit interaction (a solitary silverback and a group). Lone males are unlikely to be able to verify the presence of potential migrant females in a group without making visual contact (the importance of olfactory perception is not known, but is unlikely to be major). Likewise females, though probably alerted by auditory means, are unable to appraise a prospective new male without being close enough to make a visual inspection. The silverback of an existing group also may require inter-group interaction in order to refresh and increase the genetic profile of his group. Interactions allow for the transfer of natal sub-adult females to their first breeding groups (a behaviour with potentially mutual benefits to silverbacks of mature groups), and also for the acquisition of already breeding females from other groups (a one-sided exchange likely to be sought by one silverback and avoided by the other). Group composition, and the bonds between group members are a product first and foremost of the ecological niche inhabited by the species and the relative survival and fitness imperatives of the two sexes. This in turn influences the nature of inter-group interactions. However, in the short-term, the outcome of inter-group interactions may have a profound influence on the life-histories of all individuals in the group.

Gorillas are a prime example of a species in which difficulties in inter-group interaction data collection are likely to be encountered. They are generally shy of humans and in the case of western lowland gorillas, resistant to habituation. Their large home-ranges also make regular detection and following problematic. However, it is still astonishing that for such a high-profile species as the gorilla, only one paper exists (Sicotte, 1993) that considers inter-group interactions in detail.

Schaller (1963) recorded very little inter-unit interaction, though noted a variety of responses during encounters, including agonistic display, mingling and ignoring the presence of another group. In general, agonism was very rare and serious fights were never observed, although some wounding was noted on silverbacks. Silverbacks were most frequently involved in encounters, and females least. Blackbacks, juveniles and infants were seen to readily approach other groups and even mingle with them, and trail evidence suggested that groups occasionally nested in close proximity to each other. It was later suggested that such low levels of agonism may have been due to the fact that most of Schaller's observations were between two mature or 'established' groups (Harcourt, 1978a). While this is possible, it is perhaps more likely that ranging patterns or kin ties between the two groups led to a familiarity, engendering tolerance between members.

Fossey (1972, 1974) describes vocal and other display behaviour between gorillas of different groups, but it is Harcourt (1978a) who next gives any quantitative data on inter-unit interactions. In contrast to Schaller's apparently peaceful gorillas, Harcourt reports that 80% of 19 encounters between mountain gorilla units gave rise to agonistic displays, and that 50% of 16 led to fights with physical contact and occasional wounding. He states that silverbacks were the main protagonists in such encounters, but offers few details regarding the behaviour of non-silverback group members. In 'Gorillas in the Mist', Fossey (1983) reports on numerous inter-unit interactions, and although not quantified, describes in detail examples of violent fights between silverbacks, agonistic displays apparently used to avoid physical fights, and infanticide. However, she also describes encounters in which peaceful mingling took place. Immature individuals were observed in affiliative interaction with each other; even, on occasion, while their respective silverbacks exchanged agonistic displays nearby.

Yamagiwa (1987b) describes the behaviour of an all-male group of mountain gorillas, including encounters with other units. The nature of such meetings ranged from avoidance, through sonic displays, to close proximity display and wounding, and appeared to depend on the particular groups encountered. Watts (1989) reports on inter-unit interaction in the context of infanticidal attacks on immatures, mostly following the death of a group silverback.

Finally, Sicotte (1993) devotes a paper specifically to inter-group encounters in mountain gorillas; principally with regard to the influence of group composition on silverback behaviour. Although still finding agonistic display behaviour to be a major component of most encounters, Sicotte reports lower levels of contact aggression than Harcourt (1978a). This she considers due to having used a larger sample size, but also possibly due to changes in the demographic profile of groups in the Karisoke area. Perhaps the most important contribution of this paper, however, was the finding that a high number of potential migrant females in one or other of the groups involved in interactions predicted the intensity of response between silverbacks. This countered the suggestion of Harcourt (1978) that the length of time a group had been in existence predicted interaction intensity, with silverbacks from newly formed groups most likely to be implicated in examples of contact aggression. This report represents the most detailed quantitative study of inter-unit interactions in the Virungas, however, although mentioning the possibility that groups may occasionally mingle, it still leaves the reader with the impression that only silverbacks actively participate in interactions and gives little feeling for the ontogeny of social behaviours, agonistic or otherwise.

Eastern lowland gorillas have received even less study in this area. Yamagiwa and Kahekwa (2001) mention that, as in the Virungas, agonistic interactions, sometimes leading to fatal wounding have been recorded among silverbacks. Fascinatingly though, they also describe a social organisation among the gorillas of Kahuzi-Biega that appears to be essentially free of infanticide. Of 14 social situations that would be expected to result in an infanticidal attack (following the pattern from Karisoke; Watts, 1989) no such cases were reported. One group of females and offspring even ranged without a silverback male (following the death of their own) for 29 months, and at no point were targeted with infanticidal attacks by other group males or solitaries. For gorillas, the absence of infanticidal interactions in this population may be unique.

Virtually nothing is known of inter-unit interactions among w.l. gorillas. The longest running w.l. gorilla study, at Lopé, Gabon, recorded only 40 inter-unit encounters in almost 11 years of study (Tutin, 1996). Interactions were between groups and between groups and solitary males, and although frequently characterised by chest beats, vocalisations, and other sonic displays, contact aggression was apparent from trail evidence. That this could lead to fatal wounding was shown in the case of the principal study-group silverback, 'Porthos', who was attacked by another silverback and died of his wounds shortly afterwards. Nine of 16 interactions between groups and solitary males involved solitary males silently tracking groups for up to several days, before being discovered or surprised by researchers. Other inter-unit encounters were due to contested access to fruiting trees, and it was suggested that, although home range overlap was complete, groups in the centre of their range might have some dominance over groups nearer the boundary of their own; the former did not advertise their approach to fruiting trees, while the latter did. Bermejo (1997) comments that during the *Dialium* fruiting season at Lossi, Congo, two groups were known to have nested together, suggesting that fruiting periods may lead to affiliative as well as agonistic interactions. No clear cases of group mingling were observed at Lopé, although there was a suggestion of greater tolerance between two groups in particular, who nested in proximity and spent some time within auditory range without overt aggression. It was considered that such tolerance could possibly have resulted from one silverback being the son of the other, though no genetic proof for this has yet been obtained.

The first suggestions that gorillas may have a capacity for heightened levels of tolerance towards each other came from early reports from Mbeli Bai (Olejniczak, 1994) and subsequently, from Maya-Maya Bai (Magliocca & Querouil, 1997; Magliocca, 2000). Magliocca (2000) presents the first quantitative data on inter-unit interactions among w.l. gorillas in bais, showing 62% of encounters failing to result in any interaction ('indifference') and 29% giving rise to agonistic encounters, most of which were perpetrated by adult males.

The superb visibility afforded to researchers at Mbeli, and their subsequent in-depth knowledge of the large gorilla population using the bai make it, at least from a practical point of view, an optimum site for the study of inter-unit interactions. A potential disadvantage of the site is that the bai environment may promote behaviours unlikely to be exhibited in the forest, or alternatively repress otherwise normal forest behaviours. Making predictions about how the gorillas visiting Mbeli Bai are likely to react during encounters is difficult. Due to a dearth of data on the ranging and feeding habits of the gorillas while not in the bai, it is difficult to state with confidence whether from a feeding point of view, the bai represents a super-abundant resource to be jealously guarded, or one of many such areas, in which the abundance of food dispenses the need for any active defence. This problem is likely to confound any assessment of the role of female acquisition or defence in shaping the nature of inter-unit interactions.

Aims

The principal aims of this chapter are four-fold. The first is to describe the full range of gorilla interactions at Mbeli. This will be the first such analysis of its kind for western lowland gorillas. Encounters will be considered by type (agonistic, affiliative, neutral), by social context, according to the age/sex-class of the individuals involved, and by the overall characteristics of the groups involved. Units or individuals initiating encounters, and those emerging as dominant and submissive will be identified wherever possible.

Secondly, an attempt will be made to examine factors that may influence the likelihood and nature of interactions. Is it possible to predict who will interact with who, how, and what the outcome will be, based on variables concerning the units involved? Thirdly, findings from Mbeli will be compared with those from Karisoke (the only other major study to date). Are encounters more or less frequent at Mbeli than in the Virungas? Are levels of agonism and affiliation roughly the same at both sites, or do influences such as phylogeny, ecology or disturbance lead to significant differences in behaviour? Finally, I ask how likely behaviour exhibited in the bai is to be representative of that of the same units in the forest, or even of other western lowland gorilla populations?

Methods

The sociality of the Mbeli population can, by and large, only be measured in the context of visits to the bai. Occasionally, vocalisations can be heard from the forest surrounding the clearing, but no attempts are made to contact the individuals responsible. As such, the measurement of social interaction begins when an individual or group enters the bai. Clearly, the measurement of intra-group behaviour is possible when any group is within sight, while inter-unit interactions depend on the presence of at least two units in the clearing simultaneously. The presence of any pair of social units in the bai at the same time may result from chance, or may reflect a choice on the part of an individual or group. The presence of a unit in the bai alone may equally reflect a choice by that unit to avoid simultaneous bai use. As such, the first analysis deals with rates of simultaneous bai use (s/u) by each unit; exploring whether certain units or unit-types (group or solitary) were observed in s/u more than others. Calculating 'expected' rates of encounter in these circumstances is problematic and in most cases, no attempt has been made to do so.

Interaction research at Karisoke has employed a distance threshold to identify when an inter-unit encounter has taken place. Units there were said to have had an encounter if they passed within 500m of each other (Sicotte, 1993). In most s/u occasions at Mbeli, groups were within 500m of each other (due to the location of prime feeding areas), however given the lack of dense ground vegetation and the light conditions it is possible that units were able to see each other across any direct line-of-sight within the bai

(≤ 700m). For this reason, initial analysis of s/u uses all occasions of shared bai use without regard for distance or the likelihood that units were aware of each other.

Subsequent analysis of behaviour during s/u occasions is limited to a sub-set of s/u occasions during which units were within sight of each other, but also thought to be aware of each other (e.g., Lawes and Henzi, 1995). During data collection, a subjective assessment was made of this, based on a combination of factors including the distance between units, body orientation, length of time in s/u, and overt signs of monitoring between units. While it is possible that units may have been more aware of others in the area than might have been immediately apparent to an observer, this conservative approach was considered the best method for limiting error.

The frequency with which one unit is observed sharing the bai with another will, aside from any hypothesised effects of sociality, be influenced by the number of occasions each unit in a pair visits the bai overall. An index of association is therefore calculated in order to control for these effects. Many such indexes are available, varying according to assumptions and conditions regarding the data to be used. Several problems accompanying the use of association indexes arise from issues relating to the likelihood of a given individual being present in a social unit at a given time, due to *fission-fusion* type social systems in certain species (Cairns and Schwager, 1987). As the Mbeli data consist of independent and stable social units either visiting or not visiting the clearing, a simple index, much used by animal behaviourists (e.g., Schaller, 1972; Clutton-Brock et al., 1982) remains appropriate. The 'Half-weight' association index (known alternatively as Dice's, Sorensen's or the Coherence Index: Cairns and Schwager, 1987) has the following formula:

$$\frac{N_{ab}}{(N_a + N_b)/2}$$

where: N_{ab} = the number of occasions on which one social unit (a) was seen with another (b).

N_a = the total number of occasions that unit 'a' was seen at the bai.

N_b = the total number of occasions that unit 'b' was seen at the bai.

Indices obtained from this formula can then be compared across various treatments such as social unit identity, social unit type and size.

Having explored the frequency of simultaneous bai use, analysis focuses on the frequency and type of inter-unit interaction. There are potentially many ways of defining what is meant by the term 'interaction', each of which could have a significant impact on the conclusions drawn from the data. In this analysis, agonistic interactions include any active and overt displays of dominance or aggression and the responses to these by target units or individuals (*see* definitions in Chapter 5, pg. 201). Affiliative behaviours include play, grooming, touching, genital inspection, and copulation. A problem arises in the Mbeli data, however, as it may be unsafe to assume that all affiliative behaviours are necessarily overt. It could be argued that one gorilla seeking close proximity to another may, even in the absence of overt interaction, constitute an example of affiliative behaviour between the individuals. Similarly, the proximity of one group to another, in the absence of agonistic behaviour, could be viewed as an example of tolerance, bordering on affiliation. To this end, a sub-set of occasions is identified in the analysis of s/u by social units to identify occasions where individuals peacefully tolerated each other within a critical distance. Unfortunately, this distance criterion was only applied post-hoc, and field notes used to identify occasions. As proximity distances were not always recorded, it is possible that rates of proximity tolerance may be underestimated. Scan sample data from another study at Mbeli (Nowell, 2001) were used to obtain an average group spread for gorillas at Mbeli (median range = 30 to 35m, $N = 6$ groups). The lower end of the range was then adopted as the critical distance within which individuals or groups might be judged as exhibiting 'proximity tolerance'. Use of this criterion is nevertheless only one approach to the issue. Other possibilities might include merges, where an individual must be located closer to the centre of another group than at least one other member of that group. Data from mountain gorillas might suggest that 30m is too short a boundary within which to score affiliation. As such, the use of the 30m criterion should be seen as a somewhat arbitrary qualification and the results viewed in light this.

Scoring behaviour during s/u interactions

Problems arise at Mbeli with regard to the labelling of behaviour during inter-unit encounters. A straightforward approach used in later sections of the analysis deals only with dyads, where each independent bout of social behaviour can be scored for each pair of interacting individuals. Attempting to classify the overall reaction of a whole group of gorillas is more problematic. During a serious agonistic encounter in the forest, it may be clear that only the silverbacks of respective units are involved in the interaction, with all other members retreating to safe positions behind their silverback. However, at Mbeli, it is common for more than one individual to interact during an encounter. Furthermore, there may be a range of behaviours exhibited during a single encounter, with some individuals involved in agonistic exchanges while others engage in affiliative behaviour or close proximity tolerance. In this analysis, each encounter during which an interaction took place is scored for how many independent agonistic, affiliative, and/or proximity tolerance interactions took place, giving the number of individuals from each group involved. Perhaps crucial to this investigation is the weighting of encounters such that a true picture of their nature can be reached. The actions of a group silverback are likely, for instance, to have a much greater impact on the outcome of an encounter than those of a juvenile. Agonism between immatures may be of little consequence to the group as a whole in comparison to that between silverbacks. To this end, the behaviour of group silverbacks is taken to represent the core reaction of one unit to another, around which the interactions of all other individuals, while potentially important to the those concerned, can be seen as subsidiary or 'secondary' encounters.

Independence

Clearly there is considerable scope for data on interactions to be biased by the over-sampling of certain particular individuals or units. Wherever possible, steps have been taken to avoid any loss of independence. This can be an awkward procedure when that being measured is a discrete behavioural category, such as 'agonistic'. The simplest solution to this issue was found to be the expression of the 'mode' behaviour; thus if a unit was found to have interacted agonistically on five occasions, affiliatively on two, and neutrally on one, their 'average' behaviour was scored as 'agonistic'. Occasions on which this measure are used are identified in the text.

Dyadic interactions

Having examined simultaneous bai-use at the level of inter-unit encounters, another data set approaches the issue of social interaction by looking at every example of one individual interacting with another. This analysis concentrates on the age/sex-class combination of the pairs involved, and to a lesser extent, the behaviour of individual, named gorillas. In other words, the main unit of interest is the individual, and not as previously, the group/unit.

Although some very subtle interactions involving slight changes in body orientation or eye-gaze may have been missed by observers, this analysis proceeds under the general assumption that all overt interactions between dyads at Mbeli were recorded. Social interaction was a relatively rare event in the clearing and was thus highly conspicuous when it did occur. As a result, all occurrences recording of social behaviour was deemed greatly preferable to the use of interval sampling techniques.

The data for this section are 208 examples of interaction between two individuals from opposing groups. Each interaction is independent inasmuch as a new interaction is only scored between two individuals if a period of 30 minutes of no behavioural exchange separates encounters during the same visit, or if the fundamental context of the behaviour alters. In practice, the latter case occurred only twice, and in only four cases did a similar interaction occur between the same individuals twice in the same visit (separated by 30 minutes).

Once again, it is not possible to merely describe the number of times a certain age/sex-class combination interacted and the nature of those interactions, due to the differential proportion of age/sex-classes in the population. In order to express correctly proportioned rates of interaction, the total number of occasions on which interaction *could* take place is calculated. This method is selected as the data do not easily support an analysis of the actual time spent interacting. For the use of unit visits to be a viable control for age/sex-class proportions, the following conditions should be present:

- There should usually be no more than one independent interaction between two given individuals per visit.
- Visit length should be normally distributed, with low variability about the mean.
- Interactions should not be excessively time-dependent (i.e., an interaction can take place in less than a minute as frequently as in, say, 60 minutes).
- There should be no reason to expect that visit length affects particular unit combinations other than randomly.

These conditions were largely met by the data set, such that the following calculation could be performed: For every example of aware simultaneous bai-use between two units, the composition of each was examined at that point in the unit's history, and a count made of the number of age/sex-class combinations present. For example, a group containing a silverback, a female and two juveniles, meeting a group containing a silverback, two females and three juveniles would yield the following potential interaction values: silverback-silverback = 1, silverback – female = 3, silverback-juvenile = 5, female-female = 2, female-juvenile = 7, juvenile-juvenile = 6. In this way, each inter-unit encounter observed contributes towards an overall study total for any given combination pair, such as silverback-juvenile, and is known as the 'potential interaction index' (P.I.I.). The actual observed number of interactions between such age/sex-classes can then be expressed as a percentage of the P.I.I., and proportions subsequently examined.

In the Results section that follows, comparisons with other study sites and several other areas that could be considered as Discussion topics are included wherever their consideration is necessary prior to the presentation of further results.

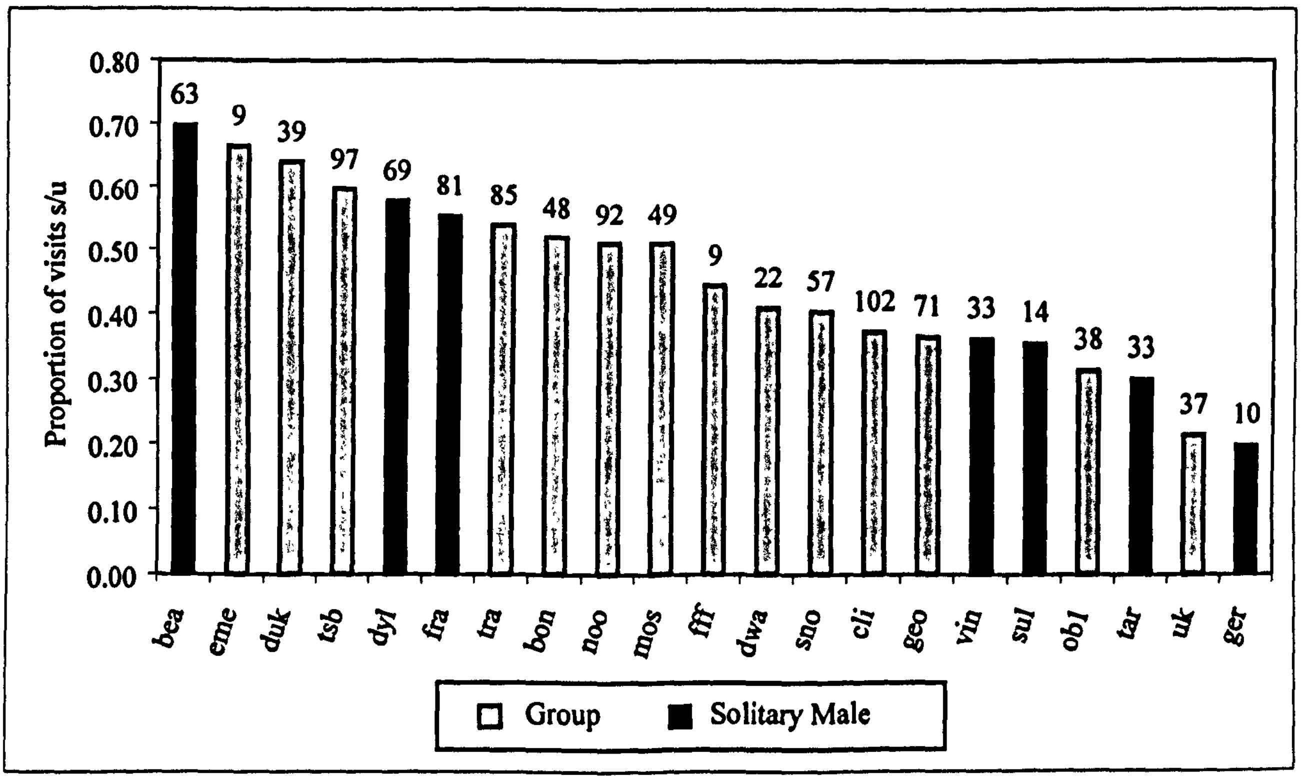
Results

Simultaneous bai-use (s/u) and unit-level analysis

Simultaneous bai-use

In order to examine the degree to which some units (groups or solitary males) may have sought out other units in the bai more often than others, the proportion of a unit's total visits that coincided with those of another unit was calculated. Figure 6.1 plots these proportions ranked by size. No units visited exclusively when the bai was empty and none made all their visits when other groups were present. Scores for s/u range from 20% of all visits to 70%. Four of the seven solitary males in the population were within the bottom third of the sample, though the other three were within the top third, with the unit most frequently in s/u also a solitary male.

Figure 6.1 Proportion of visits that were s/u by each social unit



Numbers above the bars show the total number of visits per unit. Uk = unknown units including silverbacks and groups.

A Mann-Whitney test was run to compare the median s/u proportions for groups and solitary males. Differences were non-significant ($U = 35$, N1 = 13, N2 = 7, $P = 0.41$).

Calculating proportions corrects for overall visitation rate, but not for duration of visit: a unit spending three hours in the clearing might have more chance of sharing it at some point than one only visiting for one hour. Indeed, a significant positive correlation was found between the proportion of each unit's total visits that were s/u and the average visit length for the group (Spearman Rank Correlation; $r_s = 0.534$, N = 20, $P = 0.015$). Significance is lost, however, if solitary males are excluded from the analysis; furthermore, the correlation may itself be a proximal one. Units visiting less frequently showed a lower s/u frequency than more regular visitors (s/u proportion – number of visits; $r_s = 0.602$, $N = 20$, $P = 0.005$), and visit duration correlated significantly with frequency of bai-use ($r_s = 0.608$, $N = 20$, $P = 0.004$). This suggests that a reason for lower rates of s/u in some units was a shorter visit length, which may be provoked by the unease of entering a potentially unfamiliar physical and/or social environment. With regard to the loss of significance on the removal of solitary male data, of the four solitary males in the lower third of s/u scores, Tarragon (tar) had only recently emigrated from his putative natal group when the data were collected and thus may well have exercised more caution before entering the bai. Two other solitary males, Sulatalu (sul) and Geronimo (ger), had not been seen at the bai before, only visited for a brief period and were then not seen again.

Table 6.1 gives the percentage of a unit's s/u occasions when it shared the bai with 1, 2, 3, or 4 groups simultaneously.

Table 6.1 Percentage of s/u occasions that 1, 2, 3, or 4 other groups were present

Gp ID.	Number of other social units present				Number of s/u visits
	1	2	3	4	
vin	84	8	8	0	12
duk	75	25	0	0	25
tsb	72	22	6	0	58
cli	71	20	6	3	38
noo	70	16	11	3	47
fra	68	16	16	0	45
dyl	67	22	11	0	40
tra	64	28	5	3	46
ob1	64	18	18	0	12
bea	63	26	11	0	44
geo	62	27	11	0	26
sno	61	17	22	0	23
mos	54	33	13	0	25
bon	50	30	20	0	25
tar	89	0	0	11	10
dwa	56	33	11	0	9
uk	33	17	33	17	8
eme	50	17	33	0	6
fff	60	40	0	0	4
sul	33	0	67	0	5
ger	100	0	0	0	2
Mean	64	20	14	2	-
SD	16	11	15	4	-

Solitary males shown in italics. uk = unknown groups. Mean values are for data given above the dotted line.

In order to reduce the misleading effects of small sample size in some cases, only units where the total number of s/u occasions was over ten contribute to the mean. Over half of all s/u occasions were limited to one other group, and a fifth to two other groups. Meetings between four and the maximum, five groups, were rare.

Too little is known regarding the ranging of groups when not in the bai for conclusions on sociality to be drawn from the frequency of s/u alone. A more informative approach examines the rate at which individual groups are witnessed in s/u with other known groups. Are some pairings more frequently seen than others and can the pairing of unit types tell us anything about preferences in sociality among the population?

Table 6.2 presents the s/u proportion for each social unit combined. Because visit frequency differed between units, the matrix is not symmetrical, but should be read by row, from left to right. The table exposes the effect whereby social units with visitation frequencies lower than the total number of possible pairings show disproportionately high scores. For this reason, the eight units meeting this criterion are listed at the base of the matrix and their s/u proportions should be seen as a misleading result of a low overall visitation rate.

Table 6.2 Matrix showing simultaneous bai use for each unit with each other unit as a proportion of total s/u visits

ID	*bea*	duk	tsb	*dyl*	*fra*	tra	bon	noo	mos	dwa	sno	cli	geo	*vin*	ob1	*tar*	*sul*	*ger*	eme	fff	N s/u
bea	*	*.01*	*.12*	*.13*	*.15*	*.09*	*.12*	*.15*	*.04*	-	*.04*	*.01*	*.04*	*.01*	*.01*	*.03*	-	-	*.01*	-	*67*
duk	.03	*	.10	.07	.07	.13	.03	.20	.10	-	-	.17	.07	-	-	-	-	.03	-	-	30
tsb	.10	.04	*	.05	.10	.17	.05	.10	.07	-	.04	.09	.09	.02	.05	.02	-	.01	-	-	81
dyl	*.16*	*.04*	*.07*	*	*.13*	*.07*	*.09*	*.11*	*.05*	*.04*	*.05*	*.11*	*.02*	*.04*	*.02*	-	*.02*	-	-	na	*56*
fra	*.15*	*.03*	*.12*	*.10*	*	*.10*	*.03*	*.10*	*.03*	*.03*	*.04*	*.03*	*.06*	*.03*	*.03*	*.04*	*.01*	-	*.04*	*.01*	*68*
tra	.09	.05	.22	.06	.11	*	.03	.08	.09	.05	.02	.03	.09	.02	.03	.02	-	-	-	-	64
bon	.19	.02	.09	.12	.05	.05	*	.14	.09	.02	.09	.07	.05	-	-	-	-	-	-	.02	43
noo	.13	.08	.11	.08	.09	.07	.08	*	.04	-	.04	.07	.01	.04	.03	.07	.03	-	.04	-	75
mos	.07	.07	.15	.07	.05	.15	.10	.07	*	-	.02	.12	.02	.02	.02	-	-	-	.05	-	41
dwa	-	-	-	.15	.15	.23	.08	-	-	*	.08	.08	.15	-	-	-	-	-	.08	-	13
sno	.09	-	.09	.09	.09	.03	.13	.09	.03	.03	*	.22	.06	-	.03	-	-	-	-	-	32
cli	.02	.09	.13	.11	.04	.04	.05	.09	.09	.02	.13	*	.05	.02	.04	.04	.02	-	.02	.02	55
geo	.08	.05	.18	.03	.11	.16	.05	.03	.03	.05	.05	.08	*	.03	.03	.03	-	-	-	.03	38
vin	*.06*	-	*.13*	*.13*	*.13*	*.06*	-	*.19*	*.06*	-	-	*.06*	*.06*	*	-	-	*.06*	-	-	*.06*	*16*
ob1	.06	-	.22	.06	.11	.11	-	.11	.06	-	.06	.11	.06	-	*	-	.06	-	-	-	18
tar	*.13*	-	*.13*	-	*.19*	*.06*	-	*.31*	-	-	-	*.13*	*.06*	-	-	*	-	-	-	na	*16*
sul	-	-	-	*.13*	*.13*	-	-	*.25*	-	-	-	*.13*	-	*.13*	*.13*	-	*	-	*.13*	na	*8*
ger	-	*.05*	*.05*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	na	*2*
eme	.08	-	-	-	.25	-	-	.25	.17	.08	-	.08	-	-	-	-	.08	-	*	na	12
fff	-	-	-	na	.20	-	.20	-	-	-	-	.20	.20	.20	-	na	na	na	na	*	5

With the exception of the lower 4, social units are ordered for rank by their overall s/u proportion (highest first). The dash (-) indicates zero scores. Solitary males are shown in italics.
S/u combinations that were not possible due to the timing of group break-ups and dates of first arrival at the bai are denoted by (na).

In order to better facilitate s/u comparisons between units, the 'Half-weight' Index of Association (Cairns and Schwager, 1987) was calculated for each pair-combination of social units (excluding unknown groups). Unfortunately the low number of units corresponding to some 'group types' (i.e., nascent, infant, juvenile) did not permit an analysis of the frequency of s/u against this variable. Instead, initial analyses concentrate on frequencies for groups and solitary males. To ensure that the index gives as accurate a measure of association as possible, unit pairs with a combined number of less than 20 visits were omitted from the analyses.

The median index of association scores for the three pairings were;

solitary male with solitary male = 0.041 (IQR .088)
solitary male with group = 0.031 (IQR .038)
group with group = 0.036 (IQR .049).

A Kruskal-Wallis test on the median association index for the three pairings showed these differences to be non-significant: $\chi^2 = 1.85$, df = 2, $P = 0.40$.

The data were next analysed by social group (i.e., the index of association scores for each social unit in all its s/u occasions with other units were used in comparison with those calculated for units. Solitary males were first compared against each other. Figure 6.2 plots the median of index of association scores for each male (ger and sul excluded due to low sample size). A Kruskal-Wallis test showed differences to be significant: $\chi^2 = 25.9$, df = 4, $P < 0.001$. Multiple comparisons following the formula described by Siegal and Castellan (1988), with P at 0.05, showed that Frank (fra), Bear (bea), and Dylan (dyl) all shared the bai with other social units significantly more often than both Vince (vin) and Tarragon (tar).

Significant differences were also found when association index medians were compared between groups only: Kruskal-Wallis test; $\chi^2 = 34.3$, df = 10, $P < 0.001$. Again, using Siegal and Castellan's (1988) post-hoc comparison formula, it was found that TSB group and NOO group shared the bai with other social units significantly more often than both DWA group and OB1 group, but all other comparisons were non-significant. Figure

6.3 plots the median Index of Association for each of the 11 groups included in the analysis.

Figure 6.2 Boxplot chart showing median index of association for solitary males

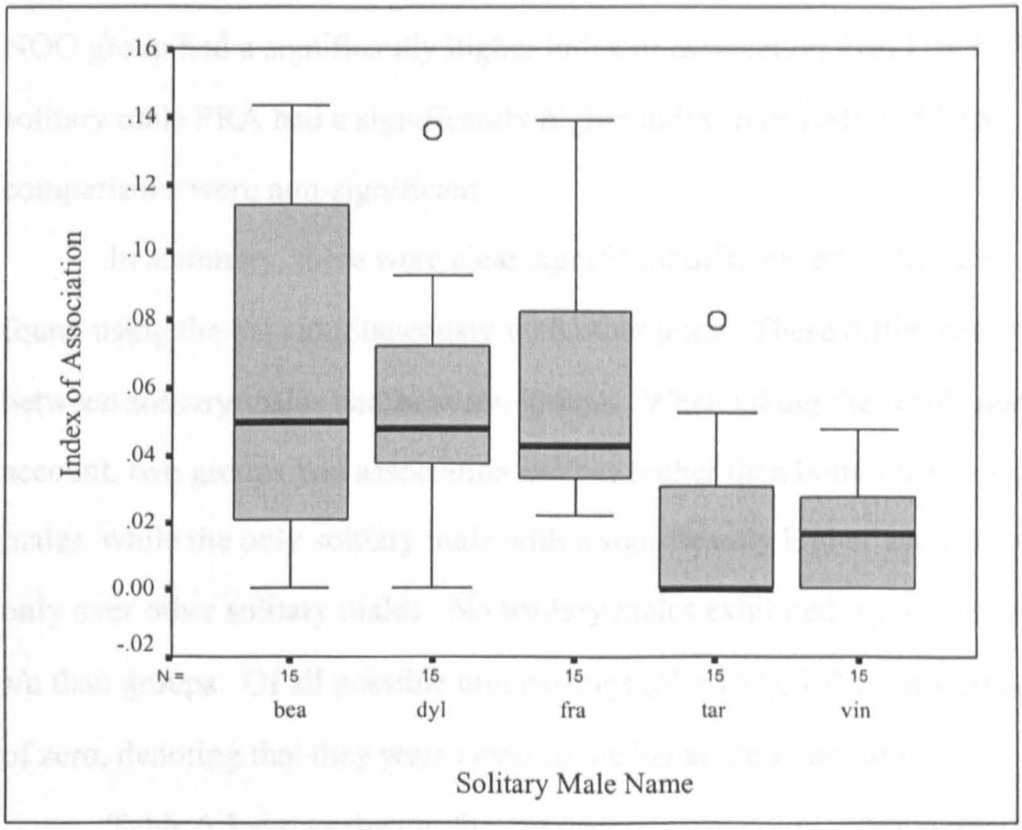
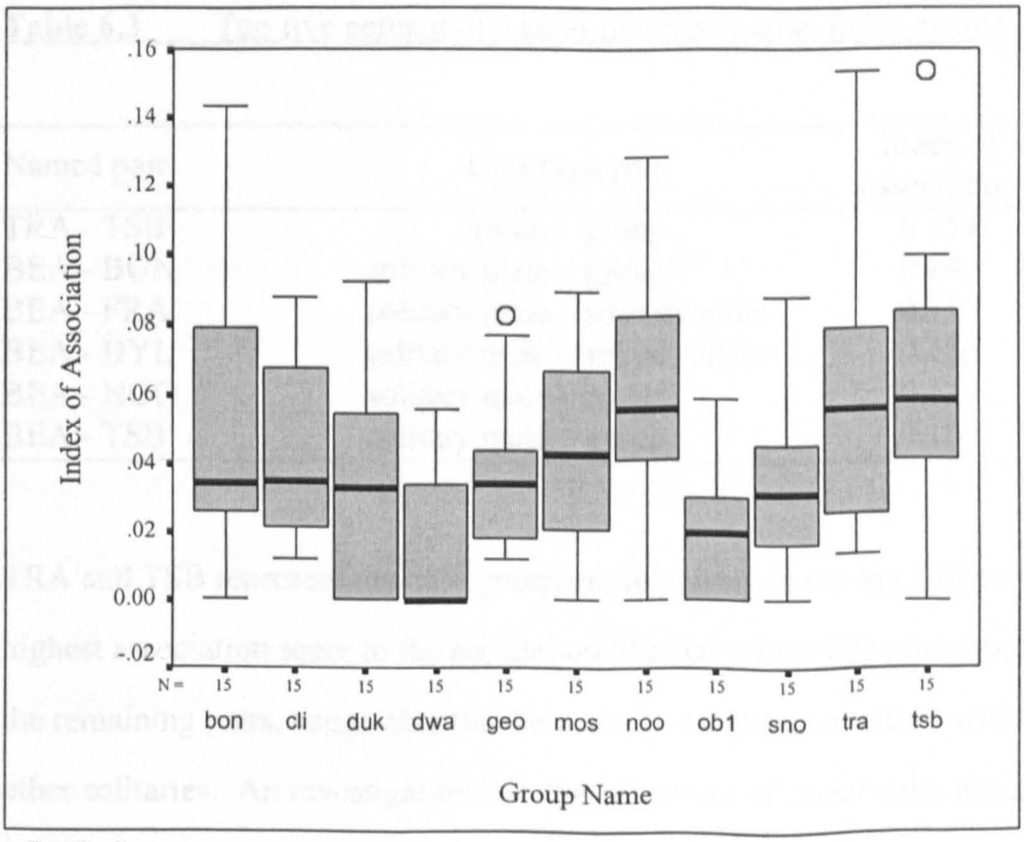


Figure 6.3 Boxplot chart showing median index of association for groups



O = Outlier

Finally, a Kruskal-Wallis test was used to examine differences in index of association across both solitary males and groups. Again, significant differences were found between units ($\chi^2 = 61.0$, df = 15, $P < 0.001$). TSB group shared the bai significantly more often than groups OB1 and DWA, and solitary males VIN and TAR. NOO group had a significantly higher index of association than DWA, TAR, and VIN, and solitary male FRA had a significantly higher index than TAR and VIN. All other comparisons were non-significant.

In summary, there were clear significant differences in the rates at which units were found using the bai simultaneously with other units. These differences were present both between solitary males and between groups. When taking the whole population into account, two groups had association indices higher than both other groups and solitary males, while the only solitary male with a significantly higher association index did so only over other solitary males. No solitary males exhibited significantly greater rates of s/u than groups. Of all possible unit pairings ($N = 157$), 16% had association index scores of zero, denoting that they were never in the bai at the same time.

Table 6.3 shows the top five percent of association index scores for distinct social unit pairs.

Table 6.3 Top five percent of named-pair association index scores

Named pair	Unit-type pair	Index of association	Number of s/u occasions
TRA - TSB	group – group	0.154	14
BEA - BON	solitary male – group	0.144	8
BEA - FRA	solitary male – solitary male	0.139	10
BEA - DYL	solitary male – solitary male	0.136	9
BEA - NOO	solitary male - group	0.129	10
BEA - TSB	solitary male – group	0.100	8

TRA and TSB represent the only group/group pairing in the top five percent, exhibiting the highest association score in the population. Solitary male Bear was implicated in each of the remaining pairs, suggesting that he actively sought interactions with both groups and other solitaries. An investigation into the behaviour of social units during simultaneous bai-use is required however, if any of the above results are to be shown as supporting or running contrary to levels of tolerance, affinity, and agonism predicted by studies of gorillas and other social primate species.

Predicting index of association rank

Spearman Rank Correlation Coefficients were calculated for association index and two dependent variables in an attempt to uncover any underlying predictive mechanism for choice in shared bai-use partners. Variables considered were:

a) the difference in size between the two units.

b) the difference in numbers of breeding females between the two groups.

In reality, these may be inseparable as there is a positive correlation between the number of breeding females per group and the total group size at Mbeli.

The principal hypothesis tested is:

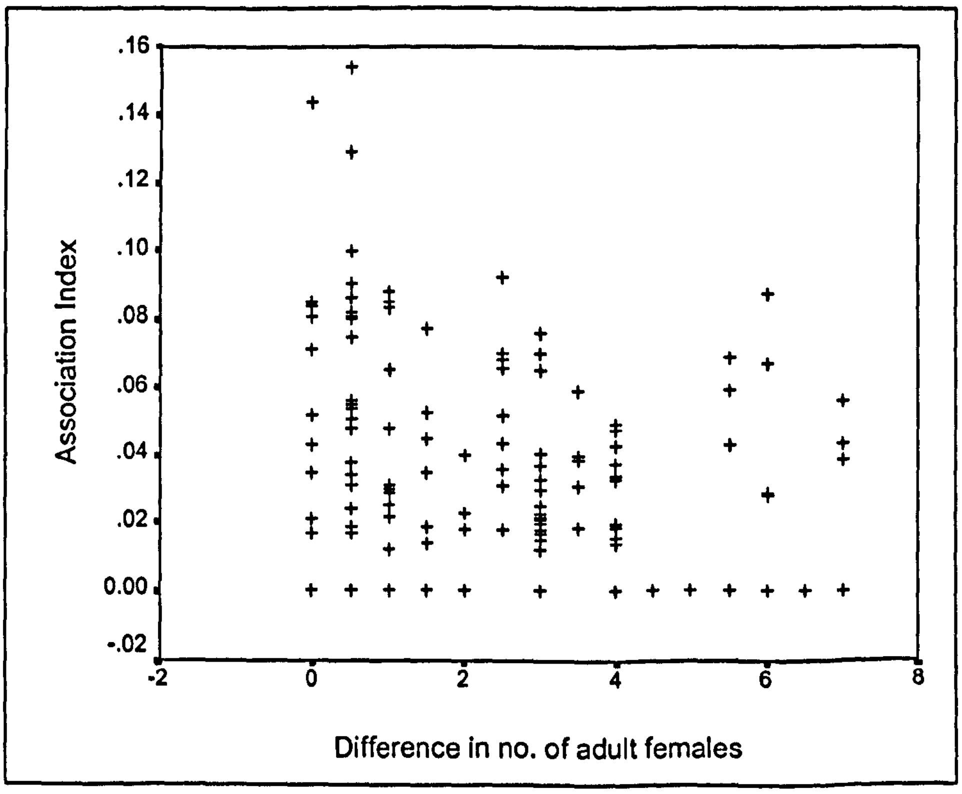
H_1. Frequency of association is significantly correlated with the difference in numbers of breeding females (and/or total unit size) between two units.

A positive correlation may suggest that smaller units target larger ones preferentially (the chances of encountering potentially migrant females should be higher in larger groups, and smaller units may be more acquisitive if they have not yet reached some optimum size or composition). A negative correlation may however suggest that large groups actively avoid small groups or units, recognising them as the most likely to seek to attract potential migrants or to elicit female transfer. Alternatively, or in addition, a negative correlation may suggest a mutual tolerance and lack of suspicion between like sized units. Naturally, the opposed motives hypothesised between larger and smaller units may work simultaneously to neutralise any effect of one or the other, resulting in the null hypothesis, that no correlation between association index and difference in group size/number of females exists.

Clearly the inclusion of solitary male – solitary male s/u should not be considered in this analysis. It is important also that tests should both include solitary-group s/u occasions, and also exclude them, in order to separate the effects of solitary males from those simply of small groups.

In all tests conducted, both group-group and group-group plus group-solitary male, and for both difference in total group size and difference in number of adult females, a significant negative correlation with association index was found. While this finding may initially appear to be of interest, as Figure 6.4 suggests (for association index and difference in number of females), significance is obtained primarily as a result of the large number of data points. Considerable scatter is evident in all such charts plotted, and as such, the correlations actually describe only a very small proportion of the data set. They are therefore unreliable in examining the hypothesis, suggesting either that the rates at which units share the bai with each other are random, or that other unmeasured variables may have a greater influence than those examined here.

<u>Figure 6.4 Scatterplot of association index and difference in numbers of females (all units)</u>



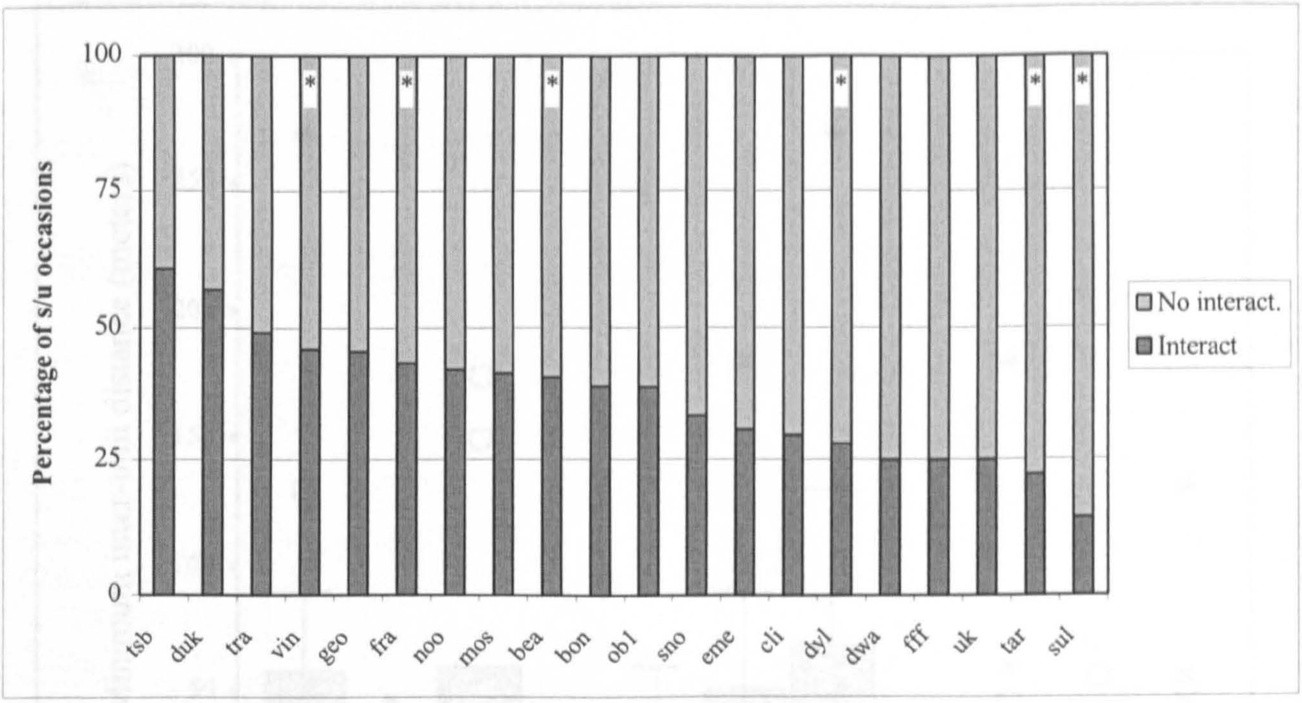
It might be predicted that units with overlapping home-ranges might occasionally travel in proximity to each other, or have a greater tolerance for each other's presence than groups from very different areas. Unfortunately, as shown in the earlier description of bai-use and ranging, data on home-range are not available, and zone of entry to the bai thought to be too weak an indicator for home-range location to warrant a statistical exploration of this issue.

Frequency of interaction during simultaneous bai-use

It was possible that social units were unaware of each others presence on 44 (11%) of a total 389 paired s/u occasions. Judgement of this was subjective, and gorillas may have been more aware than was apparent from their behaviour. However, a conservative approach of using only the 'aware' data-set for the analysis of group behaviour during s/u occasions was thought preferable to examining all occurrences. The median distance between units judged as unaware of each other was 290m ($N = 39$, IQR 95, range 60 to 400m). The minimum distance between units judged to be aware of each other (the distance between nearest neighbours, and including zero scores when physical contact was made) was 80m ($N = 341$, IQR 185, range 0 to 410m). A Wilcoxon Signed Ranks compared median minimum inter-unit distances for 13 units when aware of the other group and when judged unaware. As one of the criteria used in subjectively judging awareness was distance itself, it is unsurprising to find that unaware inter-unit distance was significantly greater than aware distance; $Z = -3.18$, $N = 13$, $P = 0.001$.

Of the 345 occasions of paired aware s/u, only 144 gave rise to social interactions. Thus on 58% of occasions where units were judged to have been aware of each other in the bai, no interaction was forthcoming. When sub-divided into unit types, interactions took place on 46.5% of occasions for group/group combinations, 41% for solitary male/solitary male combinations, and 34% for solitary male/group combinations. While the ranking of these scores may be of some interest, a chi-square test on the raw frequencies showed differences between interaction rates to be non-significant: $\chi^2 = 4.93$, df = 2, $P = 0.085$. Figure 6.5 shows the frequency of interaction and non-interaction for each unit as a percentage of all s/u occasions (where $N > 10$). Frequencies for interaction range between 14 and 61%, with a mean of 37% ± SD 12.

Figure 6.5 Percentage of s/u occasions in which interaction occurred



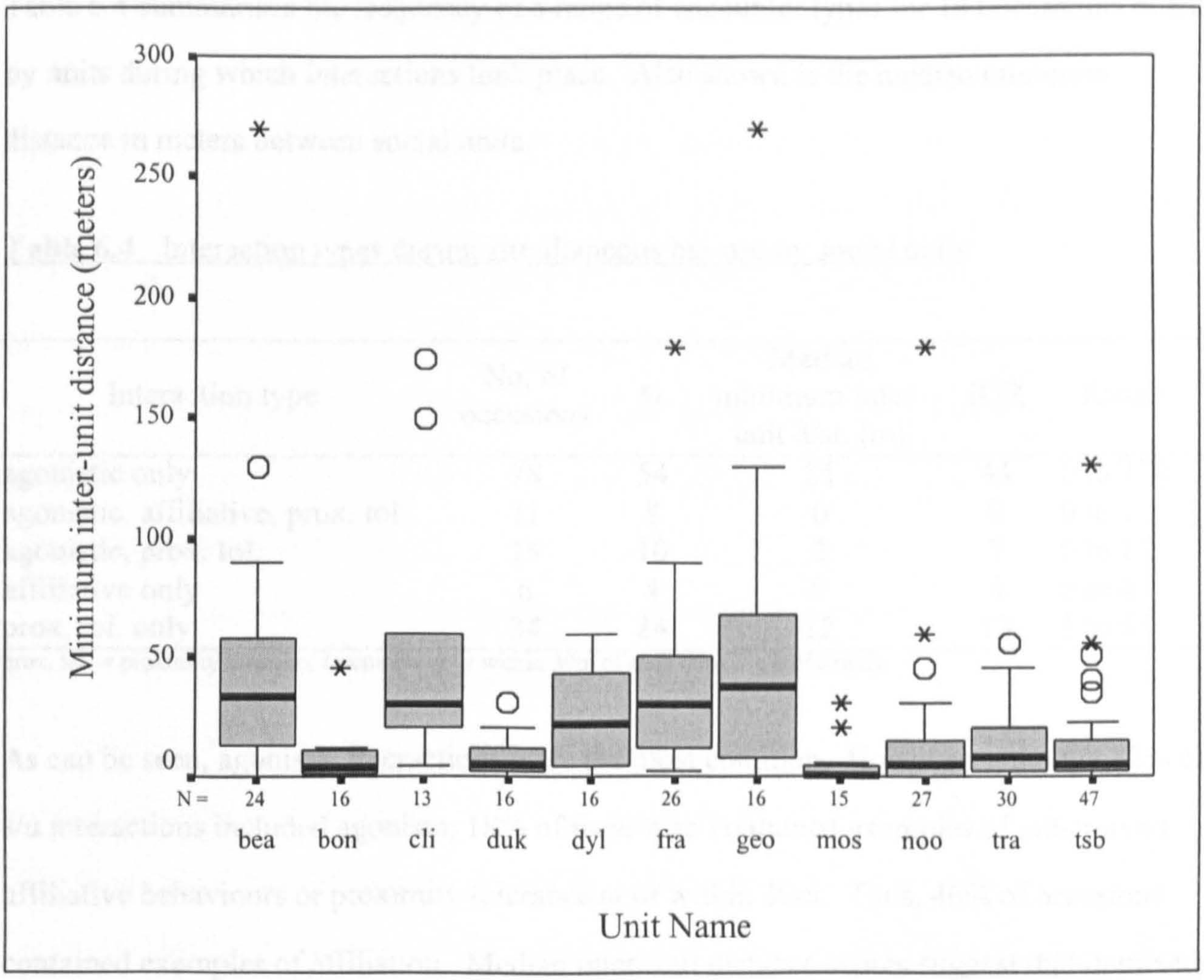
* denotes a solitary male.

Distance between interacting and non-interacting units during s/u occasions

The median shortest distance between interacting units (median = 10m, range 0 to 270) differed significantly from that between non-interacting units (median 170m, range 8 to 410); Wilcoxon signed ranks test, $Z = -2.93$, $P = 0.003$. Figure 6.6 gives the median minimum distance between interacting units for each unit where $N \geq 10$. It can be seen that most interactions took place between 0 and approximately 60m, however many units show outliers and extreme values, probably linked to long-distance displays.

No significant difference was found for inter-unit distance between solitary males and groups, though six of eight groups interacted at shorter distances than the three solitary individuals analysed: Mann-Whitney, $U = 4.5$, $P = 0.133$ (the presence of a solitary male was noted to raise inter-unit interaction distance at Maya [Magliocca, 2000]). Significant differences were however found between individual units: Kruskal-Wallis, $\chi^2 = 66.21$, df = 10, $P < 0.001$. Post-hoc multiple comparisons showed solitaries Bear and Frank, and CLI group to have significantly greater inter-unit distances during interaction than groups MOS, BON, TSB, NOO, and DUK. Distances for GEO group were only significantly greater than those for MOS group.

Figure 6.6 Median minimum distance between interacting units



* = Extreme value (more than 3 box lengths above the box).

Finally, for s/u occasions in which interaction took place (not including solitary male/solitary male encounters) the distance between silverbacks was examined in comparison to the shortest distance between the units, regardless of the age/sex-class of the individuals concerned. Minimum nearest-neighbour distance was found to be significantly shorter than inter-silverback distance: inter-silverback median = 35m, IQR 45, range 0 to 270; minimum distance median = 10m, IQR 27, range 0 to 270: Wilcoxon Signed Ranks test, $Z = -7.22$, $P < 0.001$, suggesting that on average, silverbacks maintained a greater distance from each other during inter-unit interactions than did immatures or adult females.

The nature of interactions: the social unit perspective

Table 6.4 summarises the frequency of a range of encounter types for 144 occasions of s/u by units during which interactions took place. Also shown is the median minimum distance in meters between social units.

Table 6.4 Interaction types during simultaneous bai-use by social units

Interaction type	No. of occasions	%	Median minimum inter-unit dist. (m)	IQR	Range
agonistic only	78	54	25	44	0 to 270
agonistic, affiliative, prox. tol.	11	8	0	0	0 to 1
agonistic, prox. tol.	15	10	3	7	0 to 13
affiliative only	6	4	0	4	0 to 4
prox. tol. only	34	24	12	13	1 to 45

prox. tol. = proximity tolerance (members at or within 30m of each other – see Method).

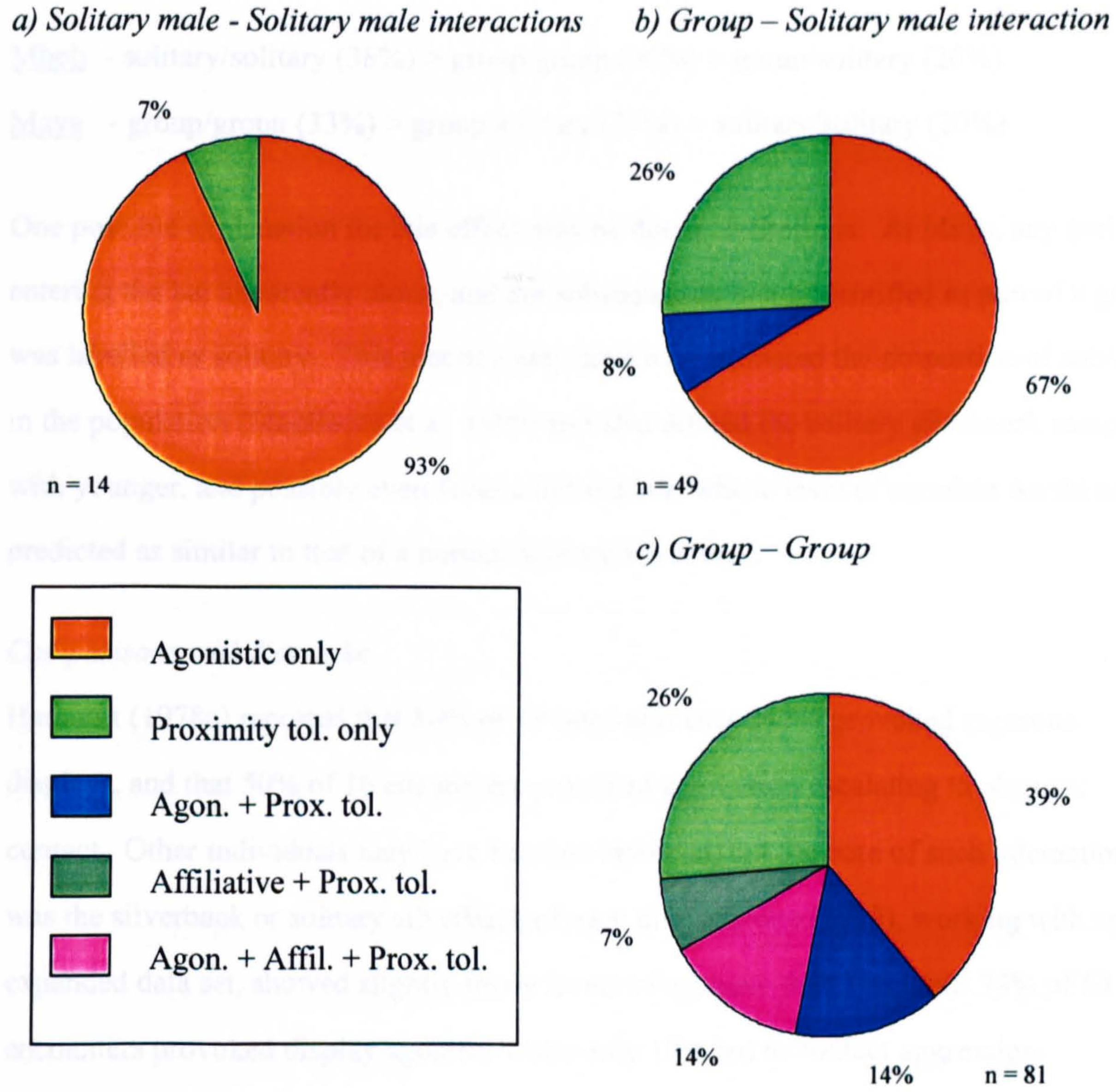
As can be seen, agonistic interactions were the most common. However, although 72% of s/u interactions included agonism, 18% of these also contained examples of either overt affiliative behaviours or proximity tolerance at or within 30m. Thus, 46% of occasions contained examples of affiliation. Median inter-unit distance scores suggest that in mixed-type encounters, affiliative behaviour is more likely to be responsible for the close contact apparent. Despite this, all encounter types except proximity tolerance had minimum inter-unit distances of 0m. Proximity tolerance was a feature in the majority of non-agonistic interactions (42%). However, if only overtly affiliative behaviour is considered, percentages alter to 84% agonistic, 5% affiliative, and 11% containing both agonistic and affiliative interactions.

It was shown in the preceding section that 58% of s/u occasions failed to produce inter-unit interactions: in other words, units may have chosen to tolerate each other's presence at the bai. These latest results appear to suggest that when interaction does take place, agonism is more likely than affiliation. However even these results can be seen as misleading. The breeding success of a silverback, as the leader of the group, is limited by his ability to initially acquire, and subsequently maintain, adult females. Extreme sexual dimorphism attests to the role of the male as both aggressive competitor for females, and protector of his offspring from infanticide and predators. As such, the behaviour of the silverback during inter-unit encounters could be viewed as diagnostic of the overall nature of the interaction, inasmuch as it is predicted that only he will be involved in any aggressive attempts to win females or protect his offspring. It is therefore possible to judge agonistic behaviour not involving the silverbacks of both units (including solitary males) as unthreatening to the cohesion of the group and the well-being of its members. Of course, this is not necessarily to imply that the agonism experienced both by non-silverback aggressor and target animals is not serious within that context, but it does permit a potentially important distinction to be made with regard to the significance of agonistic behaviour between units.

Of 104 occasions of s/u where interactions took place and where agonism was involved, 86 (83%) involved a silverback. However, only 50 (48%) involved the silverbacks of both units in the observed agonism. It may be important to now view these levels against the total frequency of s/u in which units are judged aware of each other. Of 345 occasions of s/u, 30% provoked examples of agonistic behaviour between units. However, only 14.5% involved the silverbacks of both units in that agonism, and even of these potentially serious encounters, 25% also gave rise to examples of affiliative behaviour between group members, whether overt or through tolerance of proximity.

Figure 6.7 illustrates the frequency of interaction types within the three main group-type pairings during s/u interaction encounters. The charts show a reduction in the number of purely agonistic interactions as the potential for non-silverback interactions increases. A recalculation of interaction types comparing only the number of occasions containing agonistic interactions between silverbacks and all other occasions gave the following percentages: Solitary male – solitary male, agonistic = 100%, other = 0%; Solitary male – group, agonistic = 57%, other = 43%; Group – group, agonistic = 28%, other = 72%.

Figure 6.7 Interaction type as a function of unit-type pairing



a) Solitary male - Solitary male interactions

b) Group – Solitary male interaction

c) Group – Group

Comparisons with Maya Bai

Comparing these proportions of behaviour with those recorded at Maya Bai in Odzala (Magliocca, 2000) is problematic due to inclusion there of an undefined behavioural category - "tolérance". However, it is striking that of all s/u occasions at Mbeli, 58% did not give rise to an interaction, while at Maya, an almost identical 62% of s/u occasions resulted in equivalent "indifference". Furthermore 30% of s/u occasions at Mbeli resulted in some form of agonistic interaction, while again in Maya, an almost identical 29% was recorded. However, the ranking of unit-type pairings by the proportion of agonistic interactions of all s/u occasions varied between the two sites, with encounters between solitary males responsible for the most agonistic interactions proportional to their level of s/u at Mbeli, and the least at Maya:

Mbeli - solitary/solitary (38%) > group/group (30%) > group/solitary (26%)
Maya - group/group (33%) > group/solitary (31%) > solitary/solitary (20%)

One possible explanation for this effect may be due to definitions. At Maya, any gorilla entering the bai apparently alone, and not subsequently being identified as part of a group was labelled as solitary. This practice may have overestimated the proportion of solitaries in the population (Magliocca et a., 1999) and also diluted the solitary silverback sample with younger, and possibly even female individuals, whose level of agonism would not be predicted as similar to that of a normal solitary silverback.

Comparisons with Karisoke

Harcourt (1978a) reported that 80% of 19 inter-unit encounters provoked vigorous displays, and that 50% of 16 encounters provoked aggression escalating to physical contact. Other individuals may have become involved, but the core of such interactions was the silverback or solitary silverback of each unit. Sicotte (1993), working with an expanded data set, showed slightly lower levels of agonism than Harcourt: 74% of 58 encounters provoked display agonism while only 17% led to contact aggression. Unfortunately, differences in definitions of what are considered 'encounters', or 'interactions' preclude any direct comparison of these figures with Mbeli.

Sicotte (1993) identified four main encounter types:

'Distant' – gorillas within auditory range (500m), but not physically meeting (may involve chest-beats and hoots)
'Mingling' – non-agonistic meeting of two units
'Displays' – close range displays
'Contact' – fights with physical contact made.

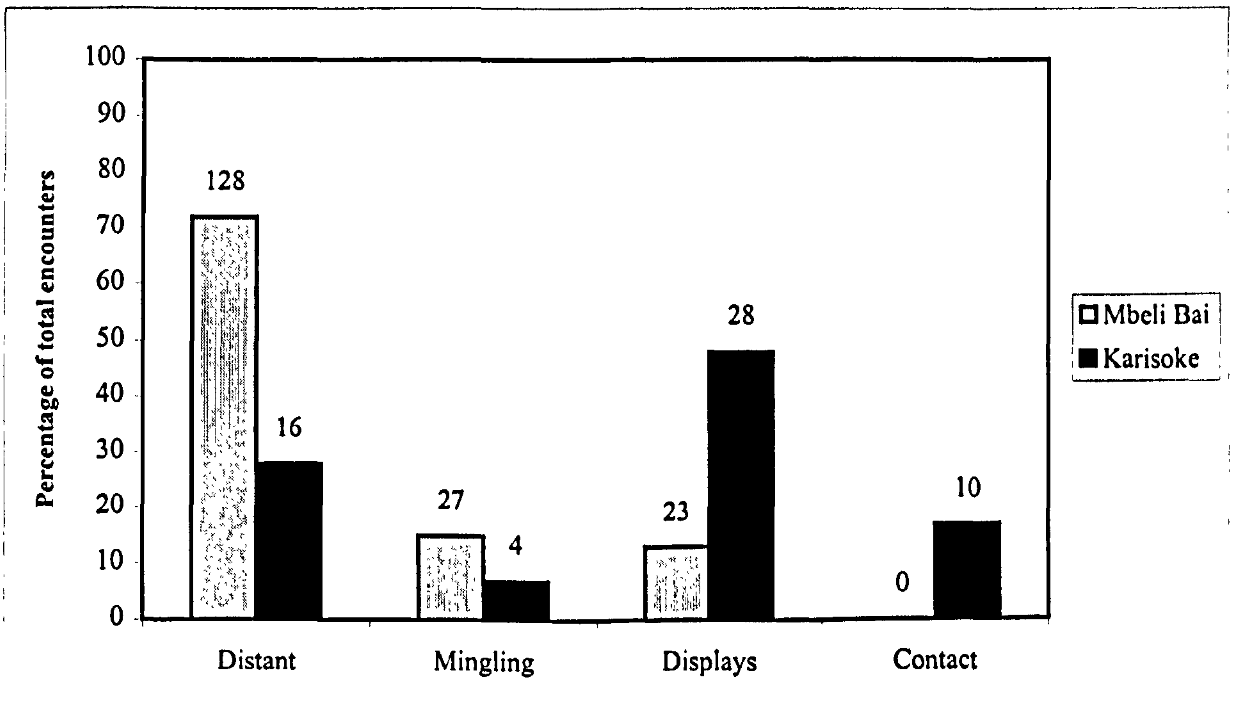
It is not straightforward to place Mbeli encounters within this system, especially as it does not reflect an increase in intensity. In particular, the establishment of a 'distant' category which includes both examples of vocal display and chest-beating, but also occasions where groups failed to interact, tends to confuse the issue on the reaction of groups to each other. For instance, a chest beat given at 100m, but not followed up by any further agonism, may indicate a disinclination to interact, but may conversely, scare the other group to such an extent that they move away from any possibility of an interaction. Comparison with Mbeli would have been better facilitated had the system included a 'no interaction' category.

To fit the Mbeli data to the Karisoke categories, all silverback to silverback displays at 50 metres or above are classed as 'distant'; instances of s/u where no interaction occurred are also placed in this class. Silverback to silverback displays below 50m are classed as 'displays', and silverback to silverback proximity within 50m is classed as 'mingling'. Expanding the close display category to 50m for Mbeli is a conservative measure, as such a distance would usually prevent visual contact at Karisoke. In the bai, with 100% visibility, such a distance may be more critical than might be the case in the forest.

Sicotte regarded each change of a group's breeding profile, whether by gain or loss of adult females, by the cessation of lactational anoestrus, or by the maturation of blackbacks into young silverbacks, as a 'new' group. In order to present a fully independent data-set, she then used the first encounter of each new group as her data point. This clearly removes the potential bias of some group-pair encounters being over-represented in the data, but at the cost of detail. Variation in behaviour was observed between the same groups on consecutive encounters at Mbeli; a factor that may potentially be important. Of 72 independent 'new-group' combinations which met on more than one occasion, three exhibited both 'mingling' and agonistic display on separate meetings: nine showed both distant display or no interaction and close agonistic display: 16 showed distant display or no interaction and close agonistic display, and two responded to each other in all three categories. Independent data points were thus generated for the Mbeli data by taking the mode silverback response for each 'new group' interaction. This yielded 179 independent encounters. Figure 6.8 shows interaction intensity levels in Karisoke and Mbeli using the system devised by Sicotte (1993).

This important chart reveals major differences in the nature of inter-unit interactions between the two sites. Most notably, there were no cases of contact aggression between silverbacks at Mbeli, whereas in mountain gorillas, such behaviour occurred in 17% of all encounters. Close range displays were over three and a half times more frequent at Karisoke, but peaceful mingling was less than half as common as at Mbeli. Distant encounters including some display behaviour but also cases where no interaction took place, were two and a half times more frequent at Mbeli than Karisoke. Furthermore, at Mbeli, approximately 76% of 'distant' encounters failed to produce any discernible interaction.

Figure 6.8 Intensity of silverback-silverback interactions during inter-unit encounters at Mbeli and Karisoke



Values above bars are the actual frequency of encounters in each case

Even allowing for some loss of precision due to the 'fitting-in' of Mbeli data to somewhat awkward Karisoke categories, it is clear that silverbacks sharing Mbeli Bai are considerably more tolerant of each other's presence than those meeting each other in the Virungas. They spend much more time peacefully mingling with each other, and during the relatively few examples of close-range aggression that do take place, none are likely to escalate to physical contact, compared to 17% of cases at Karisoke.

As shown in Table 6.5, when all Mbeli encounters by all units were analysed for silverback interaction intensity, the proportions remained almost unchanged, suggesting that little bias is exerted on the results by the over-representation of one unit or pair of units. Also given is the percentage of encounters per class using the mode for each unit-pairing, having the effect of increasing the proportion of distant display encounters and those where no interaction took place.

Table 6.5 Interaction intensity at Mbeli using all encounters, independent encounters, and mode encounter per unit-pair

	Distant	Mingling	Displays	Contact
Independent data (Mode, *N* = 179)	75%	14%	11%	0%
All encounters (*N* = 313)	78%	13%	9%	0%

Sicotte (1993) used data from Karisoke to examine the relationship between silverback interaction intensity and group composition. In particular, the number of potential migrant females and the total number of females was hypothesised as a predictor of silverback agonism levels. Sicotte chose to take the largest value for total or potential migrant females from each independent pair of interacting units, and then compared the median of these values for each category of silverback behaviour (all cases of distant display/no interaction, mingling, close display, and contact agonism).

Using the largest group size or the largest number of available females in an interacting combination as a measure for the effects of potential gain or loss in breeding opportunities may not, however, be the best defined method. For instance, two groups interacting where one group contains eight members and the other, nine, would have a considerably higher score attributed to their interaction (9) than two groups of two and five members respectively. And yet, greater agonism might be predicted in the latter interaction as the *difference* in number is greater. It is suggested that group size or adult female number differential between two groups should be a better predictor of interaction outcome than largest number alone.

At Mbeli, the relationship between silverback-silverback response to simultaneous bai-use (using Karisoke behaviour categories) and group composition was examined using the following independent variables: largest group size, difference in group size, largest number of available adult females (without unweaned infants), difference in available females, largest number of adult females (with or without infants), and difference in numbers of adult females. Clearly, it was inappropriate to include interactions between solitary males. Medians were compared using a Kruskal-Wallis test for each independent variable in turn, and the data were analysed first for group-group interactions only, and then for group-group and group-solitary male interactions (N was 99 for the former sub-set and 171 for the latter). In none of the tests performed did the difference between medians deviate from chance (with P at 0.05). This suggests that the intensity of silverback interaction was a random effect, or that other variables exerted a stronger influence on behaviour than the potential for breeding female gain or loss.

At Karisoke by contrast, a significant difference was found in the median largest number of potential migrant females, according to the intensity of silverback interactions; with the median number of potential migrants significantly higher among silverbacks that exhibited contact aggression than those that mingled (Sicotte 1993). Significance was upheld when the same test was performed on total number of females, regardless of their potential for emigration.

The degree of 'familiarity' between units at Mbeli was considered as a potential influence on silverback behaviour during s/u occasions. The zone in which social units entered the bai could not be considered as a sufficiently accurate measure of the degree of home-range overlap or 'familiarity' between units (*see* Chapter 3), and consequently, association index scores (the relative number of occasions units spent in the clearing with each other) were examined as a potential variable. A Kruskal-Wallis test ($\chi^2 = 9.92$, df = 2, $P < 0.007$) revealed a significant difference between median association index scores for unit pairings resulting from modal silverback intensity responses of either 'distant', 'mingling', or 'displays', as defined by Sicotte (1993). Median association index scores were as follows:

Distant display or no interaction – 0.039, IQR 0.037
Mingling – 0.071, IQR 0.044
Close display – 0.039, IQR 0.052

Post-hoc comparisons on the Kruskal-Wallis test reveal that the median for 'mingling' was significantly higher than that for both of the other categories. Thus it appeared that units that shared the bai more frequently were more disposed to peaceful, tolerant and even affiliative interactions.

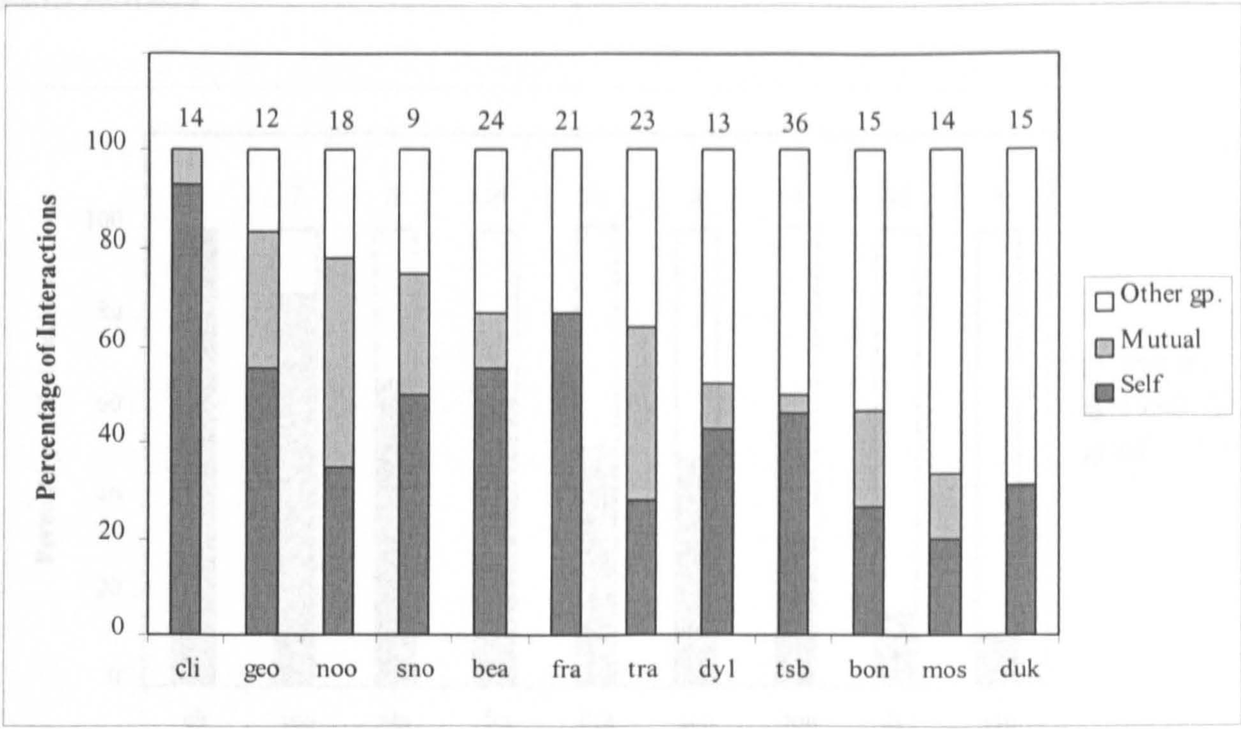
Initiation of interactions

While it takes at least two units to create any interaction, whether it be agonistic, affiliative or neutral, in the case of agonistic encounters, scoring both units as equal 'partners' in the behaviour may be misleading, as in many cases, there may be a clear aggressor unit, and a clear target for that aggression. Two methods of examining this dynamic are to identify the initiator in any encounter, and the unit deemed to have been dominant in the encounter.

Of 144 interactions, one unit or other could be identified as having been the initiator on 94 (65%). On 23 occasions (16%), both groups appeared equally responsible for initiating the interaction, and on 27 occasions (19%) no clear initiating unit could be identified. Figure 6.9 shows the percentage of interactions initiated by each unit, where the number of initiator-identified occasions was six or over (range 9 to 47). Individuals are ranked according to the total percentage of interactions initiated by that unit (self) plus those mutually initiated by both groups.

The chart shows a considerable variation in the proportion of interactions initiated by the various units. This may reflect some aspects of a unit's sociality or 'self-assurance'. CLI group, for instance, initiated 93% of their interactions, with 7% (one interaction) mutually initiated. Conversely, DUK group appeared much less assertive and only initiated 31% of their interactions.

Figure 6.9 Percentage of all interactions self-, mutual-, and other-group-initiated

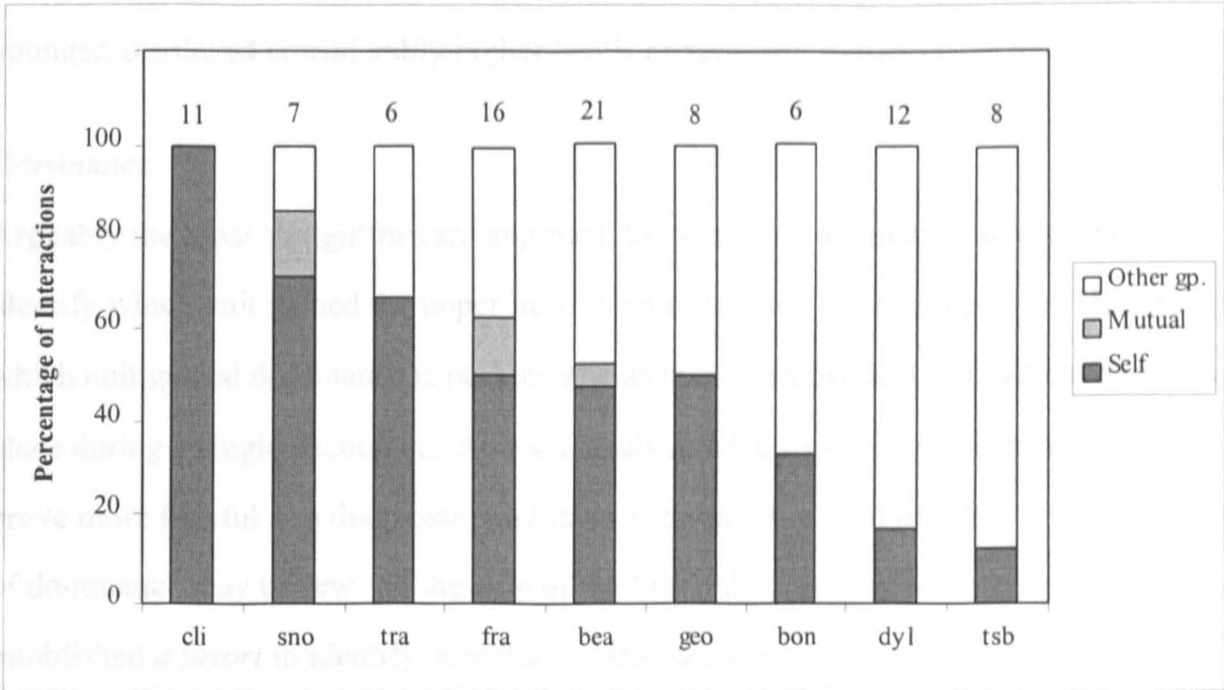


Values above bars refer to the total number of interactions in which an initiator could be identified.

When only agonistic interactions by silverbacks are considered, similar variation remains present. Prohibitively low sample sizes preclude the inclusion of some units in Figure 6.10, and differential rates of agonistic encounter have altered the ranking of initiators from Fig. 6.9. Notably, however, Clive (CLI group) was never involved in an agonistic encounter initiated by another group. At the other extreme, both the young solitary silverback Dylan and Solomon of TSB group initiated less than a fifth of the agonistic interactions in which they were involved.

Unfortunately, the sample sizes available do not allow an in-depth statistical analysis of the reasons for the variation in initiation rates among units. It is likely that a combination of variables will influence the behaviour of a unit, including the age, experience and physical stature of a silverback, whether the unit is a social group or a solitary male, the presence of older though not yet mature males in the unit, the threat of losing females to a competitor or the chance of acquiring them, the historical relationship between two units (possibly mediated through kin ties or adjacent/overlapping ranges), and the personality of the silverbacks involved (possibly influenced by conditions of social development and past experiences of interaction).

Figure 6.10 Percentage of agonistic silverback interactions self-, mutual- and other group-initiated



Values above bars refer to the total number of interactions in which an initiator could be identified.

Once again considering CLI group, the presence of three breeding females may induce strongly defensive behaviour (as may the presence of four females in SNO group). However, other groups contained more females and exhibited lower levels of agonistic initiation (i.e., DUK group). Clive is believed to have been badly injured by another silverback in August 1996, at around the time that he lost four young females to solitary silverback Max. A naturally aggressive personality may have originally led Clive into this encounter, but whether so or not, it is quite possible that the experience rendered him more nervous and aggressive in subsequent encounters. Of course, it could as easily be predicted that being defeated in an extremely violent encounter might cause a silverback to shy from further opportunities to interact with other silverbacks, though this does not appear to have been the case with Clive.

TSB group showed the lowest level of agonistic initiation, and it is interesting to note that for almost half of the study period, the group contained no breeding females at all, and even in the remaining time-span, only contained a single female with a new-born infant. The subjective impressions gained of silverback temperament during the study are largely borne out by the data. Both Clive and Caravaggio (SNO group) appeared cantankerous and aggressive, while Dylan and Solomon (TBS group) were for the most part calm and retiring. Dylan's youth might be seen as an explanation for his disinclination to initiate agonistic interactions, though Frank, who may if anything, have been even younger, displayed considerably higher levels of agonistic initiation.

Dominance

Arguably the most straightforward approach to examining agonistic interactions is to identify which unit gained the upper hand in an encounter. At a group level, identifying which unit gained dominance is problematic as many independent interactions may take place during a single encounter. As such, analysis of individual dyadic encounters may prove more fruitful as a diagnostic tool in such cases. A related problem is that overt signs of dominance may be few. In the case of the Mbeli data, no formal criteria were established *a priori* to identify dominance. Instead, a subjective assessment was made following each encounter based on the overall behaviour of the groups involved. The subordinate unit was typically identified as such if it, or most of its members retreated from the approach or displays of the opposing unit. While leaving the bai was not required, the retreat did have to consist of a substantial change of location in clear association with the approach or display/contact behaviour of the other unit. In practice, it was found that in many cases, the observer was unable to unambiguously ascribe dominance to one unit over another. Indeed, of 60 agonistic encounters that involved one or both of the opposing units silverbacks, in only 50% of cases could a dominant unit be identified.

Of the 29 encounters in which both initiator and dominant unit could be identified, it was found that the initiating group gained dominance in 66% of cases. This may suggest that units are more likely to initiate an agonistic interaction when they believe the chances of gaining dominance are favourable. However, it should be borne in mind that a retreat may signal subordination, but may also be evidence merely of a unit's disinclination to interact, for no better reason than the desire, for instance, to feed in peace.

The data are insufficient for robust analysis of the effects of group size or other variables on the outcome of encounters, though it was found that in all but 3 of 13 cases of agonistic interaction between solitary males and groups, solitary males became the subordinate unit. The outcome in group – group interactions was less predictable, with half of all interactions being 'won' by the unit with the lower total group size of the pair. In solitary male – solitary male encounters, the elder of the two males was dominant in all six interactions, though the high proportion of encounters between Bear and Frank means that a lack of independence was liable to bias the result. Data on encounter outcomes for individual groups are few and sample sizes prohibitively low. Solitary male Bear was dominant in 7 of 10 encounters, CLI group in 4 of 6, and TSB group in 6 of 8. Meanwhile, young solitary male Frank was only dominant in 1 of 10 encounters.

Summary of simultaneous bai-use and unit-level analysis

- No significant differences exist between frequencies of s/u between social groups and solitary males.
- Visit length is not a significant influence on the frequency of s/u when young or unfamiliar solitary males are removed from the data. Infrequent visitors reduce the likelihood of their meeting other units in the bai by shortening their visit duration.
- Over half of s/u events involve two units only, though up to five units have used the bai simultaneously.
- Association indices do not vary significantly dependent on whether s/u pairs are both groups, both solitary males, or one of each (N.B. solitary males and groups shared the bai the least, and solitaries with other solitaries the most).
- There is significant variation in association indices among solitary males, among groups, and across both unit types. While some groups show significantly higher association indices both than other groups and solitaries, no solitary male associates significantly more frequently than a group.
- Only one group-group pairing features in the top 5% of association index scores. The remaining groupings are all solitary male – group, with the same solitary male individual implicated in each case.
- On 11% of 389 s/u occasions, pairs of units were judged to have been unaware of each other's presence in the bai.

- No interaction took place on 58% of s/u occasions between groups judged aware of each other.
- Rates of interaction during 'aware' occasions of s/u do not differ significantly depending on whether the pairing is group – group, group – solitary, or solitary - solitary. However, group – group pairings are the most frequent and solitary – solitary, the least.
- Units interacting with each other do so at significantly shorter distances than those not interacting. There is no difference, however, between the minimum distance of interacting groups and interacting solitary males. Some individual males and some groups do show significantly greater inter-unit distances during interaction than others.
- The distance between silverbacks during interaction occasions of s/u is significantly greater than the minimum distance recorded between the groups.
- Of s/u occasions where inter-unit interaction took place, 54% were agonistic only, 28% were only affiliative (including proximity tolerance), and 18% included examples of both interaction types. However, of all agonistic encounters, only 48% involved the silverbacks of both units (translating to a mere 15% of all 'aware' s/u occasions, a quarter of which also gave rise to affiliative behaviour by non-silverback group members).
- The percentage of silverback – silverback agonistic interactions is highest among solitary males and lowest between group silverbacks.
- The frequency at which units initiate agonistic interactions varies considerably across the population. It is suggested that the character of a given silverback, mediated by factors such as past experiences of interaction, and the composition of his group compared with that of the other group, may be important in influencing whether a unit initiates fewer or more interactions.
- Levels of interaction intensity (measured by the behaviour of silverbacks only) differ greatly at Karisoke and Mbeli. Contact agonism took place on 17% of Karisoke inter-unit encounters but was never witnessed at Mbeli Bai. Close range displays were over three and a half times more frequent at Karisoke, but peaceful mingling was less than half as common as at Mbeli. Finally, distant encounters including some display

behaviour but also cases where no interaction took place, were two and a half times more frequent at Mbeli than Karisoke.

- At Karisoke greater silverback agonism correlated positively with the potential for female gain or loss. No such relationship was evident at Mbeli. However median association index scores were significantly higher in units exhibiting peaceful mingling, than those exhibiting displays, suggesting that tolerant or affiliative behaviour increases with increased familiarity between units.

Dyadic interactions

The results presented previously in Table 6.4 and Figure 6.7 all attest to the fact that an inter-unit interaction, while potentially being orchestrated and executed solely by the silverbacks of both units, can also comprise several independent interactions. Furthermore, independent interactions within an inter-unit encounter may occasionally contrast strikingly with others taking place simultaneously; juveniles may be seen playing while at the same time, blackbacks engage in apparently serious agonistic behaviour. For this reason, it is necessary, having described the overall nature of inter-unit interaction, to examine the component parts of such interactions; in other words, the behaviour of independent interacting dyads. Triadic encounters, and those involving even greater numbers of individuals were witnessed at Mbeli, but the number of such interactions was limited, and their analysis extremely problematic. As such, this section concentrates primarily on the behaviour taking place between two individuals from different units. Clearly it is necessary to examine the nature of the interactions between age/sex-class combinations, however the great number of possible combinations divide the data into very small sample sizes for each interaction type, making analysis problematic. It is therefore important to gain as much information as possible from overall levels of interaction before moving forward.

In total, 208 independent dyadic interactions were recorded, involving 55 known individuals from both sexes, and from all age-classes except infant. With the total number of gorilla unit visits at 1061, dyadic interactions took place on 20% of visits, or at 0.2 interactions per visit.

Frequency of interactions by age- and sex-class, and by age/sex-class combination

Table 6.6 shows an initial breakdown of the data into age/sex-class combinations, and gives the number of interactions for each combination class observed during the study period. The list is ranked with the most commonly interacting classes first. The most obvious character of the data is the lack of interactions involving infants. Although gorillas under three years may well have been alarmed by agonistic interactions involving their mothers, or interested in the affiliative behaviour of other immatures playing around them, their dependence on their mothers at this age ensures that they seldom stray more than a few meters from them and seek their protection at the slightest alarm. The protective behaviour of the mother also contributes to the fact that any individual interested in an infant will, by default, find itself interacting with the mother. Sub-adults of unknown sex, adult females, and young silverbacks also appear to exhibit generally low rates of interaction.

Table 6.6 Frequency of dyadic interaction per age/sex-class combination.

A/s mix	Number of interactions	A/s mix	Number of interactions	A/s mix	Number of interactions
bb-sam	23	af-juv	2	inf-sad	0
bb-bb	18	af-af	2	inf-saf	0
sb-ssb	18	af-ssb	2	inf-sam	0
bb-juv	18	juv-sb	2	inf-sb	0
ssb-ssb	16	sam-sb	2	inf-ssb	0
af-bb	14	ssb-ysb	2	inf-ysb	0
bb-ssb	14	af-saf	1	juv-sad	0
juv-juv	13	bb-sad	1	juv-ssb	0
sb-sb	10	sad-ssb	1	juv-ysb	0
juv-sam	9	sam-ysb	1	sad-sam	0
af-sam	8	sb-ysb	1	sad-sb	0
bb-sb	6	af-inf	0	sad-ysb	0
juv-saf	4	af-sad	0	saf-ssb	0
saf-sam	4	af-sb	0	saf-ysb	0
saf-saf	3	af-ysb	0	ysb-ysb	0
saf-sb	3	bb-ysb	0	sad-saf	0
sam-sam	3	bb-inf	0	sad-sad	0
sam-ssb	3	inf-inf	0		
bb-saf	3	inf-juv	0		

As outlined in the Methods section however, these figures do not account for the potential rate of interaction as a function of the number of individuals per group in each age/sex-class. Calculating the total number of individual combinations per combination type for all occasions of aware simultaneous bai-use creates what can be termed a 'potential interaction index' (P.I.I.- *see* Methods). It is then possible to express the actual number of interactions as a proportion of the P.I.I. (assuming only one encounter between any given pair of individuals per visit).

Table 6.7 ranks age/sex-classes based on these corrected proportions. All combinations involving infants have been combined in one class. Also, due to the low level of potential interactions, data for sub-adult females and unsexed sub-adults are combined to form the "sad" – sub-adult class (excl. confirmed males). Even with these classes collapsed, the ranking of the combination with the highest percentage (unsexed sub-adults with unsexed sub-adults – marked with an asterisk) can be viewed as a statistical artefact resulting from the extremely low likelihood of this combination occurring. The remaining values are, however, likely to represent a fairly accurate index for the frequency of interaction, corrected for combination potential in the population. As there may be some loss of independence to certain individuals appearing more than once in the data, a column is provided giving the number of individuals represented in each combination type. For instance, were the data fully independent, the number of individuals responsible for ssb-ssb interactions would be twice the number of actual interactions observed (2 x 16 = 32), however, only 6 individuals were implicated, suggesting that a considerable compromise to independence may be present. By contrast, the data for af-juv interactions show that no individuals were involved in more than one interaction; hence the data for this combination are fully independent.

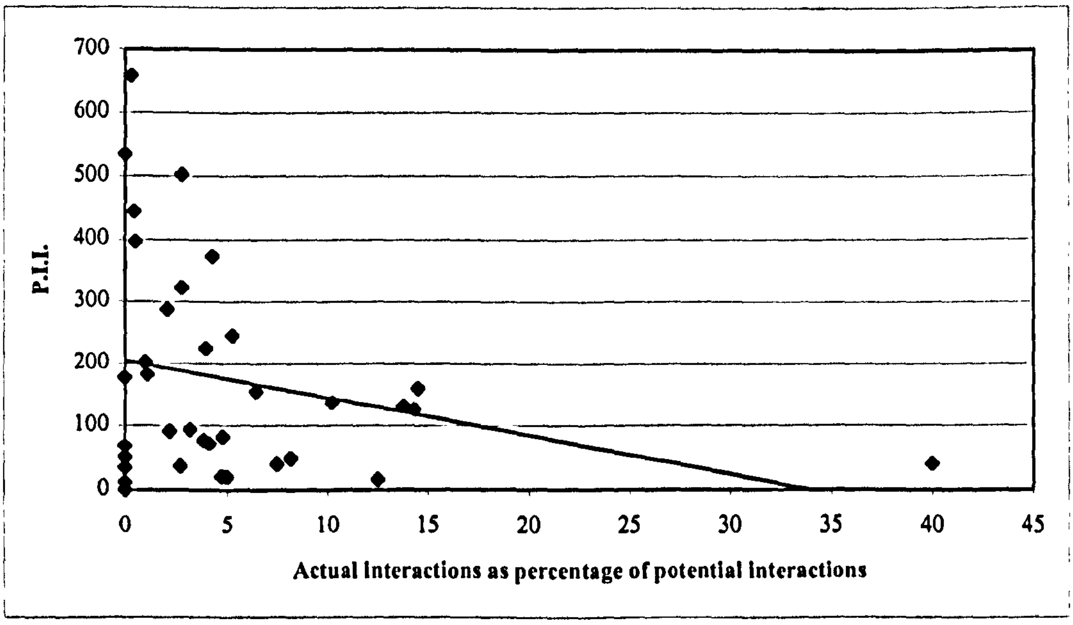
Table 6.7 Dyadic interaction per age/sex-class combination as a percentage of total possible combinations, with values for the difference in development stage, the number of individuals per class, and initiator identity

A/s mix	Potential (PII)	Actual	Percentage (ranked)	Number of individuals	Number of dyads	Difference in age-class stage	% of 'actual' that 1st of combi. initiated interaction
sad-sad	7	3	42.9*	4	3	0	-
ssb-ssb	40	16	40.00	6	7	0	-
bb-bb	131	20	15.3	9	14	0	-
bb-sam	159	24	15.1	13	15	1	54
sb-ssb	126	18	14.3	13	13	0	72
ssb-ysb	16	2	12.5	3	2	1	50
bb-ssb	137	14	10.2	11	11	1	86
sad-sam	49	4	8.2	6	4	0	25
sam-sam	40	3	7.5	4	3	0	-
sb-sb	155	10	6.5	8	10	0	-
juv-juv	245	13	5.3	9	11	0	-
bb-sad	77	4	5.2	7	4	1	75
sam-ysb	20	1	5.0	-	1	2	100
juv-sad	83	4	4.8	7	4	1	75
sad-ssb	21	1	4.8	-	1	1.5	100
bb-juv	373	18	4.8	18	17	1.5	50
sad-sb	72	3	4.2	6	3	1.5	33
juv-sam	225	9	4.0	8	8	1	78
sam-ssb	94	3	3.2	5	3	3	33
sb-ysb	37	1	2.7	-	1	1	0
af-sam	323	8	2.5	12	8	3	50
af-bb	503	12	2.4	16	12	2	29
bb-sb	288	6	2.1	9	5	2	100
af-sad	91	1	1.1	-	1	1.5	0
sam-sb	182	2	1.1	3	2	3	50
af-ssb	202	2	1.0	2	1	0	0
juv-sb	397	2	0.5	4	2	3.5	50
af – af	445	2	0.5	3	2	0	-
af-juv	659	2	0.3	4	2	3	100
sad-ysb	12	0	0	-	-	1.5	-
af-sb	535	0	0	-	-	0	-
af-ysb	68	0	0	-	-	1	-
bb-ysb	35	0	0	-	-	1	-
juv-ssb	177	0	0	-	-	3	-
juv-ysb	51	0	0	-	-	2.5	-
inf-others	1473	0	0	-	-	-	-
ysb-ysb	0	0	0	-	-	-	-

An alternative approach to the independence issue that may be pertinent to the later analysis of interaction type by age/sex-class is given in the sixth column from the left. Here, the number of independent dyads is shown, such that, for instance, in the adult female – blackback class, while independence is compromised when the number of individuals is examined (24 individuals are required and only 16 are involved), there were no duplicate dyads (12 out of 12 interactions involved a different combination of individuals).

Figure 6.11 plots the potential number of interactions for each combination type against the percentage of that number where interactions actually took place. Sad-sad interactions and those involving infants are removed from the analysis to prevent their aberrant or misleading bias on the data.

Figure 6.11 Scattergram of actual interactions as a percentage of P.I.I. against P.I.I.



A Spearman Rank test on the data failed to show a significant positive correlation (r_s = -0.229, N =34, P = 0.192), showing that interaction rate did not increase with the potential for interaction. This suggests that in some age/sex-class combinations, gorillas may be interacting more or less frequently than might be predicted on the basis of numbers alone.

Age differences

In the second column from the right in Table 6.7, the difference in number of stages between age-classes in combinations is given; i.e., a sub-adult male would have to cross three age-class boundaries (blackback, young silverback and silverback) to reach the silverback class, hence the combination 'sam-sb' is scored 3. Where there is a difference in the number of stages to maturity between males and females, the median number of stages is given, accounting for the half scores present.

Statistical methods are not appropriate for examining this variable, however the distribution of zero scores across age/sex combinations shown in Table 6.7 suggests that the highest levels of interaction are between individuals of the same developmental stage. Of the top third of combinations, 67% ($N = 12$) were 'same age', representing 49% of all actual interactions.

Sex differences

Of the top third of combinations (excluding sad-sad), 75% are between males, representing 51% of all interactions. 67% of male-male combination types were within the top third of the data. Of particular significance may be the extremely high percentage score for interactions between solitary silverbacks (ssb-ssb). Of the 40 potential opportunities for interaction between individuals of this class, interactions took place on 16 (40%). The relatively low number of potential opportunities may give some cause for concern as does the obvious possibility for bias resulting from their being only six individuals represented in the sample. Only seven solitary males were present in the population, so a lack of independence is inevitable. However, within these limitations, the data do suggest that this age/sex/social-class may interact more frequently than any other. In fact, the nearest other combination (bb-bb) had an interaction percentage of less than half that of solitary silverbacks. Solitary silverbacks also scored highly in the frequency of their interactions with group silverbacks, young silverbacks, and blackbacks. Perhaps surprisingly, combinations containing group silverbacks only appear twice in the top third of cases, while all examples of the adolescent male classes 'sub-adult male' and 'blackback' in interactions within and between each other appeared within the top third.

As mentioned, infants were never directly involved in inter-group interaction. It was more surprising to find that adult females were the next lowest ranked. Combinations involving adult females were by far the most likely in terms of the number of opportunities generated by occasions of simultaneous bai-use (3207), and yet adult females were only involved in 29 interactions (0.9%). There were only two interactions between adult females and adult females, and none recorded directly between silverbacks and adult females (though some silverback-silverback/solitary silverback interactions resulted from an apparent approach towards an adult female by one of the males). Table 6.8 gives the total opportunities for interaction for each age/sex-class with all others. Inevitably, these figures are not independent, however the comparison is a useful one nevertheless, showing blackbacks as the most frequently interactive gorillas, adult females and infants as the least frequent, with group silverbacks only attaining the median position in the ranking.

Table 6.8 Potential and actual numbers of interactions for each age/sex-class

Age/sex-class	Potential interactions	Actual interactions	Actual as percentage of potential
bb	1984	98	4.9
ssb	902	40	4.4
sam	1221	54	4.4
sad	451	20	4.4
sb	2024	42	2.1
juv	2476	48	1.9
ysb	267	4	1.5
af	3207	29	0.9
inf	1473	0	0

Initiation of interactions

The last column in Table 6.7 gives the percentage of actual interactions for each age/sex combination that were initiated by the first named class in the combination label (e.g., 54% of the 24 interactions between blackbacks and sub-adult males were initiated by blackbacks). Table 6.9 takes the actual numbers of interactions initiated by each age/sex-class (in combinations where the total *N* of interactions was 6 or over) and uses the binomial test (Siegel and Castellan, 1988) to determine if in one class initiated interaction significantly more times than the other. The resulting *P* values show that only two did so. Blackbacks initiated significantly more interactions with solitary silverbacks than vice-versa, but all interactions between blackbacks and silverbacks were initiated by the silverbacks.

Table 6.9 Numbers of interactions initiated per age/sex-class and probability of deviation from chance

Combination		Interactions initiated		P – value (binomial test)
A	B	A	B	
bb	ssb	12	2	0.013
sb	bb	6	0	0.031
sb	ssb	13	5	0.096
bb	af	10	4	0.180
juv	sam	7	2	0.180
bb	sam	13	11	0.839
bb	juv	9	9	1.000
af	sam	4	4	1.000

When interpreting such results without a hypothesis, there is a danger of inventing scenarios to fit the data, and care should be taken that equally plausible explanations could not also be found were the results reversed. In this case, a potential explanation may be as follows: The greater propensity of group silverbacks to initiate interaction with solitary silverbacks did not reach significance; however with the same proportions, only an increase in sample size from 18 to 25 would be required for significance to be reached. The primary goal of any solitary male is to attract and acquire females from established groups. In order to do so, a solitary male may shadow groups through the forest, needing only to make his presence known and then hoping that a female will seek an opportunity to join him. Exuberant displays are therefore not strictly necessary, and any behaviour that overtly provokes the group silverback may increase the risk of a violent inter-silverback encounter, and may be avoided. Group silverbacks, on the other hand, run the risk of losing females if they fail to warn solitary silverbacks away from their groups. Within this dynamic, provocative blackbacks may be able to display at and engage solitary silverbacks under the proximal protection of their putative fathers, and with a much reduced risk of reprisal. Despite their apparent eagerness to engage older males in interaction, however, blackbacks initiated none of their interactions with group silverbacks. With only six cases to draw from, it is perhaps unwise to seek overly elaborate explanations, although, it is worth noting that in several of these cases, the blackback in question was targeted after seeking close proximity to the silverback's group and sometimes displaying. In these cases, blackbacks are likely to be testing the limits of what is and is not permissible during interaction. They may also be attempting to attract the attention of females. Silverbacks may be intolerant of such proximity and behaviour, knowing that these same individuals will be potentially highly acquisitive solitary silverbacks within one to five years, and it may be beneficial to assert dominance over such males before they complete their physical development. For a blackback to be in a position to approach another group, it is likely that both groups are feeding relatively peacefully in view of each other. Thus the silverbacks of both groups may have established a degree of tolerance to each other's presence that would not be served by the aggressive defence of a blackback, unless perhaps the aggression was particularly severe.

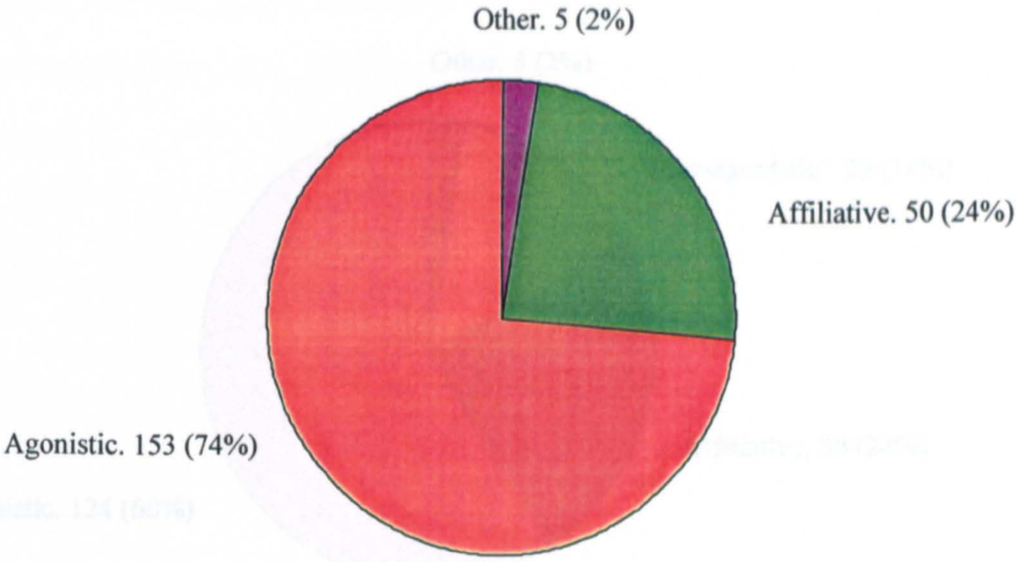
Distance and duration

In all cases, the shortest distance between two individuals was recorded. The median distance between interacting dyads was found to be 4 meters (range = 0 to 200 meters, IQR = 7), where a score of zero is given for interactions that include physical contact. As mentioned, the timing of interactions was found to be problematic, and as such, interaction frequency is expressed as a proportion of the number of opportunities to interact that were available to each individual. An attempt was made to time interactions where possible, but these descriptive statistics should be seen as a guide only. The median length of dyadic interaction was 2.5 minutes (range = < 1 min. to 171 mins. IQR = 9).

Interaction type

Interactions were judged initially as either 'agonistic', 'affiliative' or 'other' (interaction type unknown or cryptic). Figure 6.12 shows the number of interactions of each type and the percentage they formed of the total.

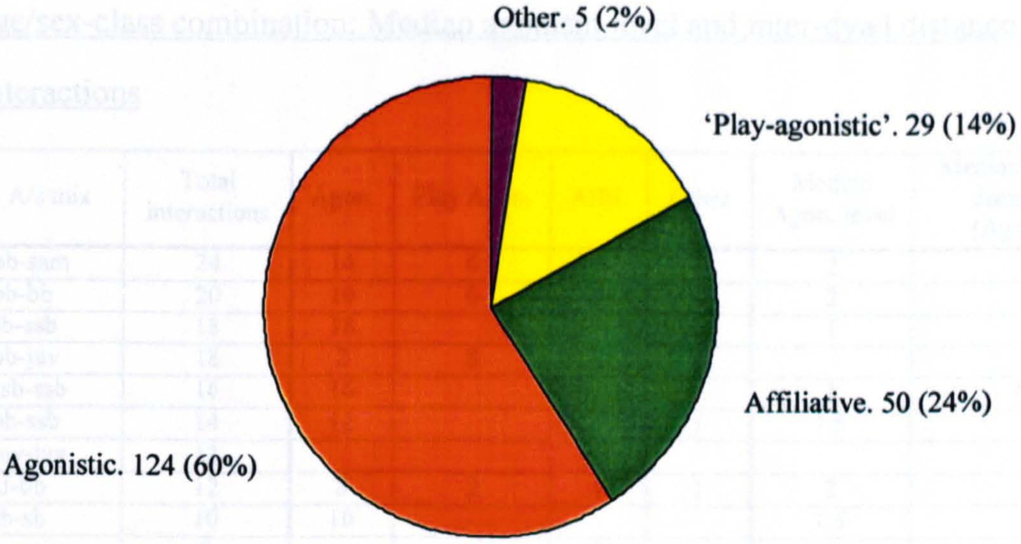
Figure 6.12 Number and percentage of dyadic interactions of each main type



No systematic attempt was made, when collecting interaction data on dyads, to account for affiliation by proximity tolerance. Hence, as mentioned in the analysis of simultaneous bai-use, these figures may in part, result from the less conspicuous nature of some affiliative interactions, and thus, their potential for being overlooked.

Also in the analysis of simultaneous bai-use, issues relating to the nature of agonism were raised. This issue is also important to the analysis of dyadic interactions. Of the 153 agonistic interactions, 29 (19%) were removed as examples of boisterous exhuberance by young males (or ‘play agonism’). This is a conservative estimate, and it is likely that more interactions may have been of this nature (N.B. Recall that in the s/u analysis, only agonism between silverbacks was judged to be of immediate importance to group stability and cohesion). While these instances do not necessarily belong in the ‘agonism’ set, adding them to the ‘affiliative’ interactions may also be misleading. Hence, ‘play-agonism’ is retained as a distinct category, with the revised figures presented in Figure 6.13. It does not, however, include play wrestling and similar behaviour among juveniles, who showed no ambiguity with regard to the nature of their interactions.

Figure 6.13 Revised number and percentage of dyadic interactions per interaction type



Interaction type and age/sex class

Table 6.10 lists the age/sex-class combinations shown in Table 6.7, giving the frequency of each of interaction in each main interaction type. Combination classes are ranked by the total number of interactions observed. Median values are shown only where the sample size for agonistic interactions was six or over. Little can be said regarding the distribution of interactions for combinations with low sample sizes, and it must be remembered that even those above the threshold for statistical comparability are still relatively low.

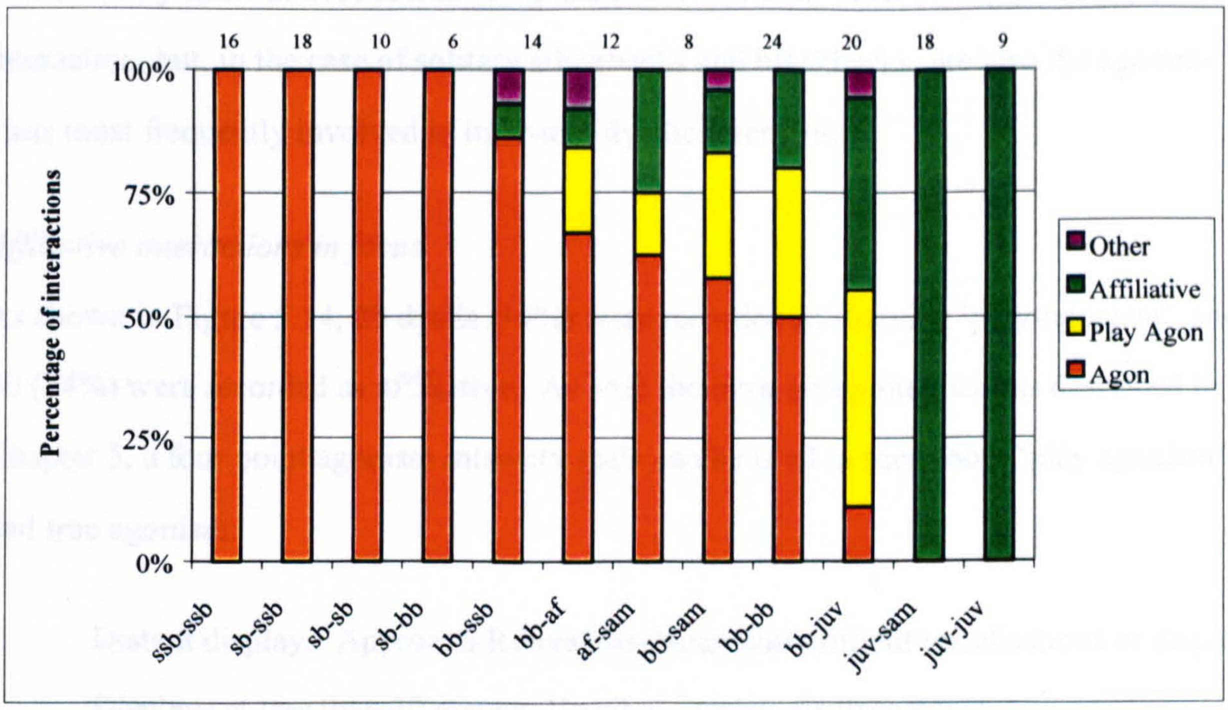
Table 6.10 Distribution of interactions across five main interaction types for each age/sex-class combination: Median agonism level and inter-dyad distance for agonistic interactions

A/s mix	Total interactions	Agon.	Play Agon.	Affil.	Other	Median Agon. level	Median inter-dyad distance (m) (Agon only)
bb-sam	24	14	6	3	1	2	2
bb-bb	20	10	6	4		2	3
sb-ssb	18	18				1	40
bb-juv	18	2	8	7	1		
ssb-ssb	16	16				1	42.5
bb-ssb	14	12		1	1	1.5	5.5
juv-juv	13			13			
af-bb	12	8	2	1	1	2	5.5
sb-sb	10	10				1.5	16
juv-sam	9			9			
af-sam	8	5	1	2		1	2
bb-sb	6	6				2	5
sad-sam	4	1	1	2			
juv-sad	4		2	2			
bb-sad	4	2	1	1			
sad-sad	3	2	1				
sam-sam	3	1		2			
sad-sb	3	1		1	1		
sam-ssb	3	3					
ssb-ysb	2	2					
sam-sb	2	2					
af-ssb	2			1			
juv-sb	2	1		1			
af-af	2	2					
af-juv	2	1		1			
sad-ssb	1	1					
sb-ysb	1	1					
sam-ysb	1		1				
af-sad	1						
sad-ysb	0						
af-sb	0						
af-ysb	0						
bb-ysb	0						
juv-ssb	0						
juv-ysb	0						
inf-others	0						
ysb-ysb	0						

Agon. – Agonistic. Play agon. – Play agonism. Affil. – Affiliative.

Figure 6.14 expresses the distribution of interaction types as a percentage of total interactions for all combinations with a sample size of six or above.

Figure 6.14 Distribution of interaction types as a percentage of total interactions



Values above the columns show the total number of interactions for each age/sex combination

This chart is useful in that it appears to indicate a positive correlation between age (developmental stage) and frequency of agonistic interactions. Only combinations with one or both individuals of silverback or solitary silverback status exhibit exclusively agonistic interactions, and the level of affiliative and play agonistic interactions increases, with only one exception, as the combined age of the participants decreases. Juveniles were implicated in the only two combinations to show exclusively affiliative interactions; in one case, with other juveniles, and in the other, with sub-adult males.

Given the subjective nature of the assessment of interaction types, there may be a danger of veering towards a circular effect whereby, for instance, any behaviour by juveniles is scored as play/affiliative *because* the individuals concerned are juveniles, and so on. However, with the exception of a marginally grey area in regard to play-agonism in blackbacks, it is believed that the effects shown in Figure 5.14 are genuine. The presence or absence of vocal, facial, and other cues usually allows for what is believed to be a relatively accurate assessment of the nature of each interaction.

The overall levels of agonistic and affiliative interaction shown in the pie-chart of Figure 6.13, can now be viewed with greater insight. The high frequency of agonistic interactions recorded is primarily due to blackbacks, solitary silverbacks, and silverbacks, who not only show almost exclusive agonism towards each other during proactive interaction, but, in the case of solitary silverbacks and blackbacks, are also the age/sex-class most frequently involved in inter-unit dyadic interaction.

Affiliative interactions in focus

As shown in Figure 5.14, 29 dyads (14%) were recorded as showing 'play-agonism', and 50 (24%) were recorded as affiliative. As with the intra-group interactions described in Chapter 5, a four point agonism intensity scale can be used to score both 'play agonism' and true agonism:

1. Distant displays. Approach-Retreat displacements without vocalisations or display.
2. Displays at less than 30 meters. Vocal or display displacements.
3. Mild contact aggression: slaps, grabs, pushes etc. Unlikely to cause injury.
4. Severe contact aggression: biting, hitting etc. Likely to cause injury

The system is designed primarily for the analysis of genuine agonism (next section), and as such, includes the category for severe contact aggression. Where the same dyad occurred more than once, the average score was taken for all its interactions. The median score for 28 independent dyads was 2, though, as Table 6.11 shows, the proportional frequency of physical contact was twice that seen in 'true' agonism, largely at the expense of distant displays (*see* page 292 – ag in focus).

Table 6.11 Frequency of agonism intensity scores for 'play agonism'

Agonism score	Frequency	Percentage
1	3	11
2	20	71
3	5	18
4	0	0
TOTAL	28	-

An extract from Field Notes, describing a particularly light-hearted bout of play-agonism between two blackbacks is given in appendix A6.1.

Returning to more standard affiliative interactions, Table 6.12 gives the social context of the 50 examples of dyadic affiliative interactions between individuals of differing units.

Table 6.12 Frequency of social context for affiliative dyadic interactions

Affiliative interaction	Frequency of examples	Percentage
Play	24	48
Greeting	12	24
Seeking proximity	9	18
Genital inspection	4	8
Unknown	1	2
TOTAL	50	-

'Play' was a mutual activity generally characterised by chasing, wrestling and displays of exuberance, occasionally accompanied by a 'play-face'. 'Greeting' describes interactions where one or both individuals, on first reaching close proximity, made some gesture of physical acknowledgement. Examples of this behaviour were identified if play behaviour did not immediately follow the encounter. In all but one case, greetings involved physical contact. On 9 of the 12 interactions, staring at the face of the other was recorded, and in 6 of 12 cases, closed lip, mouth-to-mouth 'kisses' were observed. In these situations, it was not always obvious whether mouth contact was the main behavioural element or if close eye-to-eye contact or face sniffing were more important. Staring was observed without 'kissing' so independent functions may exist, though a kiss greeting automatically entailed eye-to-eye contact and would also facilitate sniffing (*see* Appendix 7, Section II for a fuller description of staring behaviour). Six cases involved sniffing other parts of the body including the torso and the genitals. Touching of the genitals of the other with the hand was seen on three occasions (the hand is frequently sniffed following contact), and in one case the pair embraced in a full ventro-ventral hug. Cases of 'genital inspection' were distinguished from these if they were not accompanied by some form of return gesture by the individual inspected, or if the behaviour took place at some point following the initial meeting of the pair. Three of the four cases of genital inspection were among immatures, while the forth involved a juvenile female sniffing the anus of a group silverback.

Although the sex of some individuals was not certain, it is believed that all four of these cases of genital inspection involved different sex individuals.

Table 6.13 shows the age/sex-classes involved in all 50 cases of affiliative encounter. Most involve immatures in both roles, though there are several cases of adults, including silverbacks, being targeted for close proximity by immatures, and in one case, by an adult female. There were no cases of silverback-silverback affiliation, though the issues pertaining to close proximity affiliation raised in the simultaneous bai-use section should be borne in mind. Table 6.14 shows that gorillas made physical contact with each other during affiliative interactions more frequently than in either play agonism or true agonism

Table 6.13 Affiliative dyadic interactions by age/sex-class (A/S)

A/S	Play	Greeting	Seek Prox	Genital inspection	Unknown	TOTAL
juv-juv	7	5	1			13
juv-sam	5	3			1	9
juv-bb	3	2	1	1		7
bb-sam	3					3
bb-bb	3					3
juv-sad				2		2
sam-sam	2					2
sam-af			2			2
sam-sad	1		1			2
bb-sad		1				1
juv-af		1				1
juv-sb				1		1
bb-ssb			1			1
sad-sb			1			1
af-bb			1			1
af-ssb			1			1
TOTAL	24	12	9	4	1	50

Table 6.14 Frequency of physical contact per interaction type

Interaction type	Frequency of dyads making contact, of total dyads	Percentage
Agonism	6/124	5
Play agonism	4/28	14
Affiliative interaction	28/56	50

Agonism in focus

As for play agonism, every agonistic interaction between dyads was scored for intensity using the four point scale given on page 289. Table 6.15 shows the frequency of intensity scores across all agonistic interactions regardless of age/sex-class (excluding play agonism).

Table 6.15 Frequency of agonism intensity scores across all age/sex-class combinations

Agonism score	Frequency	Percentage
1	47	38
2	67	54
3	9	7
4	1	1
TOTAL	124	-

The median score was 2 (IQR 1) and the mean, 1.7 ± SD 0.6. Clearly, contact aggression is a very rare occurrence in the bai, particularly so for that likely to cause injury. The only incidence of this level of agonism was upon a blackback by a young solitary silverback. Table 6.16 shows the number of agonistic interactions in each dyad combination and also expresses these as a proportion of the potential interaction index (P.I.I.). Also median intensity scores are given for each age/sex-class combination where the number of agonistic interactions was six or over. The data suggest that interactions between adult males may be of a lower intensity than those between younger males (and young males and adult females).

Table 6.16 Median agonism intensity level per age/sex-class combination

A/s mix	Number of agonistic interactions	Interactions as proportion of P.I.I.	Median agon. level	Median inter-dyad distance (m)
bb-sam	14	0.09	2	2
bb-bb	10	0.08	2	3
af-bb	8	0.02	2	5.5
bb-sb	6	0.02	2	5
bb-ssb	12	0.09	1.5	5.5
sb-sb	10	0.06	1.5	16
sb-ssb	18	0.14	1	40
ssb-ssb	16	0.40	1	42.5

These data add weight to the hypothesis that most inter-unit agonism between immature males while still in their natal groups is more in the nature of boisterous sparring than full-blown attack. The data suggest that males in this age group may engage in agonistic exchange, including contact aggression, with little risk of escalation to a level likely to cause serious injury. As such, agonism between immature males can perhaps be viewed as quite a different phenomenon to that between fully adult males. In the majority of cases, immature males only interacted with each other during instances of inter-unit mingling or close proximity. Such inter-unit encounters may only proceed under conditions of mutual tolerance by the silverbacks of each respective group, therefore immature males may interact with each other agonistically while the general nature of the group interaction remains calm. A group silverback would be expected to intervene in any interaction that seriously threatened his son, but such interventions were very rare. Indeed, of 80 agonistic dyads (excluding sb-sb, ssb-sb, and ssb-ssb), group silverbacks intervened on behalf their group members on only three independent occasions, and only one of these was to protect a son. In one instance, silverback Solomon intervened to halt an aggressive attack by solitary silverback Dylan on Solomon's putative sub-adult son Salaam (interestingly, Solomon had done nothing to protect another immature male, the blackback/young silverback Red Stripe when he was very viciously attacked by Dylan earlier during the same encounter). In the second example, silverback Emerson charged at the blackback Bayleaf and sub-adult male Coriander from NOO group after they made repeated charges and agonistic displays towards Emerson's group and in particular his adult females. In this case, Emerson was probably attempting only to restore calm, and reacting to the seemingly mild annoyance shown by his females. The final example again involved Solomon, who charged and out-manoeuvred the solitary silverback Bear when he aggressively approached Solomon's adult female Misha, who was carrying her six month old son at the time. This was likely to have been a serious intervention to deter a potentially infanticidal attack. Thus, while still in the natal group, immature males may enjoy some degree of protection from the group silverback, who may intervene to settle disputes that threaten the overall peaceful nature of a contact or endanger a group member, though for the most part, silverbacks appear aware of the nature of immature male interactions, and tend to ignore them.

It should be remembered that immature males, within a single-male mating system, cannot gain directly from their agonistic interactions, as they are not in a position to lose or gain breeding opportunities. Some level of dominance may be asserted during these encounters although this is unlikely to be of great benefit in adulthood. While agonism between old immatures may ultimately be a result of an increase in male hormone levels as individuals near adulthood, the social value of such encounters to learning the mechanics and boundaries of interaction should not be underestimated.

In silverbacks, conversely, distant display behaviour is thought to function in part to avoid physical fights that could prove mutually deleterious or even fatal. The median inter-dyad distances shown in Table 6.16 attest to the considerably greater spacing of adult males during agonistic encounters, and in particular, combinations involving solitary silverbacks, who may be seen by group silverbacks as the individuals most likely to attempt to lure away females. The medians, unsurprisingly, differ significantly (Kruskal-Wallis; $\chi^2 = 50.6$, df = 7, $P < 0.001$), the significant differences being between 2m and 16m and above, and 3m and 40m and above.

Initiation by age/sex-class

As the age/sex-class combinations with the highest sample sizes were mostly males, whose primary social contact was agonistic, figures for agonistic initiation given in Table 6.17 differ little from those given in Table 6.9, for overall initiations. Unfortunately, the subdivision of interactions into type results in smaller sample sizes and thus, fewer classes available for comparison.

Table 6.17 Numbers of agonistic interactions initiated per age/sex-class and probability of deviation from chance

Combination		Interactions initiated		P – value (binomial test)
A	B	A	B	
sb	bb	6	0	0.031*
bb	ssb	10	2	0.039*
sb	ssb	13	5	0.096
bb.	af	6	2	0.289
bb	sam	7	7	1.0

Dominance by age/sex-class

Low sample sizes make statistical analysis of questionable value for this data set, and many combinations are excluded from Table 6.18. In the combinations presented, the only potentially important levels of dominance exhibited are by silverbacks over blackbacks and solitary silverbacks. The most telling feature of the other combinations is the relatively high number of interactions where no dominance was apparent. This again may testify to basic differences in the intensity, seriousness, and motivation behind adult silverback agonism and all other examples.

Table 6.18 Levels of dominance during inter-unit dyadic agonistic interaction for a selection of age/sex-class combinations.

Combination		Interactions dominant		No dominance exhibited	Dominance ambiguous	Total interactions
A	B	A	B			
af	bb	1	1	4	2	8
af	sam	3	0	2	0	5
bb	sam	5	2	7	0	14
bb	ssb	2	3	6	1	12
sb	bb	5	0	1	0	6
sb	ssb	10	1	3	4	18

The social context of agonistic interaction

So far, analyses have concentrated primarily on which combinations of gorillas interact the most, and in what ways. A further attempt was made during data collection to assign a social 'context' to each interaction. This was done in order to examine why interactions took place, or in other words, what were the motives behind the interactions.

When recording each interaction, a simple word or phrase was used to describe what, in the observer's opinion, the purpose of the interaction had been. Thus an agonistic interaction between two silverbacks might be further annotated with 'intervention to prevent non-group silverback from gaining proximity to group adult female'. As mentioned previously, ascribing a simple label of 'agonistic' or 'affiliative' to an interaction can at times be problematic. Attempting to assign motive relies considerably more on the formation of a subjective judgement by the observer, and thus is more likely to be prone to anthropomorphic and otherwise inaccurate interpretation. Nevertheless, to make no such attempt leaves the labels 'agonistic' or 'affiliative' empty of meaning and relatively uninteresting.

As the results demonstrate, in a great many cases, it was not possible to be precise about the purpose of an interaction, and the cover-all terms 'intimidation' and 'proximity intolerance' are used extensively. Intimidation was used extensively for occasions of long-distance display between individuals, especially silverbacks, and for other interactions where one individual seemed intent on reinforcing his or her presence forcefully on another. 'Proximity intolerance', although at times used interchangeably with 'intimidation' was used more when displays or other forms of agonism seemed to originate from one individual being ill at ease with the distance between it and another. Unfortunately, the line between these two context categories is not always particularly distinct. Furthermore, they are proximal in nature, and sit uneasily alongside the other, largely ultimate categories, in which greater interpretative precision was possible.

Table 6.19 shows the frequency of interactions in each category. Most interactions were not clearly attributable to an ultimate purpose by their content alone, but fell into the more amorphous categories of proximity intolerance and intimidation. Only five clear cases of feeding displacement were recorded, suggesting that competition over food resources was not a key motive for agonism. This is perhaps unsurprising given the abundant distribution of food plants in the bai. Only two cases of maternal protection were witnessed, possibly indicating that females largely rely on the presence of a group silverback to ensure no potentially dangerous extra-group individuals get close enough to pose a threat. Clear examples of the defence of group members other than adult females and infants were also rare.

Table 6.19 Interactions per agonistic context category

Agonistic interaction	Frequency of examples	Percentage
Intimidation.	48	39
Proximity intolerance.	36	29
Attention seeking display by immature male to adult female of other group.	6	5
Defence of adult female from approach by opposing group member.	6	5
Defence of non-adult female group member.	5	4
Feeding displacement.	5	4
Protection by adult female of own infant from boisterous other group playmates.	2	1.5
Silverback aggressive approach towards potential migrant female in other group.	2	1.5
Unknown.	14	11
TOTAL	124	-

Many of the remaining instances could perhaps be summarised as symptoms of what may be the over-riding motives of male inter-unit social behaviour, whether in its adult or immature forms; namely to prevent other males gaining access to group females and infants, to directly intimidate potential rivals for female acquisition, and to advertise fighting abilities to potential migrant females from other groups. Establishing which interactions are which may be virtually impossible, and it may be the case that even the individuals involved are not always aware of the distinction.

Notes on interactions concerning female defence or acquisition

Given below is an extract from the Field Notes for 16 June 1998, in which the silverback of SNO group (Caravaggio) approaches BON group. The silverback Bones continually moves to block Caravaggio's access to his group.

16-Jun-98

14:38 Bones grp enters with Caravaggio (Cara) 10m from them in zone 2cn. Bones is between Cara and his grp. Both silverbacks are tight lipped and tense. Cara follows the grp into the bai, maintaining close proximity. About 15m in, Bones chest beats and continues to move south-east along with his grp and Cara. When the grp reaches 3c all individuals are tight lipped, with Bones 6m from Cara. Bones is positioned between his grp and Cara. At this point Bones and Cara both sit and face each other about 6m apart. Bones starts to feed while still looking at Cara. Cara stands and heads 3m to the east. Bones also gets up but then sits back down.

14:51 Bones gets up and moves 5m more towards the south, away from Cara and towards his grp. They feed. Juvenile Muffin maintains close proximity to Martha (his mother). Over the next several minutes Bones and his grp. increase the distance between them and Cara to about 20m. Cara sits and feeds facing Bones and grp.

15:01 Bones stands with tight lips; his grp starts to move further south. This causes Cara to rise and follow with tight lip, 16m away.

15:14 Cara moves towards Bones, closing the gap between the grp and himself. When Cara is 12m from Bones, Bones gets up; both males are tight lipped. Bones remains between Cara and his grp. Cara continues to move south and approaches Bones' grp who move west. As Cara continues to follow, Bones is quick to keep up, continuing to block Cara from his grp. The silverbacks then sit about 4m apart.

15:18 Cara splash displays, actually wetting Bones in the process. Bones remains still but tense. Cara then starts to move south with Bones maintaining proximity to him.

15:21 The males are about 6m apart. As Cara moves towards the group, Bones stays between him and his group. When the two males are about 8m apart Cara splash displays again. Bones remains tight lipped as does Cara, and much side glancing takes place. Cara starts to move south towards the group. Bones again moves quickly between them. At this point the group move south away from the two silverbacks.

15:31 Cara advances to about 5m from Bones. Bones yawns twice. As both males face each other Bones slaps the ground twice with both hands. 15:37 Bones yawns twice and chest beats as Cara heads north. After two minutes Bones moves 4m towards Cara and yawns again.

15:46 Cara chest beats and does a running charge as he moves north. Bones heads south toward his females.

15:48 Cara. exits 2nc. All the way glancing back at Bones.

This is an example of one of the relatively rare occasions in which silverbacks interacted agonistically within close range of each other. Even in this example, however, it is never explicit that Caravaggio is particularly targeting Bones' adult female in his approaches.

Bones' behaviour immediately following the departure of Caravaggio gives greater credence to this idea however, being the only clear example of female herding in response to the approaches of another group silverback (*see* Chapter 5 for more details of female herding).

> 15:49 Just a minute after Cara has exited the bai Bones is next to Martha. Cara chest beats in the forest and immediately Bones lunges tight lipped at Martha who is moving and feeding 3m from him. This causes her to move south away from him, and consequently away from the site of Cara's departure.
> 15:51 Cara again chest beats from the forest, causing Bones to become tight lipped and Martha to head south more quickly. During the next 15 minutes Bones maintains close proximity to Martha and Muffin, as Cara chest beats on three further occasions.

Less ambiguous is the behaviour of solitary silverback, Bear, towards adult female Misha from TSB group in the following extract from 10 Aug 1998. Bear had approached the group steadily without provoking much reaction from TSB silverback, Solomon. He then attempted to attract Misha's attention; first with low vocalisations, and then with more vigorous displays.

> 13:33 Bear is looking at Misha and begins to generate low belch-like vocalisations. Misha glances up from her feeding.
> 13:39 Again Bear generates low vocals while staring at Misha. She looks up but then goes back to her feeding.
> 13:42 Bear is now feeding about 5m from Misha. Again, he vocalises, to which Misha only glances up . Misha gets up and turns her back on Bear. He stands as soon as she moves then sits back down when she resumes feeding.
> 13:47 Bear stands up from feeding and chest beats. She briefly looks up.
> 13:48 Misha moves back towards Solomon. Bear stands and watches her.
> 13:57 Misha is feeding 1m away from Solomon. Bear has moved to 2m from her and is looking at her; she feeds, as does Solomon.
> 13:58 Bear lunges and slaps the ground with both hands, narrowly avoiding contact with Misha. She turns her back to him. Solomon only glances at Bear, then continues to feed. Again, Bear slaps the ground with both hands. Misha turns to face him.
> 14:00 As Misha moves away from Bear he moves towards her. She then moves to the north of Solomon such that he is now between her and Bear. As Bear moves to keep up, Solomon turns around and rapidly moves towards Bear. Bear turns and runs south and Solomon follows him for about 10m. They both stop and are about 4m apart, tense and side glancing (head turning) at each other.
> 14:03 Bear slowly works up to a hoot-series and then chest-beats.
> 14:10 Bear has moved back within 6m of the TSB members.
> 14:15 Bear again hoots and chest-beats along with a short run display. TSB members look at him briefly. In the next 15 mins. Bear hoots and chest beats twice more with short display runs, and then repeats his low vocalisations.

> 14:37 Bear does a running chest-beat display past Solomon.
> 14:39 Bear runs south and chest-beats with hoots.
> 14:41 Solomon, Stripe, Moses, Misha and Bogplant move to the south and Bear becomes tense. The grp is going to have to pass Bear in order to exit. As they move south, Bear runs in front of them. Solomon and the others do not stop but keep moving and as a result, Bear backs up. Solomon is about 1m from Bear as they move south. As Misha starts to move south Bear lunges for her. Quickly Solomon moves towards Bear who recoils briefly. Bear then moves further south with TSB grp behind him.

In this example, Solomon does not actively herd Misha, but merely blocks the more extreme attempts of Bear to gain access to her or threaten her in any way. Solomon behaved similarly towards Misha in an earlier encounter in which she and a sub-adult female from TRA group had exchanged displays and blows. Solomon's behaviour on that occasion was ambiguous, as there was no attempt by Travis to approach Misha himself. In fact, Travis appeared to retreat from any contact with Solomon. Solomon's behaviour could probably be interpreted as easily as peace-keeping as the guarding of females, however, his attitude towards Misha on this and other occasions gives credence to her having been a juvenile immigrant to his group, and not as previously thought, his daughter. Indeed, no herding behaviour should be predicted between silverbacks and their daughters, given the apparent inevitability of female transfer from the natal group and incest avoidance by the silverback.

In the bai context, there was very little evidence of females actively seeking contact with silverbacks from other groups or solitary silverbacks. One exception was the sub-adult female, Leah, from OB1 group who left her group feeding in one zone of the bai, entered the forest and emerged adjacent to TRA group, who were feeding approximately 200m from OB1. She next approached group silverback Travis to 8m and began to feed. Shortly afterwards, juvenile and sub-adult females Paris and Holly of TRA group approached Leah and began to charge and display. These displays had little effect on Leah, although she did retreat slightly away from Travis and closer to the forest edge. At this point, TRA blackback, Stockwell, approached and charged Leah vigorously, causing her to scream and head back towards her own group. At no point did Travis or OB1 silverback, Obiwan, pay any overt attention to the activities of their younger group members. Several other examples of female herding were recorded by group silverbacks towards their breeding females, though this activity was almost as likely to be seen when the group was alone in the bai as it was in an intergroup context. As such, these examples are considered in Chapter 5, under intra-group interactions.

Agonistic behaviour outside the bai

All the data presented so far concern behaviour exhibited in the bai. Evidence that agonistic behaviour may differ outside of this environment may come from the study of wounding. Data were collected on all evidence of illness and injury, including the location of wounds, their type, and probable cause wherever discernible. Table 6.20 gives the frequency of the various types of health problem seen, while Table 6.21 gives the frequency of probable causes.

Table 6.20 Frequency of health problems by type

Type	Frequency of cases	Percentage of all cases
Laceration or puncture	22	42
Skin condition	17	33
Bruise, torsion, or sprain	4	8
Illness or malnutrition	1	2
Unsure	8	15
TOTAL	52	-

Table 6.21 Frequency of probable causes

Type	Frequency of cases	Percentage of all cases
Other gorilla	20	38
Pathogen	16	31
Accident	3	6
Unsure	13	25
TOTAL	52	-

Of the 26 cases of laceration/puncture, and bruise/torsion/sprain, 19 were thought likely to have been caused by another gorilla, but only two of these were witnessed by observers; both being cases of bruising on adult females by their own silverbacks. Where the infliction of injuries was not observed, cause was deduced from the severity of the wounds in question, and from their location on the body of the victim.

Consistency of location may not always be a reliable indicator of cause. Early in the study, several adult or near-adult males from different groups were seen with what appeared to be a well-healed linear wound on one or other side of the chest, over the pectoral muscles. At first these were attributed to wounding during fights, but later, the uniformity of the length, location, and low severity of the wounds hinted at an alternative explanation. Rather than being healed-over lacerations, it is believed that these were friction burns sustained during charging behaviour in the forest. During charges, gorillas typically lift their heads high and become stiff-limbed. In such a posture, the first part of a gorilla's body to make contact with any vines or other vegetation passed over during the charge, would be the chest. Being free of hair, this area is additionally vulnerable. In humans, the Marantaceae *Haumania danckelmaniana* and the Euphorbiaceae *Manniophyton fulvum* both cause friction burns and even cuts when brushed against in passing, and it is hypothesised that passage over these plants may have been a more probable cause of the lesions observed.

It is, however, hard to imagine environmental pressures capable of causing the more typical wounds seen on many male gorillas. Leopards would be capable of inflicting somewhat similar wounds but it is suggested that adult male gorillas do not, under most circumstances, present ideal targets for leopard attack (*see* Chapter 4, pg. 179), and other gorillas are the most likely cause of most of the lacerations recorded.

Of course, wounding could have been inflicted during intra-unit disputes. It can be predicted, however, that given the enormous sexual and developmental dimorphism of silverbacks to all other age/sex-classes in a group, and the rate of intra-group agonism toward the silverback by such individuals, all or most wounding of silverbacks (solitary and group) is likely to have been inflicted by other silverbacks during inter-unit disputes. They may therefore be a reliable sub-set to indicate levels of inter-unit wounding. Table 6.22 lists these 11 cases of laceration and puncture wounding thought to have been inflicted by other gorillas on silverbacks.

Table 6.22 Cases of probable gorilla inflicted wounding to silverbacks at Mbeli

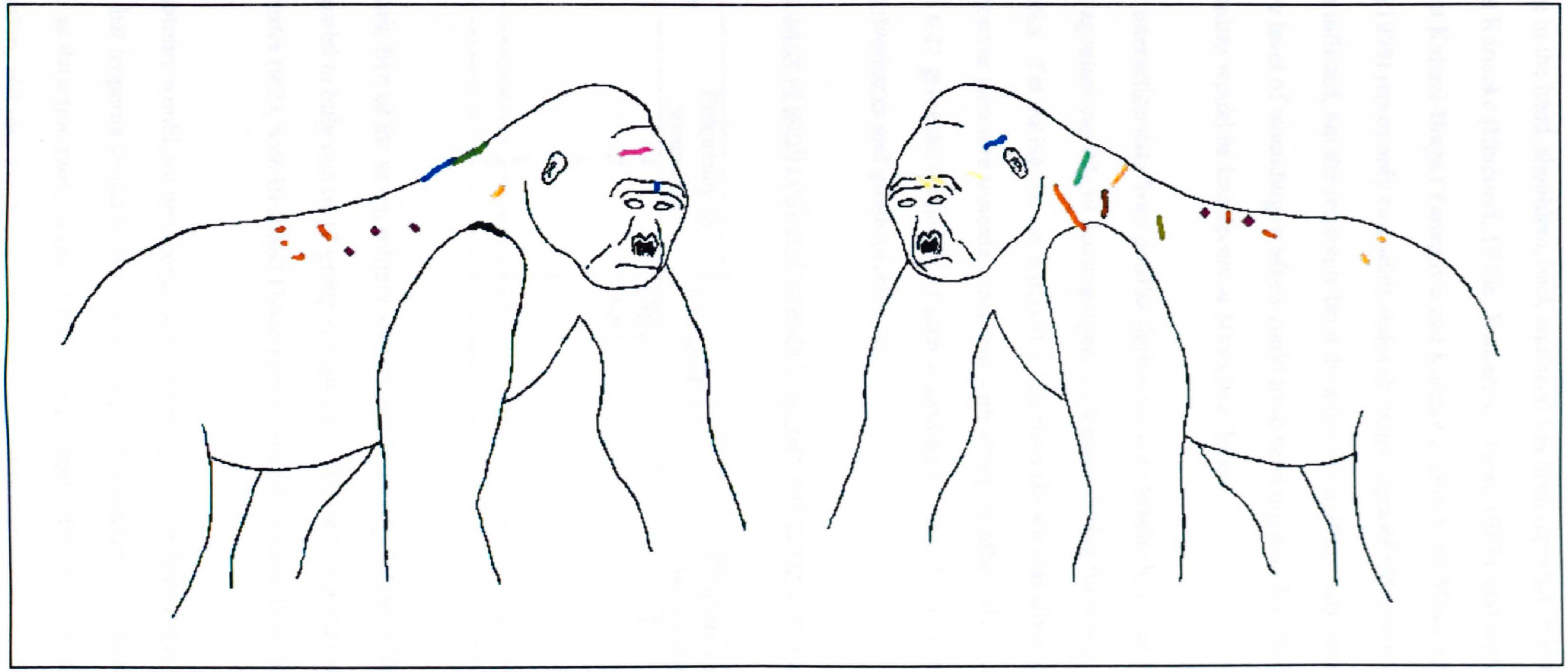
Name	Date	Status	Description
George	May 97	Healed	Linear cut on head.
Bear	Jun 98	Recent	Cuts on shoulder, rump, and neck.
Dylan	Apr 99	Fresh	3cm cut on shoulder.
Bear	Apr 99	Fresh	12cm linear cut.
Clive	Apr 99	Fresh	11cm cut at base of nape.
Dylan	Jul 99	Fresh	Cuts on brow, and deep cut on palm of right hand.
Bear	Jun 99	Recent	Cuts on brow, head (8cm) and shoulders (11cm).
Basil	Aug 99	Recent	5 small puncture wounds on back.
Frank	Sep 99	Fresh	8cm linear cut.
Vince	Sep 99	Fresh	Deep cut on neck and several scratches on back.
Bear	Oct 99	Recent	9cm linear cut.

Evidence of past wounding (scaring and deformation) was noted in 3 silverbacks (Vince, Clive and Solomon). Clive's old wounds were inflicted, probably by the then solitary silverback Max during one or more intergroup encounters in August 1996, when Max gained four sub-adult females from Clive's group. While such wounding occasionally looked severe, it was noted that silverbacks healed very quickly, even with deep cuts, and little loss of movement was recorded.

Figure 6.15 maps the location of these 11 cases of laceration and puncture wounding recorded during the study, and shows some bias towards the head, neck and shoulders. The wound map shows a greater number of small scratches and punctures lower on the back, and most linear wounds higher on the shoulders, nape and head. An interpretation of this might be that they represent an archetypal leopard attack from the rear, with the claws gripping the back and the canines slicing at the vital areas of the neck vertebrae and head. However, were most wounds caused by leopards, one would expect to see regularly spaced 'striping ' from the raking of claws across the skin, as is frequently witnessed in ungulate survivors of leopard attack. While leopard attack cannot be completely ruled out, it seems more probable that violent clashes between silverbacks may follow a somewhat ritualised course, leading to consistent wounding patterns.

The wound map shows left- and right-side projections of the body, and the wounds from separate incidents are indicated by the use of different colours.

Figure 6.15 Illustration of the location and relative size of 11 occasions of gorilla-inflicted wounding on silverbacks at Mbeli



Similar wounding to the head, shoulders, back and hand has been reported following inter-unit encounters at Karisoke (Harcourt, 1978a; Yamagiwa, 1986, 1987a, and with eastern lowland gorillas at Kahuzi-Biega (Yamagiwa and Kahekwa, 2001). At Maya bai, Magliocca et al. (1999) report only two adult males showing signs of old injury that might have been gorilla inflicted, but the relatively brief duration of the study may mean that a more comparative level of wounding to Mbeli could have been missed. It is hard to imagine why agonism would be less severe at Maya than Mbeli.

Inter-unit interaction data from gorillas during visits to Mbeli show that only one case of inter-unit agonism capable of causing injury took place during the study, and none between silverbacks. Yet during the same period, it has been shown that silverbacks sustained lacerations or puncture wounds consistent with attack by other silverbacks on 11 occasions. Table 6.23 gives the frequency of such wounding by named individual and as a total for solitary silverbacks and group silverbacks.

Table 6.23 Frequency of gorilla inflicted wounds to solitary and group silverbacks

Solitary SB name	Frequency of wounding	Group SB name	Frequency of wounding
Bear	4	Clive	1
Dylan	2	Basil	1
Vince	1		
George	1		
Frank	1		
TOTAL	9		2

As the Table shows, five of the seven solitary silverbacks in the population suffered lacerations, compared to only two of 12 group silverbacks. The ratio of actual wounding events is even greater (9:2), with Bear and Dylan both wounded on more than one occasion.

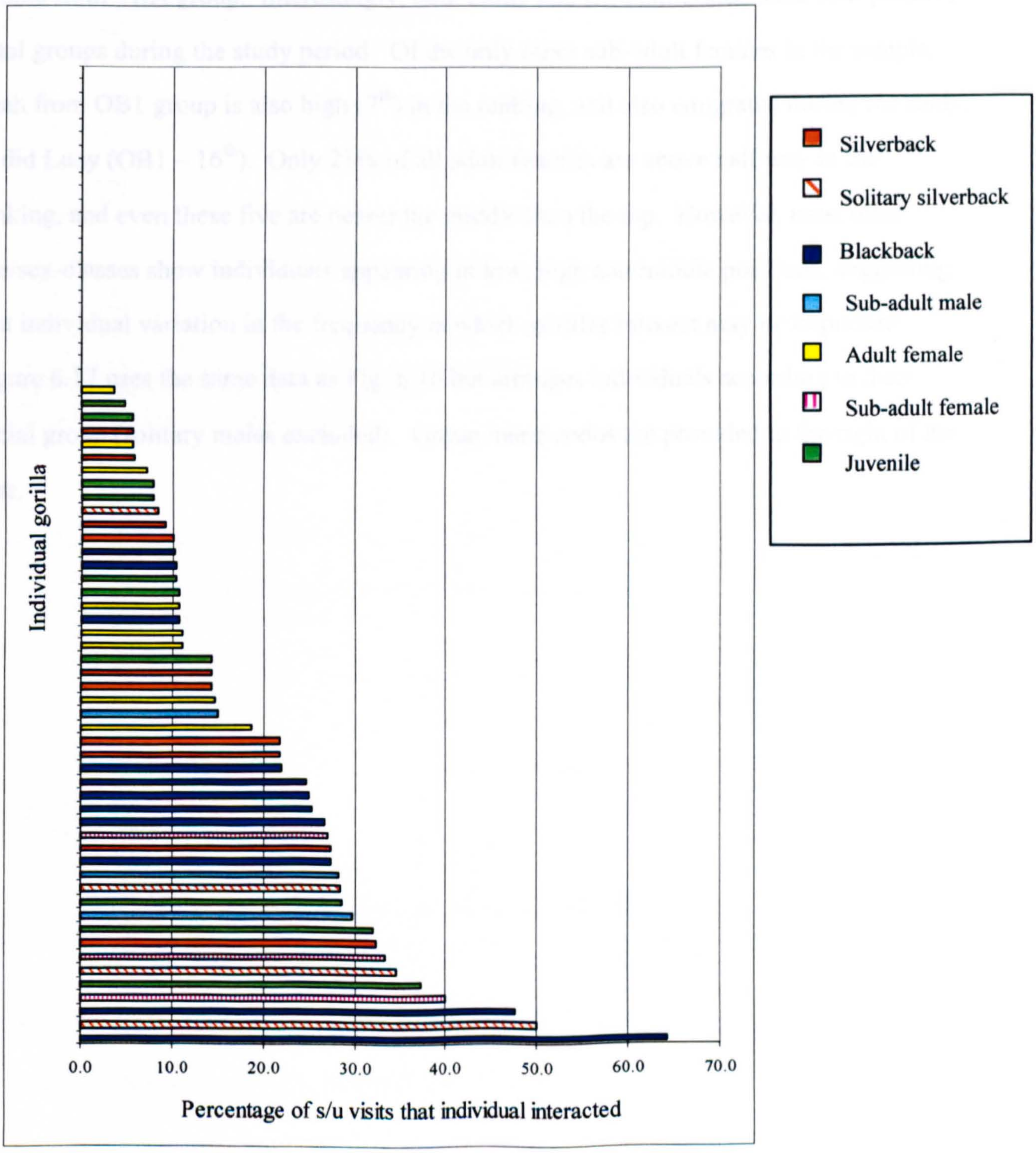
This dichotomy would not be incongruent with the predation hypothesis in that it could be argued that leopards would be more likely to attack a solitary silverback than a group silverback, as detection rates would be higher in a group. However, an entirely more plausible explanation, and one which fits with the data so far presented on the differences in agonistic behaviour in both types of male, is that the wounds are caused by other males. The differential ratio of wounding implies that one or both of the following are true: that solitary males engage in severe contact agonism with each other more frequently than any other adult combination, and/or that solitary males consistently come off worse in contests with group silverbacks. The relative rates of encounter between solitaries with each other and with groups suggests that the former may be the case, although it is perhaps less to be expected that a solitary male would risk injury in the absence of any possibility of direct gains in females. The latter is not unlikely given the putative differences in development and experience between the two types of male. Yamagiwa (1986) reports on 12 encounters between a solitary silverback and groups at Karisoke. The solitary silverback was wounded on two of these occasions – a deep cut on the left thigh, and a 3cm cut on the forehead – while no wounds were recorded from the group silverbacks.

Individual variation in dyadic interaction

Although Mbeli Bai offers the opportunity to witness many more interactions than is possible in the forest, the number of occasions on which any given individual is observed interacting is still limited. With a true independent data point consisting of an interaction between one named individual and another named individual, sample sizes drop even further, and even at an optimum site, the collection of sufficient data for a statistical analysis of individual trends and relationships is almost impossible; especially so for maturing individuals who may change age/sex-class, and thus behavioural motivation, long before sufficient data are collected. However, to ignore the behaviour of individual gorillas is to discount what may be a potentially crucial variable in explaining some of the differences in the nature of social interactions. This final section therefore briefly presents some data on levels of interaction in some of the individual gorillas visiting Mbeli.

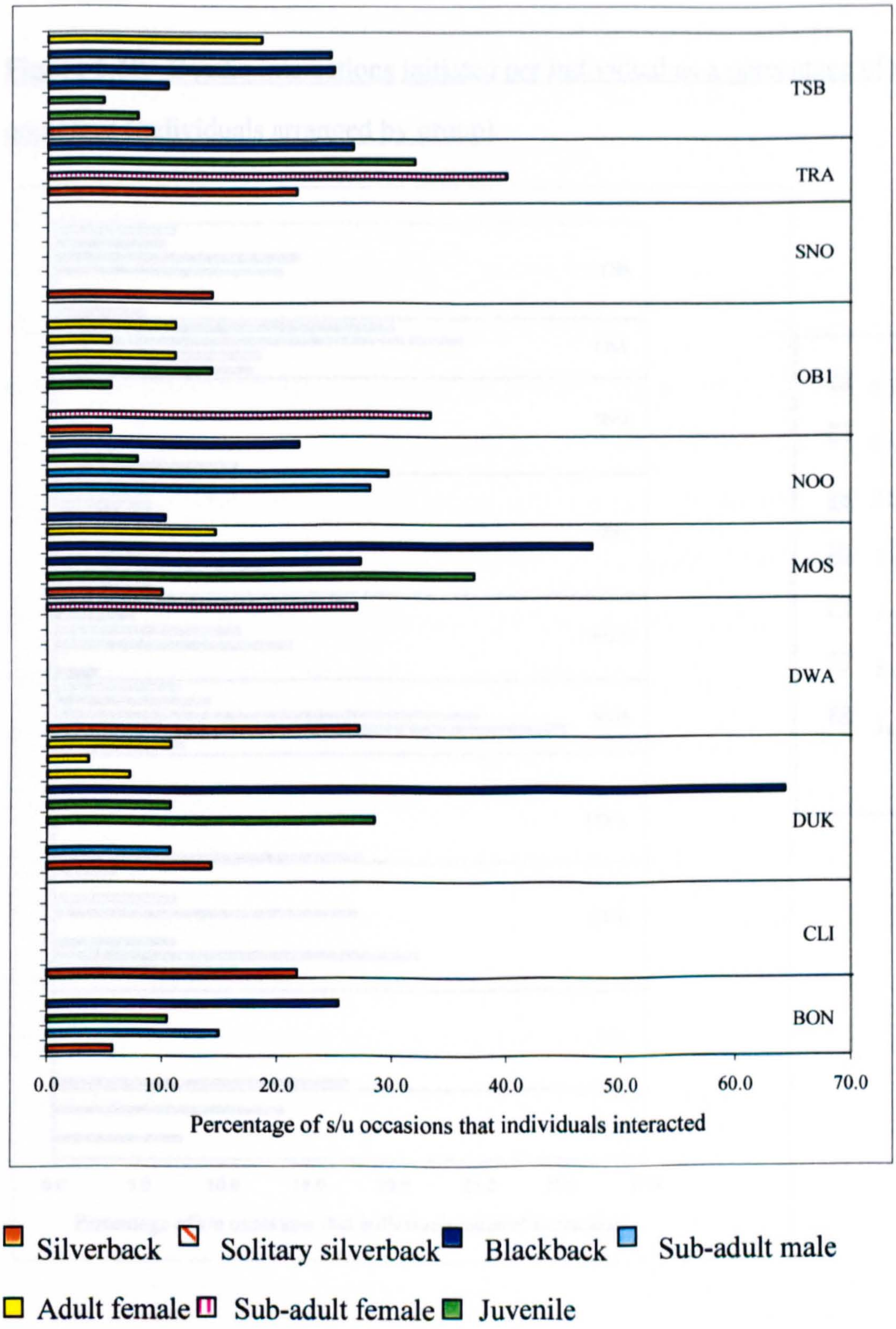
Groups in which the individual identity of most or all individuals is not known are omitted from the sample, as are individuals from groups implicated in simultaneous bai-use (s/u) on less than 10 occasions. This leaves a sample of 73 known individuals, involved in s/u on between 11 and 77 occasions (mean = 37 ± SD 21). In Figure 6.16, the total number of dyadic interactions witnessed for each individual is divided by the number of times he or she was seen in s/u. The resulting percentages are thus comparable across individuals taking into account the number of opportunities for interaction available. Individuals are not named, but a key to age/sex-classes is provided.

Figure 6.16 Dyadic interactions per individual as a percentage of total s/u occasions



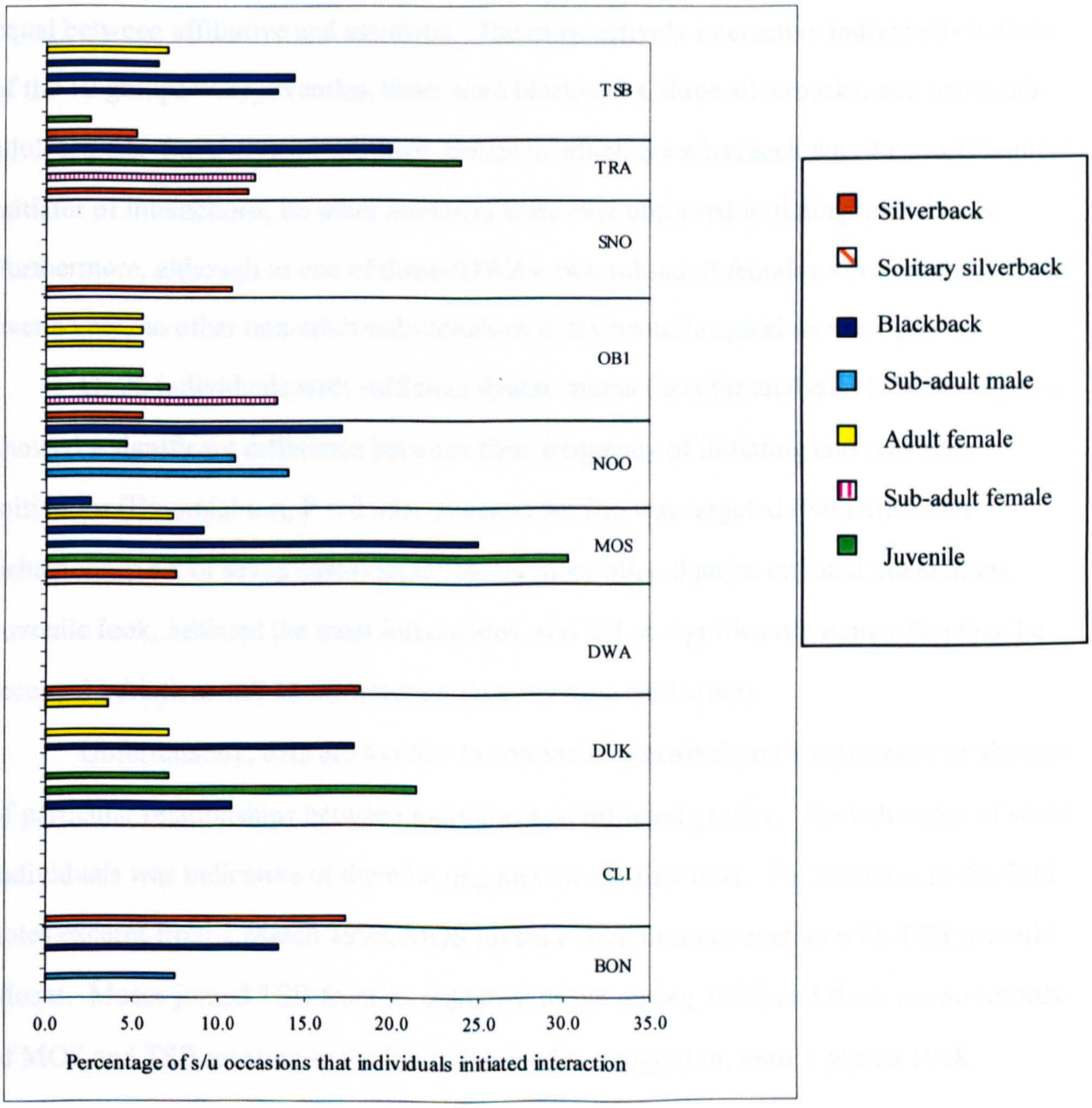
Twenty-four individuals (33%) have interaction percentage scores of zero. 67% of these are adult female, 29% juvenile, and surprisingly, 4% silverback. Of the top 5% of individuals, the individual most frequently interacting is Bird, a blackback/young silverback in DUK group, followed by solitary silverback Bear, then another blackback/young silverback (Homer) from MOS group, and finally Holly, a sub-adult female from TRA group. Interestingly, both Holly and Bird emigrated from their putative natal groups during the study period. Of the only other sub-adult females in the sample, Leah from OB1 group is also high (7th) in the ranking, and also emigrated during the study, as did Lucy (OB1 – 16th). Only 21% of all adult females are above half way in the ranking, and even these five are nearer the middle than the top. However, most other age/sex-classes show individuals appearing in low, high and middle positions, suggesting that individual variation in the frequency at which gorillas interact may be important. Figure 6.17 uses the same data as Fig. 6.16 but arranges individuals according to their social group (solitary males excluded). Group name codes are provided to the right of the bars.

Figure 6.17 Dyadic interactions per individual as a percentage of total s/u occasions (individuals arranged by group)



The frequencies of interaction shown in the preceding two charts include initiations of social behaviour, but also occasions when a gorilla was merely the target of another's behaviour. As such, they have the potential to be misleading in terms of the active sociality of a given individual. Figure 6.18 therefore gives only the percentage of s/u occasions on which individuals initiated interactions. Note that the x-axis scale is altered from the two previous charts.

Figure 6.18 Dyadic interactions initiated per individual as a percentage of total s/u occasions (individuals arranged by group)



Both the previous two charts show that in some groups (CLI, SNO), the silverback was the only interactive individual. Other groups have some quite highly interactive individuals, but also others that seldom if ever interacted. Naturally, group composition will have a strong influence on this, as, for instance, groups containing mostly adult females and their young offspring are much less likely to be socially interactive than those with several older immatures. With the data re-analysed only for initiated interactions, juvenile Iook (MOS) emerges as the individual seeking interaction more than any other. Blackback Homer (MOS), drops into second place in the ranking, while two other juveniles, Paris (TRA) and Dizzie (DUK) assume third and forth place. The initiations of all three juveniles were primarily affiliative (85, 83 and 83% respectively), while Homer's initiations were roughly equal between affiliative and agonistic. The most actively interactive individuals in three of the 10 groups were juveniles, three were blackbacks, three silverbacks, and one a sub-adult female. Strikingly, in the three groups in which the silverback was the most frequent initiator of interactions, no other members were ever observed initiating interactions. Furthermore, although in one of these (DWA), two sub-adult females were present for just over a year, no other non-adult individuals over the juvenile age/class were present.

Of 26 individuals with sufficient dyadic interactions for analysis ($N \geq 6$), only two showed a significant difference between their frequency of initiating and receiving initiations (Binomial test, $P < 0.05$). Juvenile Muffin was targeted (with affiliative behaviour in six of seven cases) significantly more often than he initiated interactions. Juvenile Iook, initiated the most interactions, and did so significantly more often than he received initiations (all 16 initiated interactions were affiliative).

Unfortunately, data are too few to comment extensively on the presence or absence of particular relationships between individuals of different groups. The behaviour of some individuals was indicative of them having met for the first time. For instance, in the field notes excerpt from 1 March 1998, MOS juvenile Iook initiates contact with TSB juvenile Moses. Moses joined TSB from an unknown origin during 1997, and there are no records of MOS and TSB meeting in the bai following his emigration, until 1 March 1998.

> 16:25 Iook approaches Moses, intently watches him feeding, then does a very close-up face to face greeting gesture (kiss). Iook looks slightly the younger of the two. Moses moves away slightly. Iook moves to stand bipedally in front of him and briefly massages Moses' head with both hands! There is absolutely no reaction from Moses. Iook bends so as to put his face directly in front of Moses' face – only few inches apart. As Moses begins to pull away again, Iook catches him gently with one arm around the back of the neck and stops him moving away. Moses looks VERY shy and uncertain how to behave in the face of Iooks gentle approaches to play. This arm/neck stopping tactic is done twice. Iook then bends low and intently watches

> Moses feeding. This is an exagerated behaviour that appears to be more about visibly showing an interest in Moses' behaviour than actually having that interest. Iook moves to the rear of Moses and touches his anus with a finger. Moses moves away slightly, and the interaction ends.

During the same contact, however, Iook greeted Bogplant, also a juvenile in TSB group, but one who had been born into the group and had shared the bai with Iook previously. Instead of the cautious solicitation directed at Moses, Iook went straight up to Bogplant and the two ventro-ventrally hugged before beginning a prolonged play session. There were many other examples of behaviour indicative of recognition between individuals of different groups. Most of these involved fast approaches towards members of other groups by immatures, and often preceded play or merged feeding sessions. During an affiliative feeding merge between FFF and NOO groups in December 1996, members of MAX group entered the bai and began to feed next to the merged groups. All of these individuals had been part of regular Mbeli groups prior to joining solitary silverback Max as either sub- or full adult females. The peaceful merge came to an end as soon as Max (who had never been seen at Mbeli before his arrival with the new females) entered the bai. Moving up towards his females with a tense expression, he was spotted by members of FFF and TSB. Immediately, his new females began to make their way back towards him, while the other merged groups began what can only be described as a panicked retreat to the forest. There was no immediate attempt to reform into groups, but only to escape the advance of Max. In this instance, the gorillas may have been reacting merely to an unknown silverback, to his powerful advance towards the groups, or in recognition of his aggressive nature following previous encounters in the forest. However, the intensity of their reaction suggests that they were already aware of his capacity for agonistic behaviour. These and many other examples are intriguing pointers to the existence of relationships between individuals and groups at Mbeli, however, considerably more data will be required to confirm this and even more so, to comment on the implications such a 'community' structure might have for the gorillas.

Summary of dyadic interaction analyses

- The frequency of dyadic interaction between individuals in the various age/sex-class combinations does not correlate with the proportion of such age/sex-classes available during inter-unit encounters. Certain age/sex-classes appear to be selective in their choice of partners for interaction.
- Among the top third most frequent age/sex-class combinations in dyadic interaction, 67% were between same-aged individuals: 75% were males, and the most frequently interacting combination was solitary male with solitary male.
- Interactions between blackbacks, between sub-adult males, and between blackbacks and sub-adult males were all among the top third most frequently interacting combinations. There were no examples of infants being involved in inter-unit interactions.
- Overall, blackbacks were the most interactive, and adult females were second only to infants as the least interactive. Silverbacks occupied a roughly central position within the range of age/sex-classes.
- Blackbacks initiated significantly more of their interactions with solitary males than vice-versa, however, in silverback – blackback interactions, blackbacks initiated significantly less often than silverbacks.
- Of all dyadic interactions, 60% were agonistic, 14% were dubbed as boisterous and provocative behaviour in older immature males, or 'play-agonism', 24% were affiliative, and 2% were not categorised.
- All pro-active interactions between silverbacks, between solitary silverbacks, between silverbacks and solitary silverbacks, and between silverbacks and blackbacks were agonistic. As the combined age of both parties in a combination type decreases, agonism is replaced by play agonism, and then affiliation. Juveniles were implicated in the only two combinations to show 100% affiliative interactions.
- Most affiliative interactions were performed by immature gorillas, and in particular, juveniles. Affiliation was most frequently expressed through play, and through greeting upon first reaching close proximity. Physical contact was made in half of all affiliative dyadic encounters, 14% of play agonistic encounters, and only 5% of

agonistic encounters. In only 1% of agonistic dyads was physical contact likely to cause injury. Most dyadic agonism was close display, followed by the distant display type.

- Immature males appear to interact at a higher intensity of agonism than silverbacks. It is suggested that younger males are able to take advantage of the tolerance shown by their respective silverbacks to each other, to interact agonistically without undue fear of dangerous escalation or the intervention of either group silverback. Silverbacks made only three interventions on behalf of group members in 80 non-silverback agonistic encounters, but were thought likely to do so should a serious threat become apparent.
- Silverbacks that did engage in agonistic interactions did so at considerably greater distances than blackbacks interacting with each other or with sub-adult males.
- Eleven cases of wounding consistent with gorilla attack were noted on silverbacks. Solitary silverbacks received nine of the instances of wounding while group silverbacks received only two. Among silverbacks, no cases of agonism likely to cause wounding were recorded during the study. The level of wounding evident on silverbacks visiting the bai suggest that agonistic behaviour may vary according to the physical or social environment, and a greater degree of tolerance is exercised while in the bai.
- Considerable variation exists in frequencies of interaction between individual gorillas. Interaction is not governed solely by predictable age- and sex-class variables, but may be influenced by an individual's personality and its past history of interactions with any other given individual.

Discussion

All examples of simultaneous bai-use by gorillas at Mbeli can be scored as inter-unit encounters under the definition employed at Karisoke (e.g., Sicotte, 1993). Indeed, it is perhaps not unreasonable to suggest that any unit entering the area and feeding in an environment where any other unit might be, at the very most, 700m away with a clear line-of-sight would be aware of the presence of the other. This being so, it is notable that no units made all their visits to an empty clearing, or were not joined by another group on one or more occasion. In other words, every unit visiting Mbeli, shared the bai at some point or other. Even without simultaneous use, the very fact of so many units visiting the bai is clear evidence of staggering home-range overlap, which in itself, may raise the chances of one unit encountering another. Considerable variation was observed in the proportion of a unit's visits during which the bai was shared (ranging from 20% to 70%). The relative proportion of a unit's s/u may be influenced by its familiarity with the clearing or its previous experience with groups already present. However, there was no difference in s/u proportions by solitary males and groups. Likewise, no relationship between total group-size and s/u proportion was found.

The overall low frequency at which social units visit the bai makes it unlikely that groups wait at the forest edge and select which other units they will share the clearing with. It is more probable that some units may avoid entering the clearing if they see certain others present. However, the former strategy might be envisaged in solitary males. The greater ease with which such males are able to meet their nutritional requirements, enables them to adjust their ranging patterns (Yamagiwa 1986). Bais may represent optimum sites for the location and approach of groups by solitary males. By remaining at a bai for an extended period, ranging close to a bai, or travelling from bai to bai, solitary males may encounter groups more frequently than by ranging solely in the forest. Furthermore, the process of following a social group through the forest commits a male to pursuing a single set of females at a time, while the bai offers the chance to approach many groups in conditions where greater visibility may reduce the chances of attack by a defensive group silverback. Unfortunately the overall number of bai visits per unit could not be used to test this hypothesis, as solitary males, when not at Mbeli, may have been ranging close to other bais. A solitary male (Bear) exhibited the highest proportion of shared bai visits (70%), with solitary Dylan also scoring highly (59%). Intra-sexual competition may account for why more solitary males did not score highly. If bais do represent optimum sites at which to attract females, then one might expect, for every male that frequents the bai often, others that are intimidated away from the area by these same males.

Calculation of the 'Half-weight' index of association permitted direct comparisons of s/u levels between units. Grouped by unit type, the highest median s/u association index score (AI score) was recorded from solitary males with each other, followed by groups with groups, and lastly by groups with solitary males. Though the differences were non-significant, they should be borne in mind in regard to later discussion of interaction type. When examining the AI scores of individual units against each other, significant differences were found however: These were among solitary males, among groups, and among groups and solitaries together. In terms of individual unit-pairings, groups TRA and TSB shared the bai with each other more than any other unit pair, but the following five highest AI scores all involved solitary male BEA as one of the parties.

Although significant negative correlations were found in tests using both the absolute difference in group-size between units and the difference in numbers of breeding females, they were not thought to explain the observed rankings in AI score. As such, the reasons for differential levels of s/u of the bai remain as yet unknown. Degrees of relatedness, familiarity and the individual character of the individuals concerned may all be implicated as variables. It was tempting to imagine, for instance, that the silverbacks of the pair of groups with the highest AI rank (TRA and TSB) were full- or half-brothers, given the slight resemblance between them. Such hypotheses will require the collection of DNA material in order to be tested, and a protocol for such collection is now in place at Mbeli. Familiarity resulting from a regularly used overlap in core home-range may also have fostered increased tolerance between some units, and there did appear to be some synchrony in at least some of the visits between TRA and TSB (*see* Chapter 3). However, it was thought that ranging patterns could not be assessed with sufficient confidence to permit a statistical examination of the influence of this variable.

It should be remembered that familiarity and tolerance may not be the only, or even the prime cause of a raised AI score. In the case of solitary male Bear, a highly acquisitive nature with regard to the search for breeding females, potentially coupled with the ability to dominate other solitary competitors at the bai could have given rise to his seeking s/u with as many units as possible. A major weakness in analysis of s/u becomes apparent in this regard; namely that simply being in the clearing at the same time as another unit says nothing about whether or not the shared use was sought by either party, or how those parties reacted to the situation. Thus, levels of simultaneous bai-use, while of interest, can only go so far in illuminating the nature and motive for interaction.

Despite the extraordinary visibility at Mbeli, it was considered prudent to remove from the data a sub-set of units that did not appear to be aware of each other's presence in the bai. Although this was a subjective and thus imprecise judgement, making allowances for a lack of awareness was thought justified. On several occasions, groups, and in particular solitary males, gave a clear impression of having looked up from their feeding to be suddenly surprised by the presence of another unit who had only recently entered the bai. Hence, the removal of 11% of the 389 occasions of simultaneous bai-use where groups were well separated and showed no signs of having spotted the other. A danger exists that units may, on occasion, deliberately ignore others, either to avoid provoking a confrontation, or out of general disinterest, but the greater danger of scoring 44 cases of s/u where awareness was questionable, within the sample measured for the presence or absence of an interaction was thought more critical.

When only 'aware' occasions of simultaneous bai-use were examined, only 42% gave rise to any detectable interaction (including distant displays). Unfortunately, it was not possible to directly compare this frequency with Karisoke data due to differences in what is taken to constitute an encounter and an interaction. Nevertheless, data from Karisoke characterise inter-unit interactions as generally aggressive and involving vigorous displays by silverbacks (e.g., Harcourt, 1978a), whereas at Mbeli, over half of all encounters between units failed to elicit any response whatsoever from either party. At Maya Bai, non-interaction was labelled 'indifference', which may be ascribing too great a degree of context to the gorillas' reactions. However, it was striking to note that the percentage of encounters failing to elicit an obvious reaction was almost exactly the same as that at Mbeli. The fact that both sites also demonstrated essentially identical proportions of agonistic interactions (29% and 30%) is further evidence suggesting the existence of a 'baseline' rate of interaction that can be predicted in an open, bai-style environment. As mentioned in Chapter 4, the density of gorillas around Maya is higher than in the Ndoki region. Furthermore, at 18ha, Maya Bai is larger than Mbeli and contains several different food plants. Variables such as these might be expected to influence the behaviour of gorillas, and yet as shown in Chapter 4, gorillas at both sites appear to share identical social systems. As such the actual proportion of group types meeting each other in the clearing (e.g., juvenile, mature, senescent groups) may be very similar and the composition of the groups themselves proportionally the same. This being so, it may be that any given interaction can be predicted to take place on a given proportion of occasions. It should not be forgotten, however, that these results may be a chance phenomenon. This possibility is given some credence by the finding that at Mbeli, the highest proportion of encounters resulting in agonism were between solitary males, whereas at Maya, solitary/solitary interactions provoked the least agonism, although the less rigorous definition of a solitary at Maya may have compounded this issue.

At Mbeli, the reason for the higher proportion of agonistic encounters between solitaries than between groups is straightforward. In addition to a silverback, groups also contain immature individuals, all of whom (with the exception of young infants) are capable of interacting, and, as the analysis of dyadic interactions shows, do so affiliatively considerably more than silverbacks. In fact 100% of juvenile/juvenile dyadic interactions were affiliative, while 100% of all pro-active silverback/silverback, solitary/solitary, and solitary/silverback interactions were agonistic. Thus, at a group level, the silverback contribution to agonism scores is diluted by the more affiliative encounters of other group members. Such an effect highlights one of the more striking features of inter-unit encounters at Mbeli; namely that behaviour during group meetings is not restricted to silverbacks. It was therefore necessary to examine each dyadic interaction individually.

When examining the frequency of dyadic interactions using percentages derived from the 'potential interaction index' (P.I.I.), 67% of the top third ranked age/sex-class combinations were of the same age-class. The apparent preference for same-age targets for interaction might be predicted during agonistic encounters as targeting an older individual might increase the risk of defeat, while targeting a younger animal might well be pointless if a linear dominance hierarchy with age already renders younger animals subordinate. With regard to affiliative interactions, the preferential selection of same-age play partners is not unusual and has been widely demonstrated previously (e.g., baboons - Owens, 1975a; chimpanzees – Van Lawick-Goodall, 1968; Mendoza-Granados and Sommer, 1995; gorillas – Stewart, 1981; Walters, 1987; Watts and Pusey, 1993; Fletcher, 1994). Attraction for play partners of differing age has also been reported (e.g., Lee, 1983; Markus and Croft, 1995) though most reports deal in particular with intra-group play behaviour where familiarity and relatedness of the individuals may permit more of such behaviour.

Of the top third of dyad age/sex-class combinations, 75% were between males. The sex-bias towards males in frequency of interaction was graphically demonstrated by the finding that adult females were only involved in 0.9% of all dyadic interactions, with only two interactions recorded between adult females. There were no examples of females communally defending access to resources. This, in addition to the evidence of female transfer given in Chapter 4, and the lack of evidence for female philopatry or dominance hierarchy presented in Chapter 5, confirms adult female gorillas at Mbeli as living within a non-female-bonded, dispersal-egalitarian social system.

Were one to predict the proportionally most frequently interacting age/sex-class combination based on the social structure described in Chapter 4, it would probably be that between solitary and group males. Solitaries have no females to lose during interactions, and require females in order to breed. They have also been shown elsewhere to actively pursue breeding groups in order to attract females. Group silverbacks must therefore actively protect their breeding potential by preventing any contact between solitaries and females. It was surprising therefore to discover that by far the most interactive combination was that of solitary silverbacks with other solitary silverbacks (all such interactions were agonistic). With relatively few solitary individuals in the population, a lack of independence becomes a potentially confounding issue, and it should be noted that in 11 of 16 ssb-ssb interactions, 'Bear' was one member of the dyad. Nevertheless, he only initiated the interaction on five of the 11 occasions.

It is initially puzzling why solitary silverbacks should expend energy and potentially risk injury in interacting agonistically with each other given that such interactions offer no potential in terms of direct acquisition of females, as might interactions with groups. Almost nothing is known about such interactions in the

Virungas, where the few data on inter-unit encounters involving solitary males have them interacting with groups (Yamagiwa, 1986b). Without comparative data from the forest, it is difficult to know whether the high levels of agonistic interaction between solitaries is linked primarily to bai-use, but this seems a probable hypothesis. Although gorillas are not considered territorial in the sense that they do not actively defend their home range, the bai, or rather access to the groups using it, may represent a resource that can to some extent, be defended. As mentioned earlier, this may simply take the form of a solitary male displaying vigorously at any other solitary male in, or around the bai, in the hope that by forcing the other to leave the immediate area, only he will be present to approach any females that may subsequently arrive.

In addition, or complementary to the behavioural correlates of social status and life-strategy imperatives of solitary males, hormone levels may play an important role. A positive relationship between androgen levels and aggression has been demonstrated in other primates (e.g., Higley et al., 1996). Data on hormone levels among gorillas are still preliminary and to a degree, contradictory. Examining urine from wild mountain gorillas, Robbins and Czekala (1997) found no differences in the testosterone levels of males aged 10 to 13 years old and those of 13 years and above, suggesting therefore that such males were hormonally alike long before reaching full maturity. However, Stoinski et al. (2002) divide age-classes differently, identifying juveniles as being below 10 years, sub-adults as 10 to 13 years, young adults as 14 to 20 years, and adults as being over 20 years. This classification gives greater definition to what is believed to be the general age-range of most of the solitary males at Mbeli (young adult). Examining urine from captive western lowland gorillas, they identified three stages of androgen change: an increase from juvenile to sub-adult (<10 to 10-13), and from sub-adult to young adult (14 to 20 yrs.), and then a decrease from young adult to adult (>20yrs.). Significantly greater androgen levels of were found in young males (14 to 20yrs.) than in the other age-classes, and aggression was noted as being ten times greater in 14 to 20 year olds than in both younger and older males. Thus the core of the solitary stage in the socio-sexual development of the male gorilla may be linked to its period of highest androgen levels. Males with well established groups are more likely to be at the upper limit of this age range or in the 'adult' age-range where androgen levels, and potentially therefore, aggression levels, are reduced. From a motivational point of view also, silverbacks of well-established breeding groups can only lose in interactions with solitaries, whether the loss be in terms of energy expended in herding females away from the solitary, displaying at or fighting him, or actually through the loss of genetic potential due to female emigration. As such, encounters with solitary males may at times be actively avoided. A group silverback should never seek interaction with a solitary male.

Agonism was recorded among immatures and was the most frequent interaction-type for dyads with blackbacks involved. Attention was drawn, however, to the rather amorphous category of 'play agonism', which described the exhibition of agonistic behaviours in what appeared to be less threatening, or affiliative contexts. A similar category has alternatively been described as "quasi-aggressive behavior" (Adang, 1984) and "para-play" (Mendoza-Granados and Sommer, 1995). Difficulties in defining play behaviour are well reported (Fagen, 1981), as is the observation that much play behaviour comprises motor patterns which in adults are considered aggressive (e.g., Loizos, 1966; Owens, 1975b). In fact, most examples of play behaviour at Mbeli involved agonistic behaviour patterns (*see* Chapter 5). Though easily labelled as 'affiliative' in younger immatures due to qualities such as repetition, exaggeration, exhibition of a 'play face', distinctions became harder to draw in older individuals. Observations of so called 'play agonism' in sub-adult and blackbacks are thus ambiguous, and due to the qualitative nature of assigning such behaviour, will probably remain so.

In agonistic interactions involving blackbacks with members of other groups, the median level of agonism was higher than that recorded between silverbacks (including solitary silverbacks). This further attests to the context-specific nature of agonism: all adult-male agonism was confined to display, while contact aggression was frequently observed among immatures. Contact aggression between adults may cause life-threatening injury, whereas none of the physical fights between immatures appeared to cause injury or even much distress. The avoidance of close-contact aggression by silverbacks was illustrated by significant differences in median inter-dyad distances during agonism.

Blackbacks interacting agonistically with each other and with sub-adult males, did so at significantly shorter distances than solitary silverbacks in all combinations with each other and with group silverbacks.

Assigning context to interactions is in many respects crucial if the description of inter-unit interaction is to have any major impact in elucidating the processes driving social structure. In practice, such labelling by context, or, what the 'purpose' of the interaction was, turned out to be extremely problematic, and often the performed actions alone were not sufficient to do more than place the behaviour into a broad category such as 'intimidation' or 'proximity intolerance'. These tell us little about whether such intimidation was aimed at, for instance, frightening away a potential rival for females or a competitor for food. However, by examining both the interaction, the age and sex-class of the individuals involved and the outcome, a clearer picture may emerge.

For the purpose of this discussion, interactions between immatures will be considered secondary, and in most senses, part of an individual's behavioural development towards the adult interactions that will have a greater direct impact on the breeding success of the individual. This is not to say that aspects such as the degree to which an immature has access to, for instance, inter-group play partners, will not influence his or her abilities to interact successfully as an adult, but simply that the analysis of context in immatures is more likely to encounter ambiguous and potentially misleading results.

Almost half of all affiliative interactions between dyads were in play, with the rest divided amongst 'greeting', 'seeking proximity' and 'genital inspection'. Of all affiliative interactions, 50% included physical contact, while only 5% of agonistic interactions did so. Neither group- or solitary silverbacks were ever witnessed initiating affiliative interaction with any non-group member. There was some evidence that immatures were more familiar and comfortable in affiliative interactions with members of some groups than others. It is too early in the study to know if affiliative encounters during immaturity have an influence on behaviour in adult life, but it will be interesting to see if frequent male play partners show greater tolerance for each other as silverbacks, or if females migrate preferentially to silverbacks that they are already familiar with.

Agonistic interactions between immature males were common, and were mostly characterised by boisterous displays and sparring. These contests were not overtly monitored or interfered with by group silverbacks, suggesting that they were largely lacking in any real menace. Such interactions are likely to be important in developing the skills, both motor and judgmental, necessary to compete for, or defend females in adulthood (Baldwin and Baldwin, 1974; Fagen, 1981). Given that adult females exhibited almost no inter-unit behaviour, it is perhaps not surprising that Nowell (2001) found play (intra-group) to be less frequent in immature females than immature males at Mbeli. Although sample size was low, females were also observed to exhibit wrestling play and chest beats less than males; thus foreshadowing adult roles (*sensu* Brown, 1988; Pereira and Altmann, 1985).

Among adult males, all active interactions were agonistic and appeared unconnected with defence of feeding resources. Furthermore, little of silverback-silverback agonism was exhibited directly during the defence or acquisition of females. At Karisoke, females transferred on 13 of 171 occasions (8%) of inter-unit encounters; a level described as 'low' (Sicotte, 1993). It is not clear what this description was relative to, but at Mbeli, it was clearly lower. No examples of female transfer were actually witnessed taking place in the clearing, despite there being 345 occasions of 'aware' simultaneous bai-use equivalent to the definition of an encounter at Karisoke. As shown in Chapter 4, female transfer is known to have taken place, and for all we are able to tell, may even have done so in the forest edge following a bai visit. The key issue though, is that adult females did not actively attempt to approach other silverbacks while in the bai, and with few exceptions, the herding of females by silverbacks did not appear to be necessary. As described in Chapter 5, females were herded on rare occasions, but this was mostly seen when no other units were present or when the other unit was distant and not interacting rather than during inter-unit interactions. The disinclination of females to attempt to transfer within the bai is probably due to the ease with which the silverback is able to monitor both the behaviour of the female and that of any other silverback. In most circumstances, cover may be necessary for a breeding female (as opposed to a natal sub-adult female) to leave the silverback she is with. At Karisoke, herding was witnessed more frequently in new groups than well-established units (Sicotte, 1993). The very low proportion of new groups in the Mbeli population may have therefore gone some way to producing the low level of herding, but ease of monitoring by silverbacks is likely to be by far the more important of these variables.

At Karisoke, interactions are generally characterised by the behaviour of the silverback, as it is typically this individual that orchestrates and dominates inter-unit encounters (Sicotte, 1993). Although this was not the case at Mbeli, independent analysis of silverback behaviour permitted a rough comparison between the sites. Startling differences were discovered: in particular, no contact agonism was recorded at Mbeli, while at Karisoke it took place on 17% of encounters. In addition, close range agonistic displays were three and a half times more frequent at Karisoke than Mbeli, while peaceful mingling took place more than twice as frequently at Mbeli than at Karisoke.

Sicotte (1993) found that the highest number of females in one or other interacting unit was related positively to the intensity level of the silverback's agonistic response, but no such correlation was evident at Mbeli. Although the number or difference in number of females in one or other interacting unit did not significantly influence the intensity of silverback response, a measure of familiarity between units did appear to be a significant variable. Post-hoc tests on the influence of familiarity as reflected by association index scores indicated that scores were significantly higher among units whose modal behaviour to the other unit during interaction was 'mingling' than to both distant and close range display. Thus it appeared that units that shared the bai more frequently were more disposed to peaceful, tolerant, and even affiliative interactions.

The apparent differences in rates of agonistic behaviour between silverbacks in the Virungas and at Mbeli do not, however, point towards a phylogenetic origin. Although no physical fights were observed in the bai, evidence of wounding on the bodies of adult, and especially solitary males indicates that, as at Karisoke, injurious conflict is a feature of male-male interactions. It seems likely then, that the bai environment exerts a moderating influence on the agonistic behaviour of silverbacks. In the same way that female transfer during inter-unit encounter did not appear to be facilitated in the bai, greater visibility is likely to be pivotal to creating conditions of increased tolerance between silverbacks. With clear lines-of-sight of up to 700m, silverbacks are able to make decisions regarding whether or not to interact. If any conflict of interests is present, a silverback may easily take evasive action and avoid confrontation. In a dense forest habitat, such detection and evasion may be compromised and 'flash-points' more likely. In the bai, only units both wishing to interact need become involved in a close encounter. The super-abundance of edible aquatic herbs in the bai probably reduces the likelihood of contest competition among units, but it is predicted that were the same abundance of plant food available in a dense forest environment though with visibility reduced, levels of agonistic interaction would rise.

The implications of this finding are simple but critical. The unique conditions encountered by gorillas in large bais represent not only a distinct habitat type but also generate a 'social landscape' very different to that in operation in the forest. This is not necessarily to suggest that gorillas multilaterally respect different rules of conduct within clearings, but that each individual recognises the altered parameters surrounding social interaction and moderates his or her behaviour accordingly. Bais offer perhaps the only opportunity for research into the interactions of units on a scale approaching that necessary for statistically valid analysis. They offer the best opportunity for examining the behavioural elements used by gorillas during interaction, and can be informative with regard to the socio-behavioural 'capacities' of gorillas, but the very conditions permitting such observation alter the nature and probably the frequency of interactions to a degree whereby it might be suggested that they be considered phenomena independent of social interaction in the more typical forest setting.

Chapter 7

Discussion

Fundamental to an overview of the data and ideas presented in this thesis is a realistic grasp and acknowledgement of the difference between those questions that can be answered, those for which the data may offer important clues and insights, and those that remain unanswered but can now perhaps be approached with greater clarity in future studies. Data were not initially collected in order to answer limited and specific hypotheses, but represent an endeavour to produce a baseline appraisal and understanding of several aspects of bai-use and gorilla socioecology. As such, establishing and maintaining structure when drawing conclusions from the work is critical. One approach to an overall consideration of these data poses the question, 'What does the bai represent for the gorillas using it?' with its necessary corollary, 'What does it mean to be a gorilla ranging where there are no bais?'. Given the gaps in our knowledge of the Mbeli population's activities outside of the bai, a more realistic approach might be, 'What are we seeing when we observe gorillas in Mbeli Bai?', and it is largely in the spirit of this latter question that the discussion proceeds.

A point made abundantly clear at the start of Chapter 3 is that, at Mbeli, we are seeing virtually nothing of a gorilla's life. With approximately 99% of a gorilla's daylight hours spent elsewhere, caution is required when drawing conclusions from the data. Impetus to continue in the face of this rather shocking statistic is provided by the knowledge that observer time spent at Mbeli Bai is rewarded with gorilla observation hours at least an order of magnitude greater than those possible at most other 'non-bai' western gorilla study sites. Put simply, there are many aspects of gorilla life that will never be elucidated through bai study, just as there are several that will never receive any illumination other than at bais.

Whether examining social interaction or bai-use patterns, a question returned to time and again is, 'How important is the bai to gorillas?'. Already we know that the vast majority of a gorilla's life is spent out of the bai, however, a) while time spent at Mbeli alone may represent little of a gorilla's life, visitation of other bais in the region may increase the overall importance of the resource, and, b) as has been noted in the study of western gorilla frugivory and keystone foods (e.g., Rogers et al., 1994; Tutin, 1996), and in mountain gorilla bamboo feeding (e.g., Fossey & Harcourt, 1977), a resource need not be used extensively or all year round to be important. With respect to the first point, it is not yet known to what degree Mbeli gorillas visit other bais. Mbeli is the largest clearing of its kind in the region, though several smaller bais are situated within an average home-range distance of Mbeli. At present, a study is being designed to monitor these clearings for known groups and individuals (Stokes, pers. comm.). However, even if some units are confirmed as using these clearings, there is no reason to predict that their use would be greatly in excess of that at Mbeli. As such, the contribution of bais to total time-budgets is still likely to be no more than two to six percent (based on a maximum of five other clearings within range of Mbeli).

What, if anything, is the main attraction of bais to gorillas? At a general level, the two main possibilities are social or trophic features. As shown throughout the thesis, many gorilla units visit the bai and shared bai-use and interaction are common. Consequently, the bai is likely to facilitate social interaction and may assume an important social role in the lives of some individuals (i.e., solitary males – Chapter 6). However, this is likely to be a proximate effect, resulting from the initial attractiveness of the clearing for trophic or other non-social reasons. Drinking is highly unlikely to be a primary motive for bai visitation, as streams are abundant in the region. Other proposed attractions are the abundance and high protein content of aquatic bai plants, or the high mineral content of some species (e.g., Nishihara, 1995; Magliocca, 2000). Although some of the plants consumed by gorillas at Mbeli do have a high nutritional value, pilot work in Chapter 3 suggests that extremely high water content and bulk may limit the contribution of these plants to dry-weight intake, providing one explanation for the relatively short duration of most bai visits. The seasonality of bai visits may hold some clues to the feeding significance of the bai, though with only three years data (one year of which is incomplete) few if any patterns can be confidently attributed to any one variable or set of variables. Indeed, the apparent effects of a *Stomoxys* fly outbreak on visit duration and frequency, and the 'mast' fruiting of *Nauclea vanderguchtii* are both offered as examples of how unpredictable or stochastic events may greatly alter bai-use patterns and hide underlying trends that might otherwise explain the primary nutritional value of the bai. Although open to the confounding influence of such events, the finding that bai-use is consistently highest during the peak fruiting season may be pivotal. Were bai plants of major importance as a source of protein and carbohydrate, then one would predict them to be exploited most during the main dry season, when few fruit are available and terrestrial herbs produce fewer shoots and may be less nutritious. The fact that the opposite effect is described, with highest visitation taking place during the fruiting season suggests otherwise, and raises the hypothesis that bai feeding, though perhaps inefficient or self-limiting for most of the year, may become an attractive option when most nutritional requirements are largely met through the consumption of energy-rich fruit.

The mineral content of some bai plants remains a potential attraction of clearings, though this hypothesis does not appear to sufficiently explain the erratic visitation patterns of many gorilla units. However, without data on bai- and swamp-use away from Mbeli, no clarification in this area will be forthcoming. Undeniably, gorillas feeding in swamps ingest significantly higher concentrations of certain minerals than are present in most of their terrestrial foods, and bai plants do sometimes grow abundantly and in dense patches, thus lowering the energetic costs of feeding, but should these factors be considered as evidence suggesting that bais are of major importance to gorillas? So far there is little evidence to suggest that bais are crucial to gorilla well-being, or proof that gorillas without access to bais (most of the western gorilla population) are at a disadvantage. Gorillas rely on large quantities of stem and green leaf material from monocotyledonous herbs to maintain health. Sites offering an abundance of such foods will clearly be attractive, whether they are found in bais, light gaps, or in non-bai swamps. That so many gorillas can be seen at bais, often with units visiting simultaneously, indicates that they exploit bai resources preferentially, either on a regular and selective basis, or whenever they happen to be in the vicinity of a bai while following 'core' or seasonal ranging patterns. However, the importance of bais may be easy to overestimate. Although more research into bai formation and 'evolution' are needed, they may represent relatively temporary phenomena, at least in relation to their attractiveness to gorillas. Mbeli is currently attractive to gorillas, but may not have been as little as 40 years ago (Chapter 2), and through sedimentation and re-colonisation (or indeed the return of large numbers of elephants), may cease to be within the next 40 years. An alternative way of considering bais may be to imagine them as the equivalent of giant fruiting trees. Some units may visit them regularly as an integral component of their home range, while others may make special visits, especially if drawn to the vicinity by other resources. Being exceptionally large and subsequently hard to defend, they can accommodate several units at once without provoking competition over food. However, they need not, in and of themselves, be a vital or 'keystone' part of any unit's nutritional requirements, even if they do provide useful dietary elements.

The nutritional aspects of bai-use were not the main subject matter of this thesis however, and it is unwise to speculate further without more data. When considering why gorillas use bais and their importance in gorilla socioecology, it may be easy to overlook less biologically imperative motives for visitation. Observations suggested that individuals in some groups were excited to enter clearings and exhibited behaviour congruent with an appreciation of some aspect(s) of the environment itself (self-play, social play, rolling). The bai was clearly an enjoyable environment for some immatures who either played or engaged in relatively light-hearted agonistic exchanges with members of other groups. Environmental features that may be appreciated during bai-use include: sunshine (may be beneficial in drying the skin during the rainy season), breeziness, cooling water on hot days, and increased visibility (relaxation of vigilance). It is unlikely, however, that environmental factors alone would be a primary motive for bai-visitation, though they may play some role in increasing the likelihood of a visit being made if gorillas are in the region. Although some individuals show agonistic reactions to other species in the bai, in general, tolerance levels between species are probably increased in an environment where inter-individual spacing can be so effectively maintained. Data on the direct effects of the climate on bai-use were inconclusive. Some gorillas showed discomfort during heavy rain, or left the bai during thunderstorms, and insect pests appeared to be more abundant and irritating on hotter days, but no data were collected on swatting/scratching rates to explore this observation further.

Ultimately, questions relating to motives for bai-use and the influence of bai-use on ranging can only be speculated on in this thesis as few data were collected with these questions expressly in mind. Whether it will be possible to collect such data as are required for this task is open to debate. It is hard to see how this could be comprehensively achieved without the use of radio-telemetry. For me, the importance of these data is largely one of academic interest, and there is little justification in risking the health of gorillas through immobilisation and the attachment of radio transmitters in its pursuit. It may be argued that bais represent important habitats for gorilla conservation, and a greater understanding of their influence is required in order to permit improved conservation planning. Indeed, it has been suggested (Magliocca & Gautier-Hion, *in press*) that the mineral content of bai plants (at Maya Bai) may make up for deficiencies due to low fruit availability, and increase the carrying capacity of the region; thus making bais key habitats for gorilla conservation. While there is a slight possibility of this being so in some areas, at Mbeli, where fruit is not uncommon, the main conservation value of the bai must surely be that, unprotected, it would permit well-armed poachers to decimate most gorilla groups in the area, as well as elephants and other wildlife. It is suggested that little other justification for the protection of areas containing bais is required.

The principal task of this thesis has been in describing the social organisation of the western lowland gorillas using Mbeli Bai. This may superficially seem a simplistic aim, but it is of critical importance in furthering our understanding of primate social systems, including the influence of ecological variables on behaviour, and ultimately, the evolution of social behaviour in both human and non-human primates. The world currently has only six species of Great Apes (including *Homo sapiens*), and it is staggering at a time when five of these are facing extinction, that not only is so little being done to prevent their loss, but also that so little is understood about their physical, social and mental capacities, systems and needs. With particular regard to gorillas, the astonishing detail of mountain gorilla studies has for many years been juxtaposed by an almost total lack of reliable data on anything other than feeding ecology in western gorillas. As discussed in Chapter 4, traditional methods of gauging group size and composition using nest-counts and dung diameters, can be extremely inaccurate and misleading, and it is possible that in the absence of reliable observational data, there have been occasions when, perhaps unwittingly, interpretations of secondary trail and nest data have been made somewhat to match what was expected or desired by the paradigm or hypothesis under consideration.

The most significant scientific consequence of the discovery of bais by primatologists has been the opportunity to use direct observations of whole groups to provide precise descriptions of group size and composition, enabling comparisons of social structure to be made with mountain gorillas. Only now is it becoming possible to consider the influence of ecological variables, and in particular the potential for greater food competition due to frugivory and a reduction in the availability of herb foods on social parameters. However, this thesis only provides one side of the picture, as it was not possible to collect data on the botanical composition of the surrounding forest. Such interpretations as are made are therefore done so on the assumption that the Ndoki forest (excluding the presence of bais) provides 'typical' conditions for western gorillas, and crucially, conditions differing in relatively well understood ways from those faced by mountain gorillas. Such botanical survey as has been conducted in the region (e.g., Fay, 1997) suggests that this is likely to be the case. Current studies are now addressing these issues through the instigation of thorough botanical and phenological surveys of the surrounding forest, and should permit us to validate or reject this assumption.

The description of the Mbeli population in Chapter 4 represents the most robust data in the thesis, and to date, the most accurate description of a western gorilla population, in the sense that repeated observations allowed absolute precision in group counts. The main areas in which data remain vague are those reliant on many years of study (i.e. demographic variables such as inter-birth intervals, age at first birth, and mortality rates).

In describing group size and structure, as well as other social characteristics, it should be borne in mind that, although precisely measured, such features may themselves be, to some degree, a product of the presence of bais in the area. It may be, for instance that group size is more likely to be higher in groups with access to bais than those without. However, given that the vast majority of the time-budgets of units visiting Mbeli are probably spent out of bais, any such effects are predicted to be minimal at best.

With all western gorilla sites compared to all data from eastern gorilla sites, no significant difference in group size was found, although the larger western gorilla groups at Lossi (Bermejo, 1999) and those of the mountain gorillas censused by Schaller (1963) almost reached significance. Within western gorillas, Lossi was clearly responsible for the significant differences in group size. Group size at Mbeli was towards the bottom of the distribution (and below several sites without bais), but it was suggested that while greater herb availability may be responsible for some of the largest site averages, other methodological factors may confuse the results. In particular, there may be a tendency to overlook small groups when using trail and nest data. Nevertheless, while observation conditions and sample size at Mbeli may have ensured that small groups were detected (thus lowering the average group size score relative to other sites), site comparisons did suggest that maximum group-size may be positively correlated with herb availability. It was also noted that populations described with higher sample sizes showed larger ranges between minimum and maximum group size, further compounding analyses. Some research groups at Karisoke are now attaining extremely large group sizes. While for the time being, feeding competition or social pressures do not yet appear to have limited these groups or caused group fission, current trends should at least raise questions regarding the influence that many years of human contact and protection may have had on demographic processes, and thus, how representative such groups are of the population as a whole.

As a general comment, comparative analyses were weakened considerably by the quality of much of the data available and in particular, the difficulty of detecting infants using secondary evidence, and weaned group size not being made apparent in some reports. As a result of these issues, it is probably premature to overly interpret these results in the light of predictions made for group size when considering the influence of increased foraging costs (e.g., Clutton-Brock & Harvey, 1977a; Wrangham, 1980; Janson & Goldsmith, 1994).

The differences between mountain gorillas and the population at Mbeli were much less ambiguous when considering group composition, the most striking being the lack of multi-male groups at Mbeli. In accordance with results from Maya Bai, no multi-male groups were identified during this study. It is suggested that many groups described as multi-male elsewhere are in fact misnomers, in which the secondary males are maturing sons who will emigrate on, or very shortly after, reaching maturity, as is the pattern at Mbeli. The use of nest and dung data in western gorillas is particularly likely to identify 'multi-male groups' where none in fact exist. The identification of such groups does little more than recognise one stage in the ageing process or 'evolution' of social groups. The potential influence of these group-types (i.e., nascent, juvenile, mature, etc) is highlighted several times in the social chapters of this thesis and its importance, especially when interpreting demographic data from small sample sizes cannot be over-stated. It would be easy to claim that the apparently lower rate of multi-male groups in western gorillas is the result of constraints on group size through foraging competition (larger groups at Karisoke were more likely to be 'multi-male'; Robbins, 1995). While this may be an issue at some level, the largest groups at Lossi, which remain single-male, suggest that group cohesion can be maintained in such groups without coalition support, and that young males may still choose to emigrate on reaching maturity rather than remain in the natal group, even where abundant herbs permit the presence of many females. Data on the demographic history of the large Lossi groups will be of key interest in this regard.

All males reaching or approaching maturity at Mbeli emigrated from their groups, and all those not leaving the population were known to have become solitary. This process appears to be voluntary, suggesting that young males perceive their chances of finding breeding success outside the natal group to be higher than within it. The opposite perception appears to be current at Karisoke, where it is even shown that males have a greater chance of breeding in their natal group than by becoming solitary (Robbins, 1995; Watts, 2000). The formation of bachelor groups at Karisoke further attests to the difficulty of gaining females as a solitary, or the hazards of such a life in respect to agonistic encounters with other silverbacks. No bachelor groups were recorded at Mbeli, and are rare or absent in other western populations. Once again, it is necessary to consider the impact of human presence on mountain gorilla demographics. One possibility to consider is that improved protection in key areas of the Virungas may create conditions of higher gorilla density, increasing the frequency of contact between individuals and groups. As mentioned in Chapter 4, a feedback effect may be in operation whereby groups with more than one male are better placed to defend their females from approaches, both by other groups and solitaries, thus reducing the chances of female acquisition by solitaries, increasing the chances of injury, and thus adding to the costs of male emigration.

No females were known to breed in their natal group, although one female copulated with her natal group silverback before leaving the group for over a year, returning, and then giving birth for the first time. Sample sizes were small, but the data suggest that both nulliparous and parous females emigrated preferentially into smaller groups, indicating that the costs of competition for resources may still be an issue influencing female transfer decisions. However, future analyses from larger samples should consider natal and secondary emigration independently, as sub-adult females may by default, be more likely to emigrate from groups of a certain size range (generally larger groups), concordant with their group-type. The apparent ubiquity of female transfer provides the first clear evidence against the presence of strong female philopatry in the Mbeli population. None of the emigrating females at Mbeli were seen to travel alone, and two examples of block transfers of all remaining members of groups in which the silverback had died suggest that the risk of infanticide exists and may influence female transfer decisions.

Finally, groups at Mbeli were stable in the sense that there was no evidence of fission-fusion or sub-grouping as a strategy for minimising foraging competition. Although sub-grouped units might be predicted to reunite for bai visits due to the abundance of food available, it is likely that evidence for flexible grouping patterns, such as separate sub-group entries to the bai, would have been detected in the course of three years, were such a strategy regularly employed by groups in the region.

If group size and structure represent something akin to the 'finished product' of a social organisation process, then interactions within groups and between units can be thought of as the mechanism by which this product is fashioned. This being so, a careful examination of the nature of interactions may say as much about the overall system as the population structure itself. This at least, was the primary reasoning behind the collection of interaction data at Mbeli. Analyses and comment on intra-group interactions were mainly limited to those of adult males and females as these were most likely to betray variation in the social organisation of the population. In the event, too few intra-group interactions were recorded to make a thorough statistical analysis possible. This was not an observational design problem, however, as there was ample opportunity to record all occurrences of such behaviour. Rather, it reflects the low frequency of within-group adult social behaviour while at the bai. Given the abundance of food at the clearing, it is an obvious concern that interaction rates were depressed by the preoccupation of adults in feeding (which conversely may have permitted higher rates of play among some juveniles). Consequently, attention was paid primarily to the presence or absence of behavioural patterns indicative of certain social states. There was no evidence for an increase in female philopatry. No dominance hierarchy or uni-directionality of agonism was recorded between females. Likewise, there was a total lack of affiliative support or coalition forming in females. The general lack of social engagement by females with any individual other than their silverback or offspring was mirrored in their extremely low frequency of interaction in an inter-unit context. Females, in many ways, appeared socially independent of each other and almost totally dependent on, and dominated by, the presence and behaviour of silverbacks. Interestingly though, there were occasions when the non-philopatric grouping of females appeared to be the central unit of gorilla social life, with the silverback acting as voluntary 'hired muscle'. This was especially so on occasions when group females would leave the bai well in advance of their silverback, and, judging by the intensity of his subsequent hooting and chest-beating in trying to locate them, may have begun to move away from the bai edge without him.

In contrast to mountain gorillas, grooming between dyads other than mothers and infants was conspicuous by its absence. Similar reports from western gorillas in captivity suggest that this may represent a genuine species variation, with causes being the importance of rest periods in mountain gorillas, and their exposure to plants such as *Gallium ruwenzoriensis* which adhere readily to hair. As in mountain gorillas, the expression of female agonism and dominance hierarchy may be unlikely to develop even if potentially advantageous, as silverback control intervention appears to be present as a means of removing the opportunity for one female to benefit at the expense of another. Under the polygynous system of gorilla social life, it is firmly in a silverback's best interest to prevent any non-progeny female emigration, both by minimising a female's motivation to emigrate (e.g., by intervening in conflicts), and also by the harassment and herding of females liable to emigrate (especially new immigrants prior to pregnancy and parturition). However, while herding of mountain gorilla females was mostly done in multi-male groups during interaction, the herding observed at Mbeli seemed pre-emptive and not necessarily linked to inter-group interaction. The absence of herding during interactions may be a result of the high visibility conditions of the bai, in which all parties are inhibited from engaging in behaviour linked to female acquisition and emigration due to the ease of policing by silverbacks. The greater potential afforded by the bai habitat for groups to become more intimately acquainted with other groups, their composition, and the propensities of their silverbacks, may also prevent highly charged situations of attempted female acquisition from arising in the first place, as silverbacks may avoid any contact with counterparts they know to be actively seeking females.

This idea is given greater credence by the lower levels of agonism observed between silverbacks at Mbeli compared with those at Karisoke, and the absence of a correlation between number of potential female migrants in a group and the intensity of silverback aggression (as seen at Karisoke; Sicotte, 1993). Meetings among mountain gorillas may be more akin to chance encounters within a given region, with agonism exacerbated by the close-quarter conditions generated by dense vegetation. By contrast, at Mbeli, high visibility allows a unit to avoid any other, either by not entering the clearing when a particular other unit is present, or leaving if a unit to be avoided arrives. Although the number of potential migrants or adult females in a group did not influence the intensity of silverback inter-unit response, it was found that the silverbacks of unit-pairs with high association index scores were more likely to mingle peacefully than engage in close or distant agonism or to avoid interacting with each other. This further adds to the evidence suggesting that the bai environment profoundly influences the frequency and type of some inter-unit behavioural exchanges. Almost 60% of shared bai-use occasions by pairs of units failed to provoke any interaction.

Interestingly, frequencies of inter-unit non-interaction and agonistic interaction were almost identical to those from the only other bai study site, Maya Bai (Magliocca, 2000). When comparing frequencies of silverback tolerance and agonism between Mbeli and Karisoke, Mbeli males were found to be much more likely to engage in peaceful mingling and much less likely to engage in agonistic display. Notably, while 17% of inter-unit interactions at Karisoke involved contact aggression between silverbacks (Sicotte, 1993), no such exchanges were observed at Mbeli. Evidence suggesting this is a bai phenomenon was provided by the record of presumed combat-inflicted injury noted on Mbeli males. It appears that although silverbacks do not engage in dangerous aggression in the bai (where its avoidance is greatly facilitated), it remains a feature of forest interactions. Injuries consistent with fighting were more frequent among solitary silverbacks than group silverbacks. Although it is possible that solitary males (mostly being younger) consistently fare worse than group silverbacks when contesting resources, it is more likely that this result is due to elevated frequencies of contact aggression between solitary males. This seems counter-intuitive given that such conflicts do not lead directly to gains or losses in breeding females, but the hypothesis is supported by the finding that solitary males were much more likely to interact with each other than any other age/sex dyad in the population, and that all such interactions were agonistic. When examining the previously undescribed phenomenon of splash display (Appendix 7, Section I) solitary males were found to use the display agonistically towards each other greatly in excess of levels predicted by their presence in the population. Data on male aggression from Mbeli provide a behavioural correlate to the finding of Stoinski et al. (2002) that male gorillas experience their second, and largest, increase in androgen levels between the ages of 14 and 20 years.

The emergence of heightened aggression between young males was observed in the high frequency of 'play agonism' engaged in by blackbacks and sub-adult males during inter-group encounters. This aggression was usually mild in nature and never provoked intervention by either male's silverback. The bai appeared to offer an ideal 'stage' upon which such bluff exchanges could take place without escalation, just as it also permitted prolonged affiliative encounters, principally between juveniles and sub-adults. It is fascinating to consider how such interactions may influence and alter the social development of individuals, and the nature of future adult encounters between allies and adversaries acquainted during immaturity. Unfortunately, although groups without access to bais may well differ in their reactions to some social situations from those with access, measuring such differences is unlikely to be possible.

This discussion concludes by asking again the question posed at the beginning of this section, 'What are we seeing when we observe gorillas at Mbeli Bai?'. Undeniably, only a tiny proportion of a gorilla's life is exposed through bai observations, and this fact, in and of itself, may place the importance of bais to gorillas in perspective. Bais like Mbeli may provide important nutrients and minerals to visiting gorillas, but there is, as yet, no evidence that group sizes or reproductive rates are significantly higher for these gorillas than those without access to bais, let alone that bais are vital to the well-being of the gorillas using them. This, however, remains as speculation, and without data on gorilla ranging and feeding outside of bais, and more accurate measures of group size and structure from other sites, little definitive progress can be expected.

If the physical importance of bais to gorillas cannot be gauged through bai study alone, then to what degree does bai study present a true picture of social behaviour in western gorillas? In general, the study of social behaviour within the group may be best served by observing well-habituated groups in the forest. Such habituation remains elusive, although progress is now being made towards this goal. In the bai, the predominance of a particular type of feeding behaviour probably dictates the frequency and type of intra-group behaviour witnessed. Nevertheless, bai study remains important to the extent that details of intra-group behaviour in response to the presence of other units are unlikely be witnessed in the forest, as is the capacity to observe all members of a unit simultaneously.

Inter-unit interaction can only ever be studied systematically and rigorously in bais. Problems associated with differential habituation levels and the obstruction of key 'players' during interaction plague this area of study, both in mountain gorillas and all other sites where visibility is compromised. The range of units, both group and solitary male, using Mbeli Bai make it a truly exceptional resource for studying the ways in which gorillas interact. However, one of the key findings of this thesis has been that such behaviour in bais is likely to be highly site-specific. This is especially so for silverbacks, who appear much more tolerant of each other than expected in the forest. Tolerance between silverbacks also has a knock-on effect on the opportunity for all other members of the group to interact, thus adding to 'the bai effect'. A conservative approach to the findings of this study as pertaining to inter-unit interaction might be that such social behaviour in bais is just that, and that what we witness at Mbeli should not be considered as representative of the bulk of gorilla social behaviour, which takes place in the forest.

This approach should not in any sense discourage us from further study of this and other topics in bais. No other opportunities for inter-unit interaction study are likely in any other environment, and inter-unit social data can still tell us an enormous amount, as long as it is interpreted in light of the caveats described. Many areas for future research at Mbeli have already been proposed in this thesis, but of particular interest would be a highly detailed examination of all social interactions using wide-angle video of whole units, alongside simultaneous close-up video of behaviour such as body positioning, eye gaze and other subtle signals in a frame by frame sequential analysis of action and reaction. Gorillas have traditionally been considered as limited in their social behaviour, especially in contrast to the highly demonstrative behaviour of chimpanzees, but I believe that much of the subtlety of gorilla social behaviour is overlooked by traditional methods of study. Bais also offer an unique chance to record the minutiae of gorilla behaviour, whether they be food processing and handedness (Parnell, 2001), details of mother/infant behaviour (Nowell, 2001), or among the topics covered in Chapter 3 and Appendices 3 and 7 of this thesis. Bais offer an unparalleled opportunity to record group size, composition and demographic change from sufficient numbers of gorilla units to account for much of the variability present in wild populations. I believe that such parameters are unlikely to be significantly affected by the presence of bais within the range of these units, and that this may represent the most important contribution of bai study to our understanding of life-history variables in western gorillas. Within a year of the submission of this thesis, the first of the infants born at the start of the Mbeli Bai Study will, if female, be looking to transfer for the first time; in five years or less, the first of the male offspring will become solitary and begin to look towards creating groups of their own. Long-term commitment to data collection at Mbeli is required, not only to ensure the protection of the gorillas and other fauna using the bai, but also to see to fruition much of the early work contained in this thesis. This will prove to be a highly important and exciting period in the study of the western gorilla.

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Appendices

Chapter 3

A3.1

The passage from the forest to the open spaces of the clearing did not appear to concern the vast majority of gorillas. However, one unusual observation concerned a juvenile from SNO group who was seen to enter the bai, but stop at the edge, repeatedly looking skyward. After returning into the forest once, he returned and again looked straight up. His whole demeanour was one of considerable anxiety and observers initially suspected that an eagle or other large bird may have been overhead. However, on immediate inspection, no birds were in the area, and the juvenile was thought to have been reacting to a highly dramatic and unusual cloud effect (shown in Plate A3.1). After looking up ten times, the juvenile ran out of the bai a second time.

Plate A3.1 Cloud formation suspected as having caused alarm to a juvenile gorilla

A3.2

In the only example of possible tool-use by gorillas at Mbeli, four individuals were seen to swat over their shoulders with bai vegetation. Juvenile Iook was observed to swish a clump of *Hydrocharis* roots over his back several times, move forward a few paces, put down the bundle and then after a few moments, pick it up again and repeat the swatting action. Blackback Homer was once seen to use a *Hydrocharis* fly-swat on his back. It can be strongly argued that such actions are merely accidental occurrences in which there happens to be a clump of vegetation in the hand prior to its being ingested at the same moment as an irritation is felt on the back or shoulders (most 'swats' are subsequently eaten). Were this so however, it might be expected to occur much more frequently given the frequent irritation of insects and ubiquitous feeding on *Hydrocharis* and other plants. The most frequent users of this 'technology' were the blackback and silverback of TRA group. The blackback Stockwell was observed using *Hydrocharis* as a swatter on five separate days (once swatting in this fashion 20 times during one visit, and five in another). The silverback Travis was seen to use *Hydrocharis* on four occasions (eight times with eight separate plants on one occasion, and repeatedly during a 40 minute period on another). This individual was the only gorilla to be seen using anything other than *Hydrocharis* for this apparent purpose, when on one occasion, he was seen swatting with a *Rynchospora corymbosa* stem. The fact that most observations of this behaviour came from two individuals in the same group suggests that more than an accidental coincidence of natural phenomena is responsible for the apparent use of fly-swats. Its use was extremely rare, however, and most gorillas did not show any evidence of being aware of greater swatting efficiency when using a plant bundle. Nevertheless, this observation offers a tantalising suggestion of genuine tool-use in gorillas, a phenomenon hitherto almost unknown in the wild (e.g., Beck, 1980).

A3.3

Tropical storms are frequently accompanied by thunder and lightening. Group-living blackbacks, Gretsky (BON) and Stockwell (TRA), both reacted to separate incidents of loud thunder by running towards the bai edge; only Stockwell exited the bai, however, looking up directly at the sky before doing so. Members of MOS group were also seen to move towards the bai edge during a heavy period of thunder and lightening. Silverbacks Clive and Bear both reacted to separate incidents of thunder by looking in the direction of the thunder-clap (Bear standing bipedal to do this).

Rain itself caused a variety of different reactions. Most gorillas continued to feed through light drizzle, but were more likely to react to torrential rain. Such a downpour effectively caused the cessation of a tense interaction between the blackbacks of MOS and BON groups, as all members sat huddled without feeding. A hunched position was a typical reaction to heavy rain. Gorillas were observed with both arms clenched around their knees, sometimes with their hands brought up by the sides of their faces. Alternatively, the arms could be wrapped over the chest, the hands sometimes seen clutching the bicep of the other arm. While in the hunched seated posture, adult female Margo was seen on several occasions to place the palm of one hand on her head for protection or warmth. Her juvenile Iook was seen using a variant of this action, placing both hands on the head, and even rubbing them backwards and forwards several times. Blackback Stockwell used the 'two-hands on head' method, and solitary silverback Vince was seen to wipe over the top of his head once with his left hand, and then to stoop forwards to wipe his brow and forehead in the grass three times in succession. Few gorillas deliberately exited the bai in response to rain, though on separate occasions, Stockwell and solitary silverback Frank exited during heavy rain, returned when it became lighter, and then left again as the heavy rain returned. Young juvenile Iook responded to one heavy downpour by huddling at his mother's back. All three juveniles of CLI group climbed on their mother's backs during a downpour and lay flat, presumably so as to receive as much body warmth as possible from them as the group began to exit the bai. Juvenile Peter, during slightly lighter rain, looked directly up at the sky such that his face was splashed by the raindrops, then gently waved one arm above his head. Although varied, most of these reactions show some evidence of the chilling effects of rainfall on gorillas. There follows a consideration of the possible effects of chilling as a proximate cause of yawing in gorillas.

A3.4

Gorilla yawning behaviour

Introduction

Yawning, or gaping behaviour identical in outward appearance to yawning, has been recorded in most major vertebrate groups (Heusner, 1946). Despite such ubiquity, the study of yawning has advanced in a somewhat disjointed manner. This is probably due to the status of yawning as a basic behavioral element that appears to lack consistent and clear functional context across the species (Smith, 1999). Several reviews have attempted to bring together the various strands of research on yawning, with varied degrees of success (Heusner, 1946; Barbizet, 1958; Redican, 1975; Askenasy, 1985; Aubin & Garma, 1988; Smith, 1999). Yawns have been generally categorized as being either 'true' or 'rest yawns' with direct physiological functions and correlates (Barbizet, 1958; Altmann, 1967; Sauer & Sauer, 1967; Angst, 1975; Deputte, 1994), or 'social' or 'emotion yawns' in which either the primary, or more usually a secondary, function of yawning is seen in the context of a social signal (Bertrand, 1969; Redican, 1975). Laboratory studies have demonstrated that yawning can be regulated through a variety of neural and endocrine paths, with dopamine, seratonin, and testosterone among the neurotransmitters and hormones found to have an effect on the frequency of yawning (e.g., Urba-Holmgren et al., 1979; Phoenix & Chambers, 1982; Yamada et al., 1990). Yawning has also been shown as an indicator of brain pathology, including encephalitis, brain hemorrhage and lesions (Wilson, 1940; Nash, 1942; Heusner, 1946; Barbizet, 1958). Few of these studies, however, offer much insight into selective pressures that may have shaped the evolution of the pattern.

In humans and many other vertebrates, yawning has traditionally been thought of as a means of maintaining or increasing oxygen levels to the blood, especially following periods of reduced activity (Barbizet, 1958; Redican, 1975). However, Provine et al. (1987a) offer evidence questioning a respiratory role of yawning. Provine et al. (1987b) showed that in humans, yawning is most frequent during the hour before sleeping and the hour after waking. However, stretching behaviour, which is commonly associated with yawning, was only found to be more frequent in the hour after waking, suggesting a mechanism preparing the body for activity after a period of rest. The authors suggest, in light of this asymmetry in temporal pattern between yawns and stretches, that yawns may have emerged as a para-linguistic signaling device, communicating drowsiness and the desire for rest in humans (Provine et al., 1987b). The importance of such signaling is reinforced by the well described but little understood phenomenon of yawing contagion in humans; a feature not as yet confirmed in other species.

Altmann (1967: p332) identifies three main types of yawns in non-human primates: the 'true yawn', implicated in a basic physiological function such as oxygen levels in the blood, triggered by drowsiness and fatigue; yawns given during situations of elevated tension or anxiety (sometimes known as 'tension yawns') arising from the mental state of an individual; and 'threat yawns', where the purpose of the action appears to be the exposure of the teeth (particularly the canines) as an aggressive display indicating an individual's capacity for fighting and inflicting bite wounds. Troisi et al. (1990) point out, however, that it may be difficult to differentiate between types, especially as some individuals may yawn (tension yawns) as a direct result of a threat yawn by a conspecific. Yawns have been clearly shown in some circumstances to be under voluntary control (Anderson & Wunderlich, 1988). The function of yawns as a social threat is reinforced by the common observation of higher frequencies of yawning in male primates than females (e.g., Hall & DeVore, 1965; Bertrand, 1969; Redican, 1975; Hadidian, 1980; Troisi et al., 1990), and a positive correlation between yawn frequency and dominance rank in some species (*Macaca fascicuaris* - Troisi et al., 1990; *Macaca nigra* - Hadidian, 1980). Yawning as a threat has been largely ruled out for humans. Men and women do not differ in their frequency of yawning, and it is suggested that a lack of sexual dimorphism in canine size for the species may be implicated in this.

Gorillas, by contrast, show extreme sexual dimorphism, males having massive canines (Dixson, 1981), which are known to serve occasionally as formidable fighting weapons. The popular public image of the gorilla would suggest that any mention of this behaviour should be listed under 'display behaviour'. Illustrators and photographers eager to capture the might and ferocity of silverbacks have frequently resorted to recording their subjects with mouths wide open and long canines bared, such that it has become an extremely familiar image (e.g., Willoughby, 1978). Scientific comment on yawning in gorillas is extremely scant and rather vague. Schaller's (1963) records describe silverbacks yawning repeatedly in situations judged as tense due to the presence of a human observer (p204). In a more ambiguous exhibition of yawning behaviour by another gorilla (p310), during which aggressive threats were made at the observer (chest beats and branch snapping), there was also evidence of fear or tension (defecation), thus blurring the line between threat and tension yawn types. In one record, Schaller (1963; p138) appears to describe a 'true' yawn, made by a silverback, on briefly rising from a prostrate position, stretching one arm, yawning, then lying back down. Dixson (1981; p132) reiterates the tension yawn function and claims that gorillas are not known to yawn as part of an aggressive display.

As far as I am aware, there are no published accounts of yawning in non-human primates that consider temperature or atmospheric pressure as variables when seeking proximal agents in the triggering of yawning behaviour. Temperature has been recorded on rare occasions as a background variable but has not been the focus of any research. Baenninger (1987) reports that captive lions yawned most between 70 and 74°F (the ambient temperature of their quarters), with frequencies lowered at temperatures above or below this, and that captive mandrills showed no correlation in yawn frequency to the slight changes in ambient temperature they experienced. It is likely that most researchers would predict, if anything, a positive correlation between temperature and yawning, with warm environments likely to cause drowsiness. At Mbeli, the observation that many bouts of gorilla yawning appeared correlated to a drop in temperature (typically accompanied by rain and wind), plus the author's personal experience of yawning in apparent response to exposure to cold air, prompted a systematic attempt to record all cases of yawning in order to examine the variables influencing its exhibition.

Method

Data collection began in October 1998, and comprised the recording of all gorilla yawns. Information noted were; gorilla identity, age/sex-class, date, time, temperature (recorded in the bai edge at chest height), weather conditions, and any social interaction or situation occurring before or during the yawn or any other activity of the yawning subject.

On some occasions, several yawns were exhibited by an individual during a limited period and under constant environmental conditions. An independent sample was obtained by counting such occurrences as single yawning 'bouts'. Unless a conspicuous change in weather conditions was observed, yawns made in a sequence on any given day were judged as part of the same bout. Where several yawns within a bout straddled more than one hourly time period, the median of the hourly temperatures for the whole period was obtained. Air temperatures during yawning were then compared with the mean temperature for that hourly period, taken from the three-year study-period records. A Wilcoxon Signed Ranks test was used to identify any deviation from chance between these averages, and testing was two-tailed. For the purposes of the main analyses, records from infants are excluded due to the very different daily activity patterns and physical circumstances of individuals still reliant upon their mothers for food, locomotion, and to some extent, shelter and warmth.

Results

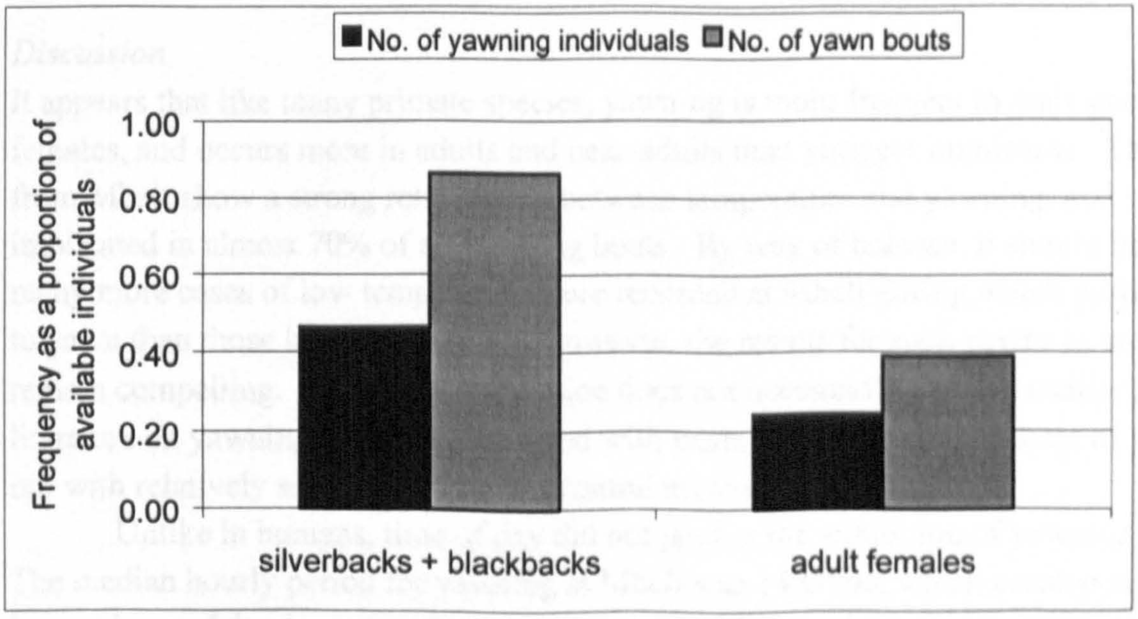
From October 1998 to October 1999, 19 temporally independent yawns or bouts of yawning were recorded from 14 individuals (7 silverback, 3 blackbacks, 2 juveniles, and 2 adult females), from 10 social units. From the 19 records, median ambient temperature at 'time of yawn' was 22.6°C. (range 21 to 29), while the median of the average temperatures for those time periods over the whole study period was 27.2°C. The differences were highly significant (Wilcoxon Signed Ranks test; $Z = -3.58$, $N = 19$, $P < 0.001$). Data collection was continued following my departure from Mbeli and with the addition of 30 new records, the difference between yawn temperature and average temperature remained significant ($Z = -5.64$, $N = 49$, $P < 0.001$).

Using the expanded data-set, two individuals stood out as more frequent in their exhibition of yawning: both blackback Frank and adult female Jewel contributed seven bouts each to the data-set (28 individuals contributed in total). The number of individuals of each sex performing yawns was very similar; 14 males and 11 females (and 3 sex undetermined): however the total number of bouts per sex differed more, with 27 bouts by males, 17 by females, and 5 unknown. The difference in actual numbers of known-sex yawning bouts was non-significant (Chi-square with Yates Correction for Continuity: $\chi^2 = 1.84$, $df = 1$, $P = 0.175$). However, when considering only silverbacks, blackbacks and adult females (for whom sex is known with absolute certainty), the ratio of males to females in the population is 0.6:1, indicating that there are over one and a half times more adult females that silverbacks and blackbacks. Figure A3.1 shows the number of yawning bouts and the number of yawning individuals for adult females against the male classes blackback and silverback combined. Frequencies are expressed as a proportion of the total number of individuals of those sex-classes in the population.

Statistical testing is not appropriate for such derived values, but the chart indicates that for both the number of individuals and the number of yawn bouts, male frequency is approximately double that of females. The number of yawns per bout ranged from 1 to 8 (median = 2). The median number of yawns per bout for males (taking medians from each individual) was 2 (N = 14, range 1 to 7) and for females was 1 (N = 11, range 1 to 2). While the difference was not significant (Kruskal-Wallis test: $\chi^2 = 3.26$, $P = 0.071$), this result and the difference in range between the sexes does suggest a trend towards a sex bias.

Of weaned non-adult individuals in the population, only four (juveniles) were recorded yawning, contributing six records to the data-set. No other age-classes other than blackbacks, young and mature silverbacks, and adult females were observed yawning. Although not included in the main analysis, eight records of yawning by infants were taken (from six individuals). Only three of these were associated in any way with rainfall, and although still suggesting a trend, differences in yawn temperature and average temperature were not significant (Wilcoxon Signed Ranks test; $Z = -1.82$, N = 8, $P = 0.069$). In five of the eight, the infant was dorsal on the mother's back at the time of the yawn.

Figure A3.1 Frequency of yawn bouts and yawning individuals by sex, corrected for proportional representation of males and females in the population.



Yawning occurred during all hours of the day except 7, 8, and 9:00hrs: the mode hourly period for yawning was 16:00hrs and the median period 14:00hrs. In total, 33 yawning bouts (67%) were associated with rainfall (raining either during or shortly prior to the bout). In three of these, a potential social context was also noted, and in six, the yawning individual was noted to be resting (in addition to the observed rainfall context). Four cases were linked to a social context but without rain, and five with a rest period without rain. No potential cause was discernible for seven bouts of yawning. Of the seven bouts potentially with a 'social' context, two concerned proximity to a sitatunga (possibly creating tension or fear in the gorilla): one took place during proximity between two silverbacks of different groups: one bout was made by a silverback as he herded a new immigrant female back towards the nucleus of his group (Plate A3.2b): three were during intra-group situations where tension between individuals was discerned.

Plate A3.2 (a) Young silverback, Bird, yawns during rainstorm. (b) Silverback Basil yawns while herding adult female, Martha.

a) Temperature/pressure/posture yawn *b) Tension/anxiety or threat yawn?*

Discussion

It appears that like many primate species, yawning is more frequent in male gorillas than females, and occurs more in adults and near-adults than younger immatures. The results from Mbeli show a strong relationship between temperature and yawning, and rainfall was implicated in almost 70% of all yawning bouts. By way of balance, it should be noted that many more cases of low temperature were recorded at Mbeli during which gorillas failed to yawn than those in which they did, however, the results for such yawns as were recorded remain compelling. Of course, correlation does not necessarily equal causation; the literature on yawning is already saturated with examples of proximal causes of yawning, but with relatively scant regard for the central mechanism(s) involved.

Unlike in humans, time of day did not predict the exhibition of yawning in gorillas. The median hourly period for yawning at Mbeli was 14:00hrs, which corresponds to the hottest hour of the day using three year averages. No observations of gorillas in the first hour of the day, or preparing to sleep at the end of the day were possible, however; conditions that may well add have added temporal skew to the data.

Some evidence of what might be termed 'rest yawning' was recorded however (probably in proximal response to fatigue or drowsiness), although such cases were very few. Yawns in a social context were also poorly represented and in most cases, ambiguous. In the case of silverback Basil herding new immigrant female Martha back to his group, his frequent yawns could be viewed as an aggressive display (accompanied as they were by chest-beats and charges). However, as mentioned in the introduction, such situations may also create levels of tension and stress in the individual, that may be more important triggers for yawning than aggression *per se.* It is particularly noteworthy that in the hundreds of aggressive displays performed by silverbacks at Mbeli, both against other silverbacks and individuals of other age/sex-classes, yawning was never recorded as a typical component of agonistic behaviour patterns, unlike chest-beating, ground and water slapping, charging, and other facial/postural signs of aggression (*see* Appendix 7). This is perhaps a curious finding given the extreme sexual dimorphism of the species (including that for canine size), the high level of competition among males for females, and the ubiquity of several forms of agonistic display evolved specifically to advertise fighting ability. Given the possibility of tension yawns in response to social situations, and the major proximal variable of temperature/rainfall, no unambiguous cases of threat yawning can be said to have occurred at Mbeli.

The data from Mbeli are insufficient to explain the yawning phenomenon in the population, but the observed relationship with temperature drop/rainfall does prompt the theoretical exploration of two main hypotheses that may do so (*see* Figure A3.2). These may be of use also when considering yawning in other primates (including humans) and a wider range of vertebrates. The hypotheses are not mutually exclusive, and the second contains a 'sub-hypothesis' pertaining to the degree to which the mechanism proposed may or may not have evolved specifically for the function with which it is connected.

The unifying element of the two theories is the narrow channel known variously as the 'eustachian tube', the 'auditory tube', or the 'pharyngotympanic tube' which originates at the middle ear and opens into the naso-pharynx. The primary function of this structure is to maintain equilibrium between ambient atmospheric air pressure and that in the middle ear. Equal air pressure is a necessary requirement for the tympanic membrane (ear drum) to vibrate correctly. As air is absorbed by the tissues of the middle ear, a fresh supply is required regularly if a vacuum is not to be formed. The *tensor palati* muscle is attached to the membrane of the eustachian tube, and its activation during swallowing or yawning opens the tube to allow a bubble of air at ambient pressure to enter from the larynx, refreshing the supply and equalizing the pressure in the middle ear (e.g., Laskiewicz, 1958; Akesson, Loeb & Wilson-Pauwels, 1990; Brooker, 1992). Humans undergoing large changes in air pressure report the sensation of pressure or 'mugginess' in the head. This is particularly associated with scuba diving and travel to high altitudes such as air travel or when driving into a mountainous region. At such times, the discomfort and even pain resulting from the difference between ambient and middle-ear pressure can be remedied by swallowing or yawning, thus allowing the pressure to equalize on either side of the eardrum. Some people are especially sensitive to pressure differences in the ear and report discomfort resulting from changes in air pressure caused only by changes in the weather (e.g., www. ivillagehealth.com/experts/ent/qua/0,11816, 242110_173997,00.html).

The simplest explanation for the majority of the yawning observed at Mbeli is that low pressure fronts responsible for bringing rain and low temperatures (typically in the form of sudden storms) create a pressure imbalance in the middle ear of some gorillas, depending on their sensitivity to pressure change or the presence or absence of any condition compromising the function of their eustachian tubes. Gorillas experiencing this then yawn to equalize the pressure and reduce any discomfort. Although not the causal agents in this phenomenon, rain and temperature drop may exacerbate the condition somewhat through their effect on a gorilla's activity pattern. The observed response of sitting still in a huddled position during heavy rain means that gorillas stop eating at these times, and any chance of aerating the eustachian tubes through swallowing is lost. While this mechanism for yawning is attractive because of it's simplicity and the added weight of research into eustachian tube dysfunction in humans, other factors may be at work or even take precedence over it.

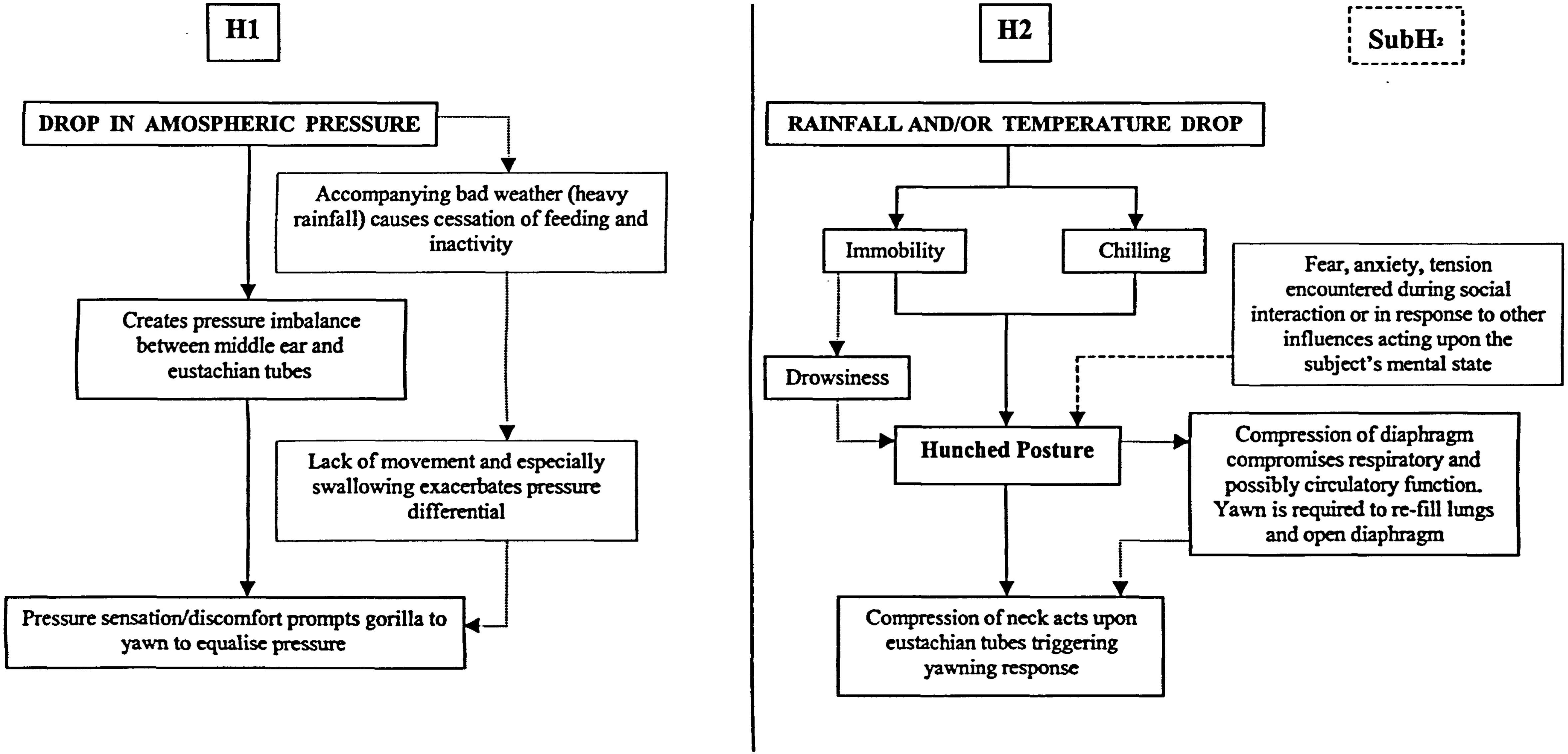
The second hypothesis is unconnected to pressure change, but involves postural variables triggered by the onset of low temperature or rain. As mentioned, in gorillas at Mbeli and in the Virungas, heavy rain prompts a cessation in feeding and the adoption of a motionless seated position (pers.obs.; Schaller, 1963, p259). While the inactivity of gorillas at such times could, in and of itself, produce drowsiness that in turn triggers a yawning response, it is hypothesized that the postural element of the response to rain may have more direct effects. A common response of many species to chilling of the body is to hunch the torso, draw the head down, and in humans and other primates, to draw the extremities closer to the heart, reducing heat-loss to the core by wrapping the arms across the chest and reducing the surface area of the body. During the shivering response also, the head and torso may take on a hunched posture. I suggest that the very act of drawing the head downwards and hunching the shoulders up may exact muscular changes in and around the neck and jaw, and possibly even have a modest compression effect on the air within the eustachian tubes. For a structure so sensitive to pressure, it may be that even slight auto-compression can create sufficient pressure to trigger the yawn response as a remedy. An attraction of this idea is that is lends itself equally well to the phenomenon of yawning in response to situations of tension, anxiety or fear ('tension yawns'), which, as for cold, may produce a hunched posture with its attendant muscular effects and possible compression of the eustachian tubes.

The sub-hypothesis takes the supposition that cold or tension/anxiety cause the body to effect certain postural changes. Common to both cases may be a hunching of the shoulders and sinking of the head, and also a compression of the diaphragm, caused primarily by the tense, hunched posture of the torso, possibly reinforced by the wrapping of the arms across, or tightly by the side of, the chest. While these actions may benefit the subject by retaining core body temperature, or protecting the vital organs from attack (note that a shivering response may accompany both cold and anxiety), they may have a compromising effect on the respiratory or even circulatory systems. Provine's (1987a) experiments at altering the oxygen and carbon dioxide content of air breathed by humans in an attempt to regulate yawning frequency, may have been somewhat naïve in implying that a respiratory function to yawning could be adequately explored through chemical manipulation alone. Few vertebrate species are ever likely to meet circumstances in which the chemical composition of the air they breathe is altered. By contrast, many species may face situations in which the mechanical process of breathing may be restricted in some way.

This idea, as before, suggests that the eustachian tubes may act as triggers for the yawning response. In the last example, however, the compression or activation of the tubes was seen as an 'accidental' response to posture. In this hypothesis, I suggest that, in addition to equalizing air pressure in the ears, the eustachian tubes may have an evolved function in triggering yawning in response to a posture that could threaten or compromise respiratory/circulatory function. Yawning in such situations, which may be proximally caused by tension, cold, drowsiness and fatigue, appears to open the diaphragm, fills the lungs again, stretches the muscles and reverses brain hypoxia (e.g., Askenasy, 1985). Figure A3.2 summarises the two main hypotheses and the third sub-hypothesis in chart form.

While these remain very tentative suggestions towards an ultimate causal mechanism and selected function for yawning in gorillas, humans and other primates, they may provoke further useful research. Further physiological examination of the sequence of events during yawns would be of interest, as would a more controlled investigation into the effects of posture on respiratory function and frequency of yawning. Unfortunately, posture was not systematically recorded either at the time of, or prior to, most yawn bouts at Mbeli. It is suggested that future studies of yawning include data on temperature, barometric pressure, and posture and activity as standard variables.

Figure A3.2 Hypotheses raised by yawning data from Mbeli (dashed lines indicate an alternative or subsidiary effect)



A3.5

Many gorilla reactions to sitatunga reflected a greater sense of alarm towards males than females, and in some cases reactions were extreme. Duke's group were feeding peacefully when they spotted an adult male slowly making his way towards them in a stream. All members became highly agitated and most stood bipedally to watch the antelope, with the blackback barking several times. As the sitatunga passed the gorillas and began to move away from them, the group relaxed and resumed feeding. However two hours later, another adult male sitatunga traced the same route towards the gorillas. The silverback did not see him until he reached 14m, and then stood bipedal to scan. The blackback once again panicked and in the resulting pandemonium, silverback Duke threat-barked at the antelope. All members of the group then ran in a panic to the forest. The sitatunga continued upstream calmly, never once having shown any aggressive intent. Duke's group were agitated by the proximity of an adult male on another occasion. This time, however, following an initial bunching of members and standing to scan, they relaxed back into feeding. Solitary male Frank was also forced to exit the bai when an adult male sitatunga (the same individual that had most frightened Duke's group) approached him. Frank stood and chest-beated towards Muir, but then lost his nerve and scrambled away from him. At this, Muir ran towards Frank while barking. Frank rapidly exited the bai and Muir returned to his slow progress through the bai. It is possible that groups may show different responses to such stimuli depending on the past experiences of the elder members of the group.

Members of OB1 group became alarmed at sounds of movement in the forest edge, not having seen an adult male sitatunga moving at the edge shortly before-hand. The group then rapidly bunched together, infants going dorsal on their mothers, and entered the forest almost on top of the sitatunga. Shortly afterwards, loud threat-barking was heard from the SB and the sitatunga emerged into the bai. A barking response was also noted from silverback Mosombo, towards adult male Kurt when approximately 30m away.

A.3.6

Gorilla/sitatunga relations seemed particularly calm in respect of Jemimah, the most frequently seen adult female sitatunga, who fed 4m from members of TSB group without any tension arising (*see* Plate 3.3, pg. 62), and on two occasions also fed within the same distance of solitary silverback Bear, who glanced up but then resumed feeding. Silverback Basil fed peacefully within 7m of Jemimah, and juveniles Wendy and Peter were observed to stare at her, though without alarm, as she fed 6m from them. Infants and juveniles showed interesting reactions to sitatunga. Iook, during a bout of playful behaviour in proximity to adult female Miranda, stood bipedally looking at her from 17m and clapped her hands. Juvenile Wendy from CLI group clapped hands many times as a female sitatunga fed 10m away, though regained her mother's back when the sitatunga approached slightly. Interestingly, adult female Primrose from DWA group was also observed to stand bipedal and clap hands towards a female 20m from her. Displacement activity was also noted in young gorillas. One infant watched a female sitatunga from his mother's back and frequently stood and stretched his arms over his head in a pensive but no less interested manner indicative of an internal conflict between fear and curiosity.

A final set of observations concern agonistic reaction. On a few occasions, silverbacks displayed briefly at female sitatunga that neared their group, but of more interest was the behaviour or blackbacks. Homer in particular was observed to take on a 'tight-lip' face and charge at Miranda. This was despite no other members of his group appearing tense. He stopped 15m from her and she stared at him briefly before resuming feeding. He was also seen to chase Miranda for 25m on another occasion. Miranda was the target of more chasing from sub-adult male Coriander. In these and similar instances, the young males appeared to be acting not in fear of alarm, but in high spirits and bravado. Female sitatunga may have provided a satisfying and possibly even entertaining practice ground for display behaviour in individuals undergoing dramatic physiological and endocrinological changes.

A3.7

On independent occasions, males have barked at river eagles (*Haliaetus vocifer*), once when one landed in the bai noisily 20m away, and once when the eagle flew only a few metres above a silverback's head. An eagle flying low over adult female Jodie caused her to scream and wave her arms in the air and on two occasions the over-flight of an eagle caused infants to seek dorsal or ventral contact with their mothers. While large predators, river eagles were never observed taking mammal prey at Mbeli and even colobus monkeys did not appear to view them as potential predators, therefore the reactions of gorillas seemed based on uncertainty or surprise rather than any need to be fearful. Similar reactions to low flying birds are reported from mountain gorillas (Schaller, 1963). A hammerkop (*Scopus umbretta*) flying low in the direction of blackback Homer caused him to crouch and then flee, and the same gorilla was greatly troubled by the persistent proximity of a feeding white-necked stork (*Ciconia episcopus*), frequently lunging at it and remaining vigilent. Silverback Mosombo barked and stared at the same bird when it landed near him. Juvenile Wendy ran towards a squacco heron (*Ardeola ralloides*) with uplifted arms, causing it to fly off. On another occasion she became alarmed at a nearby egret (*Egretta sp.*), climbed on her mother's back, then stood bipedal, slapped her left arm with her right hand, then clapped at the bird as she had previously done to sitatunga. Silverback Vince also became distracted by the proximity of an egret, and three times lunged at it, twice accompanied by barks. Egrets are known to pick insects directly off the bodies of sitatunga and other mammals (pers. obs.) and it may be that an egret attempting to do so with Vince in the past rendered him more sensitive towards them than might otherwise have been the case. Finally, juvenile Paris was twice seen to calmly observe birds; once when a heron walked 5m from her, and on another occasion when a group of hornbills flew high overhead.

Chapter 5.

A5.1

2 Jan 1998

10.34 The group is feeding in a fairly tight formation when Redstripe suddenly begins to chase Salaam north. Redstripe gives cough grunts as he does so and Salaam gives a couple of whining screams. They move at a fast walk, - about the only method possible in the deep mud of the zone. After 10-15 meters, Salaam turns round and crouches down facing Redstripe and begins a plaintive whining screaming with his mouth open, all teeth showing. Redstripe is standing quad 1m away facing him with a tight-lip face. After about 20 secs of the screams, Salaam begins cough grunting. Both Redstripe and he are all but facing straight at each other but they both avoid direct eye contact at this time. Redstripe then turns 90 degrees to Salaam and relaxes a bit. Salaam stops vocalising and reaches out with his right arm to gently touch Redstripe on his right-side ribcage with his knuckles. Redstripe does not respond to this gesture. Salaam then gets up and moves a little way from the group to feed. He increases the distance steadily until he is about 50m from the otherwise quite tightly formed group.

This observation suggests that Salaam was upset by the attack and that it did not in any way constitute play aggression. The touching action is one of very few examples of conciliatory behaviour witnessed in such situations.

A5.2

One interaction between a silverback and a blackback concerned bb/ysb Bird and silverback Duke, of DUK group, is of interest.

9 Jan 1999

> Duke + Bird feed 4m from each other. Duke gets up and approaches Bird at a calm walk. Bird begins to cough-grunt. Almost immediately after this, Duke also cough grunts. Just as Duke reaches him, Bird waves out one arm over the feeding patch in-front of him then retreats with more cough grunts. Duke then sits 1m from Bird's old spot and begins to feed.

Bird appears to recognise the context of Duke's approach, even in the absence of gesture, display or vocalisation, and makes a pre-emptive vocal attempt at defending his position. The curious gesture before the inevitable abandonment of the patch suggests a frustrated last claim to the spot

A5.3

The only example of 'affiliative interaction' between sb and bb was in the coalition defence of a sub-adult male (Salaam) from an aggressive attack by a solitary male (Dylan).

4 Aug 1997

12:47 Salaam is the furthest individual from the centre of his group and the nearest to Dylan. As Salaam walks within 8m of Dylan to catch up with the rest of his group, Dylan becomes tight-lipped and then begins to chase him. Salaam runs south-east, and screams once. Solomon is quick to notice this activity and heads rapidly towards Dylan and Salaam. As he does so, Redstripe joins him. As the joint approach of the two males reaches 10m of Dylan, he calls off his attack on Salaam and retreats.

A5.4

The only intervention witnessed in the context of blackbacks and adult females was by elder blackback Gretsky, in defence of Martha, an adult female with whom he had emigrated into NOO group. The initial agonism was initiated by younger blackback Parsley, a natal resident of NOO group.

23 Apr 1999

12:26 Parsley is walking behind Martha and cough-grunts. Martha suddenly swivels round to face Parsley. Cannot hear cough grunts but, from her facial expression, think they are given. She turns back around though and continues walking. Parsley stops momentarily at this but then continues to follow 5m behind her. She nears Gretsky and Parsley moves off slightly to the other side of Gretsky, 10m away.

12:27 Gretsky gets up from his feeding and, cough grunting, walks towards Parsley. Seeing him approach, Parsley turns his back, but Gretsky continues on and sits 1-2m to Parsley's right-side. Gretsky stares hard at Parsley for about 10 seconds, while Parsley looks ahead only, avoiding eye contact. Parsley looks very uncomfortable and seems to want to move away, but is disinclined to do so. When he finally begins to turn gently away from Gretsky (12:28), Gretsky cough-grunts aggressively, stands bi-pedally and brings both arms down on Parsleys back in a hitting/push-down fashion, clearly making contact, although by now Parsley is also cowering from the attack. We see water splash up as Parsley is forced close to the substrate, which is clearly waterlogged. Immediately after pushing Parsley to the ground, Gretsky moves off and back towards the other members of the group who are now feeding.

A.5.5

The following extract from the field notes relates the clearest example of silverback intervention in adult female agonism. In CLI group, Clive is the silverback and Jodie and Winona adult females.

11-Feb-99

13:59 Jodie and Winona are about 15m from each other with their infants when for no apparent reason, Jodie charges at Winona and they begin to fight. Both stand

> bipedally and slap their arms at each other; their mouths are wide open and they are screaming and attempting to bite each other. After 15 seconds, silverback Clive clambers from a Hydrocharis marsh and charges at the pair. At his approach, the females separate and Jodie begins to move away from Winona and him. He runs past Winona and goes straight for Jodie. She runs away from him and screams looking back at him as he closes on her but she is almost immediately overtaken. He pins her down with his open mouth on her head and shoulders. He then moves 90 degrees round her to get in a better position over her, then stoops low and appears to pin her to the ground once again with his teeth, mouth wide open. He does not appear to be aggressively biting her head but simply holding her down with his teeth. The rest of the group are highly agitated and we hear cough grunts. The three juveniles approach the pair, standing 4m from the attack and watching. Lyle (Jodie's offspring) puts one hand on the shoulder of Winona's juvenile, possibly for reassurance. Then, during the 15 seconds Jodie is held down, Lyle approaches, and standing bipedally in front of Clive, puts his hands on Clive's head, possibly in an effort to push him off his mother. Shortly after, Clive rises up and pulls away. Jodie sits in a hunched position looking very miserable indeed. Lyle sits next to her and occasionally stands with one hand holding her shoulder hair and leans in toward her ventrum in a rather touching conciliatory manner, possibly also seeking to suckle to comfort himself. Jodie holds up her left hand and licks the outside edge of her palm. After doing this, Lyle reaches up and gently touches the place, which does not seem to be punctured, with one finger. After this, Jodie licks the place again. She also has several wet patches on her head which look to have been made by Clive's teeth, though again, there seems to be no blood or laceration. After a few minutes she gets up and walks forward bipedally while holding her limp left hand in her right.

'Control interventions' are said to occur when no clear assistance is given by the intervening party to either actor in a dyadic dispute (Watts, 1992). In this interaction, Clive clearly supported the victim of the original attack, by deliberately punishing Jodie. As noted earlier, Jodie was an immigrant to the group in 1996, but it seems unlikely that Clive's targeting of her in this case was connected to her status in the group.

A5.6

The following field notes extract gives an example of silverback herding of an adult female despite there being no other groups in the bai.

18-Jan-97

> 9.14 Dukes group is feeding, relaxed, with a fairly wide group spacing. Adult female Butch is furthest from silverback Duke - 50-60m away. He suddenly gets up and strides towards Butch. As Duke nears her, Butch cowers in the grass. He rushes past her and lashes out with his left arm, though no real contact made. He sits on the far side of her with a tight-lipped expression. She sits up again and he does a short run up to her side. She begins to feed. He then does another short run past her to the east and lashes out at her in passing. She screams, then begins to slowly walk back towards the rest of the group). He follows 4m behind her. She stops once half-way back to the group and he does another short running display to her side. She continues on back to join the other females and sits close to Ella and Bessie. Duke stares hard at her, then returns to the marsh close to his original position and feeds.

Chapter 6

A6.1

The following extract from Field Notes, describes a particularly light-hearted bout of play-agonism involving Bayleaf and Parsley, blackbacks in NOO group, and Bird – a slightly older blackback in DUK group.

> 26-Aug-98
> 9:58 Bayleaf approaches Bird. Bird gets up from feeding. They both look towards each other, then continue feeding.
> 10:01 Bayleaf rolls on his back. Meanwhile Parsley approaches Bird and starts chasing him. Coriander also joins in on the chase. When Bird turns to face the others, Parsley approaches Bird to 1m. Bird turns and starts to run with Parsley following. When bird turns to face Parsley, Parsley hits Bird on the head twice and Bird play-bites Parsley. Both then break contact and sit.
> 10:03 Parsley stands, chest beats, then grabs at Bird, but is pushed away.
> 10:04 Parsley chest beats and rolls, as if enjoying the interaction.
> 10:05 Parsley approaches Bird, who gets up and begins to wrestle for a moment. Bird then breaks contact and starts to run towards the south. Bayleaf follows Bird but gives up shortly, waving arms briefly above his head then sitting. Parsley approaches to 1m and Bayleaf again moves towards Bird. Bird and Parsley start grabbing at each other. Bird pushes Parsley to the ground and slaps him on the head several times. Parsley then starts chasing Bird again towards the south. They then wrestle.
> 10:12 Bird breaks contact with Parsley and starts to run north with Bayleaf chasing him. Bird turns and faces Bayleaf and they slap at each other, their mouths open. Contact is broken and Bayleaf starts chasing bird again.
> 10:29 Parsley chases Bird with Bayleaf following behind. Bird turns and slaps Parsley on the head. Parsley and Bayleaf then wrestle with each other.
> 10:41 Bayleaf exits 7e.
> 10:43 Parsley and Bird exit in same zone.

Appendix 7

Gorilla Display Behaviour

Preface

The main body of this thesis describes the social structure of the Mbeli population, and discusses the dynamics of both intra- and inter-group interactions in the Mbeli gorilla population. This extended Appendix section concerns some of the actual behaviours exhibited by gorillas during those interactions, and at other times while in the bai. As a general reference resource, Table A7.1 gives a list of the main displays and other behavioural elements exhibited by gorillas at Mbeli. However, a detailed examination of all behaviours observed is clearly beyond the scope of this thesis, and as such, two main areas have been selected for closer consideration. Firstly, the ‘splash display’, an unusual display form hitherto unknown in wild gorillas, is described in terms of both form, function, and distribution. The other area examined is that of eye gaze and gaze aversion behaviour. This leads to an exploration of certain physical characteristics of body shape and pelage in silverbacks, that suggest an alternative functional hypothesis for gaze avoidance in particular. In this context, further observations regarding silverback physiology and the benefits and costs of secondary sexual traits and dimorphism are introduced. While data on splash displays present a relatively complete picture of this behaviour, the rest of the chapter is, in essence, descriptive and intended to point the way forward to a more detailed study of what may represent a rich and fascinating field.

Table A7.1, although not exhaustive, presents a list of the main social and non-social behaviours of the Mbeli gorillas, including displays, facial gestures, play behaviours, vocalisations and some behaviours connected with feeding and drinking. Including frequencies per age/sex-class, corrected for their representation in the population is too large a task for this thesis, though at a later date, with more data available, it should be possible to produce such an Ethogram for comparative use with other populations and for further exploring the variation and nature of these behaviours.

<u>Legend to Table A7.1</u>

🔴 Agonistic behaviour (aggression; responses to aggression; complaint).

🟡 Play agonism (containing agonistic elements but not pursued with menace).

🟢 Affiliative (behaviours clearly conducted during self- or social-play; greetings; non-agonistic mother/offspring behaviour; non-agonistic sexual behaviour).

○ Non-social behaviours (self-directed or in relation to other species/environment).

◍ Context unclear, highly variable or ambiguous.

Table A7.1 Summary table of social and non-social behaviours witnessed in Mbeli Bai

Behaviour	SB	AF	BB	SAM	SAF	JUV	INF	Notes
Chest-beat	🔴	🔴	🔴 🟡 🟢	🔴 🟡 🟢	🟢	🟡 🟢	🟢	Also non-social (excitement, ebullience, other species)
Chest-beat with charge	🔴	🔴 🟡	🔴 🟡	🔴 🟡 🟢	🔴 🟡	🟡 🟢		
Charge	🔴	🔴	🔴 🟡 🟢	🔴 🟡 🟢	🟡 🟢	🟡 🟢	🟢	
Ground slap	🔴		🔴 🟡 🟢	🔴		🟡 🟢	🟢	
Splash display	🔴		🔴 🟡	🟡 🟢		🟢	○	
Stiff limb stance or walk	🔴	🔴	🔴 🟡 🟢	🔴 🟢	🔴	🟡 🟢		
Lunge (no contact)	🔴	🔴 🟡	🔴 🟡 🟢	🔴 🟡 🟢	🟢	🔴 🟢	🟢	
Hit	🔴	🔴	🔴 🟡 🟢	🔴 🟡 🟢	🟡	🟢		
Bite	🔴	🔴	🔴 🟡 🟢			🟢		
Force/hold down	🔴	🔴	🔴 🟡 🟢			🟢	🟢	
Tight lip expression	🔴	🔴	🔴 🟡 🟢	🔴 🟢	🟡 🟢	🟡 🟢	🟢	
Stare	🔴	🔴	🔴 🟡 🟢	🔴 🟡 🟢	🔴 🟡 🟢	🔴 🟡 🟢	🟢	See Chapter 7.
Head-turn (crest?) display	🔴		🔴 🟡 🟢	🔴	🔴	🟡 🟢		See Chapter 7.
Cower		🔴	🔴		🔴	🔴	🔴	Defensive reaction to attack
Arm-up defence		🔴	🔴	🔴	🔴			Defensive reaction to attack
Scream		🔴	🔴	🔴	🔴	🔴	🔴	JUV/INF – most in alarm or tantrum at mother
Cough grunt	🔴	🔴	🔴 🟡 🟢	🔴		🔴		
Threat bark	○		○					At sitatunga, eagle, egret, and heard in the forest.
Question bark	◍		🔴					At sitatunga, otter and humans. BB once in supplantation
Hoot series	🔴 ◍	◍				◍		SB hoots towards AF of other group. Gp member location
Hoot series w/ chest-beat	🔴 ○							Display (esp. forest) and to locate gp members. Elephants
Whimper/whine				🔴		🔴	🔴	INF/JUV suckling difficulties/weaning
Belch	🟢	🟢	🟢					Contact, location. Many probably unheard

Behaviour	SB	AF	BB	SAM	SAF	JUV	INF	Notes
Play wrestle/box			🟢	🟢	🟢	🟢	🟢	
Chase	🔴	🔴	🔴 🟡 🟢	🔴 🟡 🟢	🟢	🟢	🟢	
Play mount				🟢		🟢	🟢	
Body-head patting (other)			🟢	🟢		🟢	🟢	Rare
Back scratching (other)				🟢		🟢		Rare
Clap		🔴		🟢	🟢	🟡 🟢	🟢	AF-AF agonism once only. Sitatunga. Self & Social play
Pirouette			🟢	🟢	🟢	🟢	🟢	
Play face expression			🟢			🟢	🟢	
Fear/alarm face		🔴	🔴		🔴			Usually seen during severe/physical attack
Pout/sulk face						🔴	🔴	Usually due to weaning/discipline/ignored by mother
Genital inspect/touch (other)			🟢		🟢	🟢		Same sex and opposite sex combinations
Embrace			🟢	🟢		🟢		Not including mother/infant. Mostly between JUVs
'Kiss' (face-to-face touching)		🟢	🟢	🟢	🟢	🟢		
Touch others face with hand			🟢			🟢	🟢	
Groom infant		🟢						Rare. Usually just head/face
Groom adult						🟢	🟢	Rare. JUV-JUV seen once only
Self-groom	○	○				○		Mostly of injuries or skin conditions
Fly-swat use	○		○			○		Only four individuals
Object play						○		Carrying and tossing ball of roots
Rolling on back	○		○	○	○	○	○	
Yawn	●	●	●			●	●	See Chapter 3 for details
Swat insects with hand	○	○	○	○	○	○	○	Usually from head, neck, and shoulder region
Wash food	○	○	○	○	○	○	○	
Coprophagy	○					○		
Drink (direct from source)	○	○	○					
Drink (from hand)	○		○	○	○	○		
Bipedal scan	●	●	●	●	●	●	●	Social situations and at other species

Part I

Splash display: A behavioural adaptation to an aquatic environment

Introduction

This section explores in detail the observation, at Mbeli Bai, of a new addition to the communicative ethogram for wild gorillas. Preliminary observations (Olejniczak, 1996; pers. obs.) suggested that gorillas visiting the bai were deliberately making use of water as a communicative 'tool'. The phenomenon was of particular interest as it appeared to offer an example of a nonhuman ape/water 'interaction' that exceeded the more usual conditions of such interactions that can best be summarised as 'water tolerance due to locomotive and/or dietary necessity'. There appeared to be no comparable records of splash display in the literature for wild apes, prompting a more thorough examination of the form and function of this behaviour at Mbeli.

Prior to the collection of data, a definition of the behaviour was adopted in order to set criteria for the inclusion of an observation in the data-set. The working definition used was as follows:- *A 'splash display' entails the deliberate bodily agitation of running or still water in order to create a visual impact.* This definition was purposefully left free from stringent conditions prior to data collection so as to avoid limiting observations before a more precise understanding of form and function were achieved. The term 'splash display' in the methodology and results is given to denote a 'display of splashing' rather than suggesting behavioural function. Ascertaining the degree to which these displays fulfil an intentional function was, however, the primary aim of the study.

In order to explore the possibility of an independent function for splash behaviour, it was necessary to examine the nature of another gorilla display type; the 'ground slap'. This display has been noted in many captive groups and from several field research sites (e.g., captive groups: Gould (in Ogden & Schildkraut 1991); Hoff, Nadler & Maple 1981; wild groups, Schaller 1963; at Lopé and Nouabalé-Ndoki, pers. obs.). Given the resemblance between the ground slap and some forms of splash display, data on this display are presented for comparison, addressing to what degree some splash displays may be more accurately described as ground slap displays executed in an aquatic environment.

Methods

All data were collected from the observation tower situated on the edge of the bai. All occurrences recording (Martin & Bateson 1993) was used throughout, as the frequency with which gorillas exhibited the display would have ensured that scan or focal sampling methods would have missed most, if not all, occurrences. For each observation of splash behaviour, the following data were collected:

1. Date and time.
2. Style used to create the splash.
3. Name, age, sex and social group of actor.
4. Name, age, sex and social group of target gorilla (or species, if not gorilla).
5. Context (agonistic/affiliative/play etc.). These contexts were judged subjectively based on the overall situation in which the behaviour took place (i.e. was the animal

alone or with conspecifics? Were other better known behaviours observed during the same bout that allowed the context to be 'labelled'?).

6. Distance between actor and target (metres estimated by eye, usually to the nearest 5m).
7. Reaction to the behaviour by target animals.

Occasionally data for one or more of these categories were missed during observation and this is reflected in the variable number of total observations given in the results. It was found impractical to time the duration of the behaviour as incidents were hard to predict and exhibitions of splashing were generally fleeting. In the results, the term 'splash display' refers to a single action of splashing. The term 'splash bout' is given to denote an independent incident of splash behaviour, possibly containing more than one 'splash display', but pertaining to a single target or context. Multiple bouts directed at the same target on the same day were considered independent if they were separated by 1 hour or more of non-social behaviour. A 'gorilla-unit visit' is a discrete entry to the bai from a gorilla group or a solitary individual

In some of the analysis shown in the following pages, true independence of data points was obtained (i.e. results came from mean scores for individual gorillas). Unfortunately, the data, despite representing all occurrences of splash display over the 31 month study period, were frequently insufficient to allow for statistical analysis. Where this is so, tables and charts have been used to show overall frequencies for the various categories described, with the number of individuals responsible given alongside.

For Figure A7.4 it was necessary to correct the observed frequencies of splash bouts given by group individuals and solitary males to take account of the frequency with which individuals from these two categories were seen in the bai. This necessitated obtaining a combined measure of the population structure and visitation rate. Each gorilla-unit visit during the study period was examined, and for each visit the total number of group-living and solitary males of eight years and above was counted. The total number of times individuals from both unit types (groups and solitaries) were seen was then used to create proportions of the total gorilla visitation rate. Finally, the observed frequencies of splash bouts in the two categories were divided by the proportions obtained.

Results

Frequency

A total of 90 splash displays were observed during the study period. These resulted from 57 independent bouts. Splashing was exhibited at a frequency of 0.08 displays, and 0.05 display bouts per gorilla-unit visit.

Styles

The following styles were employed by gorillas in generating splash displays:

<u>One-handed splash:</u> The weight of the body is supported either wholly on the feet, or on the feet and one arm. One arm is raised and brought downwards forcibly such that the open palm of the hand strikes the surface of the water at an acute angle. The action sends a large plume of spray up and forwards. These plumes may reach a height greater than the

animal itself. The display can be executed stationary, or while charging. Two-handed splash: This display is similar to the one-handed splash, but always involves the gorilla adopting a bipedal stance before bringing both hands down to strike the water at the same instant. This display also creates large plumes of spray, but may be less directional. It is also likely that the display has a greater auditory impact than the one-hand slap. It can be executed stationary, or while charging. Two-hand mixing: This display, seen most clearly during slow motion video playback, involves the gorilla bringing its two hands simultaneously towards each other through the water in front of the body until the palms almost touch or pass each other, crossing the arms. The arms are then separated again and the action is repeated several times, creating an impression of 'mixing'. The display can be executed stationary, or while charging, but creates less spray than either the one- or two-hand splash displays. One-handed pull-back: One hand is forcefully brought down, palm first, into the water and back towards the gorilla's body. Appears to be of limited impact. Two-handed pull-back: As above, but with both hands swept back through the water simultaneously. Body splash: A highly dynamic display which involves the gorilla either running or leaping into deep standing water (up to approx. 1.5m in depth). When leaping from a stationary position, the arms are sometimes swung behind the body first, in order to gain momentum for the jump. A large plume of spray or 'bow-wave' usually results from the display. Leg drag: The gorilla leaps across a small channel, from one vegetation mat to another. In so doing, the legs sweep through the water sending a plum of water forwards and to one side of the gorilla's body. Using this style, the gorilla is able to execute a display without having to be bodily in the water at the time. Run: In this display the gorilla runs through shallow water, creating a bow-wave and many small plumes of spray. Differs from the body splash in the duration of the display and the depth of the water. Back-hand slap: A variation on the one-hand splash using the back of the hand rather than the palm. Slosh: The back of one hand is used to make gentle splashes, away from the body.

Plate A7.1 shows a solitary silverback performing a body splash display in Mbeli Bai. In this example, the target of the display was a younger solitary silverback, who was feeding about 40m away. Note the 'tight-lipped' expression of the silverback (*see* next section). The stream at this point is approximately 1m deep.

The body splash, one-handed splash and two-handed splash were the most common styles of display used. Four styles were only exhibited by one individual each. For the category 'run', qualification as a deliberate splash display is in doubt, but the remaining three styles, while highly likely to have been adapted originally from the primary one- and two-handed splash styles, show sufficient variation in limb orientation to be viewed as distinct styles. Table A7.2 shows the frequency with which these styles were employed and the number of individual gorillas contributing to each count.

Plate A7.1 A solitary silverback performing a body splash display in Mbeli Bai

Table A7.2 Frequency of exhibition for 10 styles of splash display

Splash Style	Frequency	Percentage	Number of contributing animals
body splash	23	35	8
two-handed splash	14	22	10
one-handed splash	12	18.5	7
two-hand mixing	6	9	2
leg drag	3	5	2
slosh	2	3	2
run	2	3	1
one-handed pull-back	1	1.5	1
two-handed pull-back	1	1.5	1
back-hand slap	1	1.5	1
TOTAL	*65	-	35

*The total frequency count is lower than the 90 displays previously mentioned as the style of some displays was not recorded

Displays using only the hands accounted for 57% (N = 65) of the sample. Of the 79 displays for which data were recorded, 61% were exhibited during a charge, while 39% were from a stationary position (body splashes were counted as stationary if the actor was observed to leap into or through a body of water from a stationary position without advancing further than the initial leap). For the body splash category, displays were significantly more likely to occur during a charge than from a stationary position (Chi-squared test with Yates' Correction for Continuity, $\chi^2 = 14.09$, df = 1, $P < 0.001$), whereas for two-handed splashes the difference narrowly missed significance ($\chi^2 = 3.50$, df = 1, $P = 0.06$): for one-handed splashes there was no significant difference in the number of displays with a charge and those without ($\chi^2 = 2.08$, df = 1, $P > 0.05$).

Table A7.3 shows the distribution of splash display styles for each observed individual. The two-handed splash was the only display type used by all displaying age/sex-classes. Of the three most frequent styles, body splash was the most restricted in terms of age-class. Although this style was used to produce 35% (23/65) of all splashes, 91% of body splashes were made by silverbacks. Furthermore, no body splash displays were made by animals from age-classes younger than 'blackback' (8-12yrs). The median distance between a splash displaying individual and his or her target was 24m (N=18, range 2-135, IQR = 24.5).

Table A7.3 The splash styles of individual gorillas.

name	age/sex	body	run	2hs	1hs	2hm	hld	1hpb	2hpb	slosh	bhs
bones	sb	1									1
caravaggio	sb			1	4						
clive	sb	5		1							
george	sb	3			2						
obi-wan	sb				1						
bear	ssb	4	2	1	1	5	1				
sulatalu	ssb	1									
dylan	yssb	3									
frank	yssb	4		1	2				1		
bayleaf	bb			1							
gretsky	bb							1			
homer	bb						2				
parsley	bb	2		3		1					
red stripe	bb				1					1	
sahadouche	sam			3							
salaam	sam				1						
courtney	sad			1						1	
coriander	juv			1							
lyle	inf			1							

1hs: one hand splash. 2hs – two hand splash: 2hm: two-hand mix. hld – hind leg drag: 1hpb – one hand pull back: 2hpb; two-hand pull-back. bhs: backhand slap.

Actors

Splash displays were exhibited by 20 individuals during the study period. Of the 57 splash bouts, 47% were given by four individuals. These were Bear (solitary silverback), Frank (young solitary silverback), Caravaggio (group silverback), and Parsley (blackback). When the total number of splash displays is calculated for each individual, Bear, Frank, and Caravaggio between them make up 50% of the 90 displays witnessed. The solitary silverback Bear was responsible for the most splash bouts and also the most displays overall (28% of 90 non-independent displays).

Table A7.4 indicates a potential positive correlation between the age (developmental stage) of male actors and the frequency of splash exhibition. These figures are of limited value, however, without first considering the distribution of age/sex-classes in the population (i.e. is it possible to predict the frequency of display based on the relative numbers of animals from each age/sex-class visiting the bai?).

Table A7.4 The frequency of splash display bouts by age/sex-class categories

Age/sex-class		Frequency	Percentage	Number of contributing animals
silverback	SB	20	35.1	7
solitary silverback	SSB	9	15.8	2
young solitary silverback	YSSB	10	17.5	2
young silverback	YSB	0	0	0
adult female	AF	0	0	0
blackback	BB	9	15.8	5
sub-adult male	S.AM	6	10.5	3
sub-adult (sex unknown)	S.AD	1	1.8	1
juvenile	JUV	1	1.8	1
infant	INF	1	1.8	1
TOTAL		57		22

Abbreviations after age/sex-class names serve as a Legend to Figure 7.1 and subsequent charts

Proportions based on the visitation rate of each age/sex-class to the bai (the visiting population) were calculated (*see* Methods). The total number of splash bouts (in this case, 56) was then multiplied by each proportion in turn to generate expected frequencies of display for each age-class. The method by which proportions were calculated and the frequencies obtained are shown in Table A7.5.

Table A7.5 The proportion of the visiting population in each age/sex-class with expected and observed frequencies of splash bouts

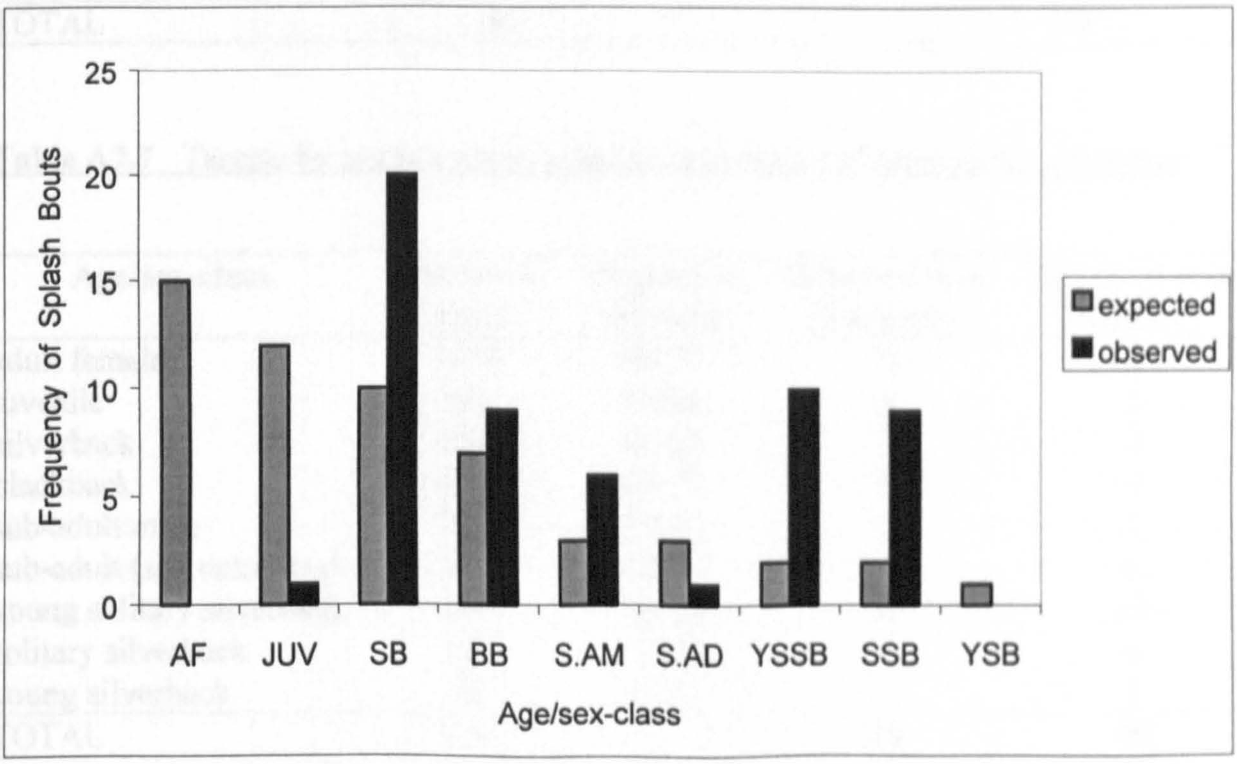
Age/sex-class	Number of visits	Proportion of visits	Expected bout frequency *	Observed bout frequency
adult female	1050	0.277	15	0
juvenile	781	0.206	12	1
silverback	675	0.178	10	20
blackback	481	0.127	7	9
sub-adult male	235	0.062	3	6
sub-adult (sex unknown)	211	0.056	3	1
young solitary silverback	145	0.038	2	10
solitary silverback	133	0.035	2	9
young silverback	86	0.023	1	0
TOTAL	3797		56	56

* 56 (the number of splash bouts) multiplied by the proportion of visits

Disparity between expected and observed frequencies can be seen more clearly, however, in Figure A7.1. Many of the animals within the age-sex-class 'infant' were frequently carried by their mothers, and could not be expected to have an equal opportunity for display exhibition. For this reason, they are excluded from the analysis.

While the data in this case do not allow for a statistical analysis of the differences between expected and observed display frequencies, it appears that for some age/sex-classes, there may be considerable discrepancies. Group silverbacks displayed twice as often as their presence in the visiting population would have predicted, while both solitary male classes displayed four times as often. Meanwhile adult females, though the most numerous age/sex-class in the population, were never observed to exhibit splash displays.

Figure A7.1 Expected and observed numbers of splash bouts per age/sex-class



Targets

In total, there were 20 gorilla-individual targets. Table A7.6 gives the frequency with which age/sex-classes were targeted with splash bouts. Non-gorilla targets are described later. Once again, it is necessary, prior to drawing inferences from these results, to examine the degree to which the observed frequency of targets, by age/sex-class, differed from expected frequencies. The expected bout frequencies are given in Table A7.7, and a visual comparison shown in Figure A7.2.

Table A7.6 Targets of splash bouts: frequency of bouts received by each age/sex-class

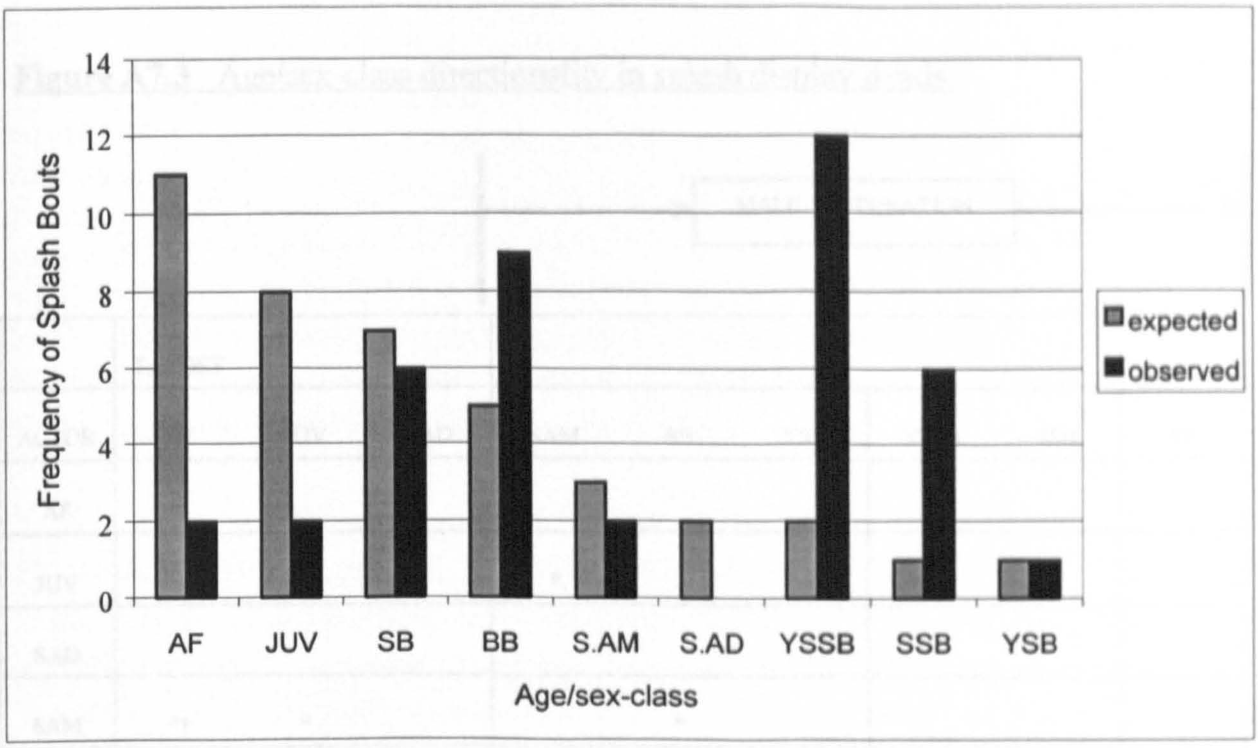
Age/sex-class	Frequency	Percentage	Number of contributing animals
silverback	6	15	5
solitary silverback	6	15	1
young solitary silverback	12	30	2
young silverback	1	2.5	1
adult female	2	5	2
blackback	9	22.5	5
sub-adult male	2	5	2
sub-adult (sex unknown)	0	0	0
juvenile	2	5	2
infant	0	0	0
TOTAL	40		20

Table A7.7 Targets by age/sex-class: expected and observed frequencies of display

Age/sex-class	Number of visits	Proportion of visits	Expected bout Frequency	Observed bout frequency
adult female	1050	0.277	11	2
juvenile	781	0.206	8	2
silverback	675	0.178	7	6
blackback	481	0.127	5	9
sub-adult male	235	0.062	3	2
sub-adult (sex unknown)	211	0.056	2	0
young solitary silverback	145	0.038	2	12
solitary silverback	133	0.035	1	6
young silverback	86	0.023	1	1
TOTAL	3797		40	40

The chart shows that both solitary male classes are six times more likely to receive splashes than their frequency of presence at the bai would predict. Adult females appear as splash targets (albeit, rarely) despite never having been seen to exhibit the display themselves. Group silverbacks, while the most prolific of the actors, were targeted at almost the same frequency as expected.

Figure A7.2 Expected and observed target frequency of splash bouts per age/sex-class



Directionality of displays

Figure A7.3 shows the direction of dyadic splash display interactions, and indicates that splash displays, already shown to be largely the preserve of mature or adolescent males, are also targeted primarily at these same age/sex-classes. Age/sex-classes in the left-hand column represent actors while column headings are targets. The box and arrows denote maturation in males from sub-adult to group silverback. While solitary silverbacks (SSB) may be as old or even older than group silverbacks (SB), they are more likely to be in the process of seeking females after having left their natal groups.

Of 41 recorded splash bouts for which data were available, 29% were made by individuals of an age-class younger than that of their target, 39% were by animals older than their target, 20% were made by animals of similar age and the same social status (i.e. group or solitary) as their target, and 12% came from animals whose ages could not be differentiated (SB/SSB) but whose social situation differed. Of the 11 splash bouts exhibited by non-silverback gorillas, only one was aimed at a silverback (in this case, a young solitary silverback).

As mentioned, these display bouts are not corrected for the bias generated by the possibility of some scores resulting from the same individuals. All of the display occasions for solitary animals (of any age) were performed by just four individuals. However, although one animal displayed only once (an unknown male who visited the bai for only a few weeks), of the remaining three regular visitors, one displayed one and a half times more often than predicted, while the other two displayed three and a half and four times as often as predicted (predicted values generated by dividing the total number of observed splash bouts by the total number of splash actors). If the class YSB is ignored (the age/sex-class was targeted once and never seen to give splash displays) then the chart more clearly indicates that the display, already shown to be largely the preserve of mature or adolescent males is also targeted primarily toward these same age/sex-classes.

Figure A7.3 Age/sex-class directionality in splash display dyads.

MALE MATURATION

	TARGET								
ACTOR	AF	JUV	SAD	SAM	BB	YSB	YSSB	SSB	SB
AF									
JUV				•					
SAD						•			
SAM	•†	•			•				
BB	•†				••••		•		
YSSB					•		••	••••	••
SSB				•			••••••		••
SB		•			•••		•••	•••	••

SOLITARY STAGE

• : Number of splash bouts. † : Same individual changed age/sex-class during study

The social context of displays

Of the 57 observed bouts of splashing, 73% were exhibited in inter-unit contexts, 5% were in intra-group contexts, and 21% were used in a non-gorilla-dyad context, or were possibly directed at unseen individuals (inside the forest edge). Of these latter cases, nine (from seven individuals) showed no apparent target, and one display each was directed at an otter (*Aonyx congica*), a bongo (*Tragelaphus euryceros*), and a human observer.

Splash bouts were observed from 20 known individuals. Of these, 16 individuals displayed in gorilla-dyad contexts. When the frequency of splash bouts exhibited in inter-unit and intra-group contexts was compared for each of these individuals, an inter-unit dyadic context was found to be a significantly more likely setting for display (Wilcoxon signed ranks test, $Z = -3.13$, $n = 16$, $P < 0.005$).

The functional context of splash displays

The subjective labelling of each splash bout produced four categories that describe the nature of a display or bout of displays. These were as follows:

1. Agonism: Threatening or aggressive behaviour. Also other behaviours indicative of a heightened level of tension or fear.
2. Exuberance: Sub-titled 'self-play', this entails a non-directed show of excitation and apparent 'high spirits'.
3. Social play: Play behaviour involving two or more gorillas.
4. Bravado: Represents a behavioural context in which adolescent males, still in their natal groups, display at adult females in the group. These displays appear to be given in a light-hearted, provocative spirit, consistent with 'showing off' in a non-threatening environment (neither the targets of these displays nor the group's silverback paid much attention to these displays). Somewhat similar to the 'play agonism' seen in other interactions at Mbeli.

In the analysis, a fifth category, 'other species', is included to cover all display bouts directed towards any non-gorilla, animal target. As noted previously, of three observations in this category, one was directed towards researchers on the observation tower and was closest to 'bravado' in nature; the second was directed towards a bongo and appeared 'agonistic', while the third example was directed at a Congo clawless otter by a blackback male. This was an unusual observation that defied all but a very liberal reading of 'self-play'. The seated gorilla was feeding at the edge of a stream down which an otter was swimming. As the otter drew parallel (3m away), the gorilla began to gently slosh small waves towards it with the back of one hand. While clearly a display, this appeared to be a curious attempt to induce a reaction from the otter, rather than intimidation.

Table A7.8 shows the behavioural context of 57 splash bouts. There were several observations where no target or context was identified and the display could not be confidently ascribed to a category. These are labelled 'unknown'.

Table A7.8 The behavioural context of splash bouts

Context	Frequency of bouts	Percentage	Number of contributing animals
agonism	38	67	13
unknown	6	10.5	5
exuberance (self-play)	6	10.5	5
social play	2	3.5	2
bravado	2	3.5	2
other species	3	5	3
TOTAL	57		29

The table clearly shows that the great majority (two-thirds) of display bouts took place in an agonistic context, both in terms of the number of bouts and in the number of contributing individuals. Table A7.9 shows the distribution of age/sex-classes within the behavioural contexts of splash display, and illustrates that all agonistic displays were performed by males from the age-classes 'blackback' and older. It can be seen that the non-agonistic occasions were, in all but one case, performed by animals of age-class 'blackback' or younger.

Table A7.9 Distribution of age/sex-classes within behavioural contexts of splash display

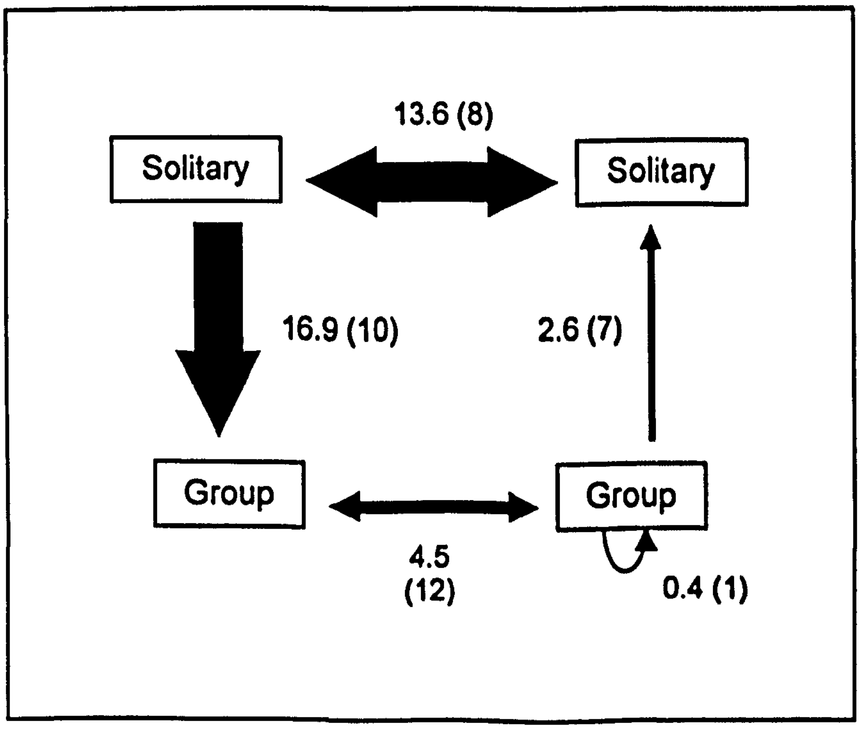
A/S	Agonism	Exuberance	Social play	Bravado	Other species	Unknown
SB	15 (5)	1 (1)				4 (3)
SSB	18 (4)					1 (1)
BB	5 (4)	1 (1)		2 (2)	2 (2)	
S.AM		3 (2)	1 (1)		1 (1)	1 (1)
JUV			1 (1)			
INF		1 (1)				
TOTAL	38 (13)	6 (5)	2 (2)	2 (2)	3 (3)	6 (5)
% of bouts	67	10.5	3.5	3.5	5.0	10.5

Figures before brackets are the frequencies of splash bouts for that context/age/sex-class.
Figures in brackets are the number of individual animals contributing to the total frequency. SSB here includes the YSSB class.

Rates of display by groups and solitary individuals

Figure A7.4 shows the frequency and direction of solitary and group male (≥8yrs) splash display bouts, following a conversion whereby the proportion of group and solitary individuals visiting the bai is taken into account (*see* Method). The width of the arrows is drawn to scale and the 'U'- shaped arrow denotes intra-group bouts.

Figure A7.4 Frequency and direction of male (>8yrs) splash display bouts (corrected for proportional visitation rate of group males and solitaries)



Values in brackets are the actual number of bouts prior to conversion.

Figure A7.4 illustrates the importance of splash displays for solitary males relative to group males. Proportional to their numbers, group males used splash displays infrequently, whether in an intra-group or inter-unit context. Solitary males splashed almost as often between themselves as they did towards group individuals. This bias towards use of the display between solitary males is accentuated when the availability of either group or solitary male targets is considered.

Availability of targets

While the overall proportional adjustment used to generate values for Figure A7.4 corrects the frequency of display bouts for both unit types (solitary and group individuals), it does not permit a proportional examination of the likely targets of display. However when the four solitary males from the population are looked at individually, a trend can be detected. If all occasions of multi-gorilla- unit visits to the bai are investigated (i.e. all visits by a given solitary male when other gorilla units were present), it is possible to calculate the proportion of these visits when group or solitary units were present, or 'available' as targets for splash display. On many occasions, solitary males shared the bai with both groups and other solitary males at the same time, but as Table A7.10 shows, groups were the most likely to be present.

Table A7.10 Status of 'other social unit' when solitary males shared the bai with other units

Name of solitary individual	Visits with other solitary individuals in bai	Visits with groups in the bai	Proportion of solitaries to groups
Bear	46	56	0.82
Dylan	37	57	0.65
Frank	47	75	0.63
Sulatalu	8	12	0.66
TOTAL	138	200	2.76
			Mean = 0.69 ± 0.04 (SE)

The table shows that solitary males were present in the bai more often with group units than they were with other solitary males. These figures, however, treat group units as single entities when, clearly, they are made up of more than one individual. For the year 1998 (the middle year of the study period) the mean group size at Mbeli was 6.4 weaned individuals (n=12). If the scores for 'group units in the bai' from Table A7.10 are multiplied by the mean group size ($x = 358, 365, 480, 77$; $\Sigma x = 1280$), it is plain to see that from the point of view of the availability of target individuals, weaned group individuals are almost an order of magnitude more likely to be those seen by a solitary male during his visits to the bai than are other solitary males. Given the vastly inflated availability of group individuals as targets for display, the high rate of solitary to solitary displays becomes considerably more compelling.

The effect of displays

The reaction of gorillas targeted with splash displays was frequently ambiguous and little precision was possible during data recording. The reactions to 40 splash displays are given in Table A7.11. The following types of reaction were observed: *Attention*: refers to a target exhibiting behaviour indicative of having been made aware of the display (e.g. glancing or hesitation) but taking no further action; *No reaction*: refers to one of three possibilities: a) target was not aware of a display having been given, b) target was aware of a display but remained impervious to it, and c) target was aware of display and chose, tactically, to ignore it (unfortunately, it was not possible to distinguish between these three states, and as such, the category is of limited value); *Retreat*: refers to a target distancing itself from an actor; *Approach*: also denotes direction of movement but does not necessarily imply threatening or agonistic behaviour; *Fend-off*: describes a single incident when a target was physically wetted by a splash and raised an arm to protect itself, while showing an open mouthed expression in apparent annoyance or fear (this 'arm-up' defensive action is also used by gorillas to protect themselves from solid projectiles (Schaller, 1963).

Table A7.11 Reactions to Splash Display

Reaction	Frequency	Percentage	No. of individuals
attention	14	35	7
no reaction	14	35	6
retreat	8	20	7
approach	3	7.5	3
fend-off	1	2.5	1
TOTAL	40		24

The lack of precision possible when recording reactions made these data of little value besides inferring a few general points. Splash displays were never seen to lead directly to contact aggression, and in most cases could not even be traced as causal factors in an escalation of tension. In 70% of cases, displays produced no visible reaction or simply gained the overt attention of the target without further action being taken.

Ground slap displays

The 'ground slap' is a frequently observed element in the display repertoire of gorillas. The similarity of the one- and two-handed slash displays to ground slaps raises the question of whether splashes represent little more than an accidental bi-product of a terrestrial display performed on an semi-aquatic substrate. Data on ground slap displays were recorded throughout the study period following a similar protocol to that for splash displays. For comparative purposes, some data are shown alongside summarised results for splash displays. Unless stated to the contrary however, only the standard one- and two-handed splash displays are used for such comparisons: when testing for contextual or other variations between the use of ground and splash displays, other splash styles were thought too dissimilar in form for comparisons to be made.

Sixty-nine ground slap displays contributed to 45 temporally independent bouts. Only two styles of ground slap were observed. These are the '*one-handed slap*', in which one arm is raised to, or above head-height and then brought down forcibly, with the open palm (or fist) striking the substrate powerfully; and the '*two-handed slap*', which is identical to the one-handed slap except that both hands are brought downwards to strike the substrate simultaneously. In 50 cases where the style of ground slap was recorded, one-handed slaps accounted for 24% of the sample and two-handed slaps, 76%. One-handed splash displays, by comparison, were seen roughly the same number of times as two-handed splash displays.

Of one- and two-handed splash displays, 59% (13/22) were exhibited in an inter-unit context and only 9% (2/22) in an intra-group context. For ground slaps, inter-group contexts remained at a high frequency of 50% (15/30) of the sample, however an intra-group context was considerably more frequent than for splash display, representing 30% (9/30) of the sample.

Agonism was the most frequent context type for both splash and ground slap displays. However, as Table A7.12 indicates, ground slaps were used considerably more often during social play than one- or two-handed splash displays.

Table A7.12 Comparison of one- and two-handed splash displays with ground slaps, giving the percentage of all bouts in each social context

Context	% of 1- and 2-handed splash bouts	No. of contributing individuals	% of ground slap bouts	No. of contributing individuals
agonism	45.5	7	33.5	7
unknown	14	3	20	5
exuberance (self-play)	22.5	3	17	5
social play	9	2	22.5	5
bravado	4.5	1	7	1
other species	4.5	1	0	0
TOTAL	N = 22	17	N = 30	23

In addition to possible basic functional aspects of the two displays, this difference may be attributable to the age-class of the actors concerned, and in particular a disinclination among younger individuals (those primarily responsible for play-type displays) to approach deeper streams too closely. The number of individuals behind these data (*see* Table A7.13) are extremely low, and little can be said without a larger sample size. Nevertheless it is interesting to note that no gorillas younger than blackbacks (<8yrs) were ever observed using the 'body splash' display, in which the whole body is launched into a pool or stream.

Table A7.13 Percentage of ground slap and splash display bouts by age/sex-class

Age/sex-class	% of one/two handed splash bouts	No. of contributing individuals	% of ground slap bouts	No. of contributing individuals
silverback	36	4	33	5
solitary silverback	14	2	7	1
young silverback	0	0	0	0
blackback	14	3	27	3
adult female	0	0	0	0
sub-adult male	27	3	10	3
sub adult (sex unknown)	0	0	10	2
juvenile	5	1	10	2
infant	5	1	3	1
TOTAL	N=22	14	N=30	17

Finally, in order to explore the possibility of a difference in the functional intra-dyad distance between ground slap and splash displays, a comparison was made which included all splash styles, but only examined cases in an inter-unit, agonistic context. This was the most frequent context and was also less likely to show statistical interference resulting from the behaviour of immature animals. Although much larger sample sizes would have been preferable, the results show that for ground slaps (N=7) the median intra-dyad distance was 6 metres (range 2 to 20), while for splash displays (N=32) the intra-dyad median distance was 26.5 metres (range 2 to 150). These differences were significant (Mann-Whitney U-test; $U = 51.0$, $p<0.05$), suggesting that splash displays may be selected primarily for longer distance display use, where the value of a strong visual element is more likely to be required.

Discussion

Is water used intentionally as a display device?

Splashes that met the definition set out in the introduction, were seen 90 times during the 1681 hours that gorillas were in sight. All splashes were the result of deliberate locomotive patterns associated with agonistic display, play, or travel. That this is so, however, does not necessarily imply that the splashes themselves were made deliberately in the pursuit of a desired goal, communicative or otherwise. To explore whether the observed splashes were made deliberately and constituted a fundamental element of the behaviours in which they were seen requires an examination of the style and context of those behaviours.

Styles

The extreme rarity of splashes suggests that they are not a by-product of everyday motor patterns. Small splashes are frequently generated during food washing, but none of these examples were included in the data as they were clearly incidental to the principal aim of the behaviour – rinsing mud from edible aquatic herbs. Normal travel within the bai does not generate splashes of the magnitude of those recorded in the data. Gorillas typically move carefully on the floating mats of vegetation and wade across deep streams with extreme caution. The principal terrestrial gait of the gorilla is a quadrupedal walk: running is usually seen only during play, flight or display. In the bai, running is even less common due to the hazards presented by the unstable substrate. Thus one of the most ubiquitous elements of the gorillas' dry-land display repertoire, the fast charge, is severely compromised in a semi-aquatic environment.

Of the 10 behavioural styles seen to produce splashes, six (one- and two-handed pull-back, two-hand mixing, leg drag, back-hand splash and slosh) appear to have no dry-land equivalents. Indeed, without an aquatic substrate these behaviours would be either impossible to perform or have little apparent display purpose. The observation of a gorilla sloshing water towards an otter in particular, is a good indication of an understanding of the potential of water as a medium for 'communication'. The three main styles – the 'body splash' and the one- and two-handed splashes, which combined, represent 75% of all observations, each have potential dry-land correlates in the form of 'the charge' and the one- and two-handed ground slaps.

It can be argued that the 'body splash' is little more than a charge display taking place in a semi-aquatic environment, an idea supported by the observation that significantly more body splashes were made during a charge than without. However, it is important to reiterate that the 'charge' referred to in splash displays bears only slim resemblance to the fast charges seen on dry land (pers. obs.), being very short and often little more than a brief lunge forwards. It would also appear paradoxical to imagine that a gorilla wishing to perform a charge display would deliberately launch itself upon a substrate (deep water) which more than any other, will invariably shorten the duration of the charge drastically, and may leave the animal in a compromised position with regard to subsequent approach or retreat.

Of all the splash styles observed, the one- and two-handed splash displays most closely resemble dry-land displays. Dry-land ground slaps are commonly seen in captive gorilla groups (Ogden & Schildkraut, 1991) and are also well known in the wild (pers. obs.; Schaller, 1963). They commonly consist of a single explosive slap against the ground with one or both palms simultaneously. In a forest setting, the display can be thought of as sonic, visual, or a combination of both. It creates a loud reverberating thump which, at least in human/western lowland gorilla interactions, is usually heard rather than seen. In the Virunga Volcanoes, ground slapping has frequently been observed at the end of a chest-beating charge at observers, where the visual element seems predominant (Schaller, 1963). Ground slaps identical to these were also witnessed in the bai and it is tempting to surmise that the one- and two-handed splash displays were examples of such displays in which the hand happened to strike water rather than solid ground or vegetation mat. Evidence to the contrary comes first from a subtlety in execution. Dry-land ground slaps, for maximum effect, are likely to require the flat of the hand to strike the substrate on a horizontal plane. This action when performed in water will, unless the animal is travelling forwards at the time, send as much spray backwards as forwards. Yet the plumes generated by this behaviour at Mbeli all appear to spray upwards and forwards, away from the actor, suggesting that the palm is angled before hitting the water. It is interesting to note, however, that Schaller (1963) mentions that in some ground slaps exhibited by mountain gorillas at the end of chest-beating display runs, the hand "...may be carried into a sweeping movement which causes vegetation and dirt to fly". While seemingly not the habitual style of ground slapping, this description, of all terrestrial display styles, most closely resembles that of the splash display.

Secondly, a comparison of certain parameters for one- and two-handed splash displays and ground slaps shows several differences. In the bai, the splash displays in question are significantly less likely to be exhibited with a charge than without one, whereas standard ground slaps are just as likely to be accompanied by a short run as not. This may reflect little more than the difficulties encountered in executing a charge in water, but may suggest that where the added visual impact of a splash is not available due to the nature of the substrate, the addition of a short charge reinforces the impact of the display. In other words, a charge accompanying a one- or two-handed splash may be physically hard to execute, and/or may be unnecessary as the display already includes its own striking visual element.

Intra-dyad distance

When intra-dyad distance was compared for splash displays and ground slaps in agonistic, inter-group contexts, it was found that slash displays were employed at significantly greater distances. Although the data for comparison were not corrected for independence by considering the mean distance for known individuals, the results are likely to be a good representation of the true picture (when average intra-dyad distances for 'splash' were calculated with fully independent data, the median value was found to be within 3m of that from the non-independent data). Thus it would appear that in a swampy bai setting, splash displays may be selected over ground slaps when dyad members are further apart. More data are required to confirm this effect, but if genuine, it may reflect, a) that splash displays are not selected at close range to avoid undesired escalation of an interaction towards contact aggression, or that b) ground slaps delivered from a distance lack sufficient visual impact to achieve their purpose. At the very least, splash displays can rival, and to a human observer, frequently surpass, the extreme forms of terrestrial agonistic display (charges, ground slapping, branch breaking and chest beating). It is perhaps interesting to note at this point, that threat barks and other explosive agonistic vocalisations were very seldom used by silverbacks within the bai, though they were frequently employed in the forest surrounding it. While some vocal displays such as the hoot-series, roar, wraah, scream, threat and question bark can carry over a considerable distance (over 1km in some circumstances - Schaller, 1963; Fossey, 1983; pers. obs.) they appear to be inappropriate or unnecessary during inter- and intra-group encounters in open areas where visibility is not obstructed. This may suggest that powerful vocal displays are physically more costly to produce and less sustainable than those generated by the percussive use of the limbs.

The strong similarities of ground slaps and charges with one- and two-handed splashes and body splashes, both in form and function, suggest that the majority of splash displays are linked closely with displays made on dry-land. While splash displays may for the most part represent adaptations of dry-land displays, the data support the existence in splash displaying of a discrete communicative display form entailing the deliberate splashing of water to create a visual impact.

The function of splash displays

All observed splashes, with the sole exception of the 'run' could be classified as 'displays' (Wilson, 1975; Beer, 1977) in that they were the intentional result of a behaviour pattern modified to convey information. Three quarters of the display bouts where a context was clear (excluding unknowns) were agonistic and were all made by males from the age-class of blackback upwards. Only one bout of agonistic splash display was targeted in an intra-group context (a silverback displaying at a juvenile); all others were in inter-group situations (excluding 'other species' displays). A significant bias towards the use of splash displays in inter-group contexts was also found when all behavioural contexts were considered. Agonistic expression and other intra-group communication is more likely to be served (particularly in the case of a silverback towards his group members) through the more subtle use of vocalisations (Schaller, 1963; Fossey, 1972, 1983; Seyfarth et al., 1994), gaze (Yamagiwa, 1992) and group spacing/body position (*see* this Appendix, Part II).

A correction of the observed frequency of display bouts, taking account of the frequency with which age/sex-classes were seen in the bai, showed that solitary silverbacks (of any age) were six times more likely to perform the display than individuals of any age living in groups. Only four individuals made up the solitary contingent of the population at Mbeli, so bias may be generated by a lack of independence for these bouts. However the distribution of displays among these individuals does suggest that these animals are considerably more likely to exhibit splash display than any others.

When expected frequencies of splash bouts were calculated for each age/sex-class, based on visits to the bai, it was found that solitary silverbacks and fully adult group-silverbacks all displayed considerably more than predicted. This suggest that social status and hormone levels were important factors. Adult females never exhibited splash displays despite being the most likely to do so based upon their proportional representation in the visiting population. Juveniles were similarly under-represented.

Similar differences were found when comparing the age/sex-classes of animals targeted for splash display with expected frequencies. Adult females and juveniles were targeted, but considerably less than predicted. Once again, solitary silverbacks were targeted much in excess of their predicted levels. Interestingly, group silverbacks were targeted very slightly less than predicted, suggesting that while frequent exponents of the display, they make less appropriate or attractive targets. Of all splash bouts for which a target animal was identified, 45% (18/40) were solitary males, despite this social class constituting a mere 7% (278/3797) of individual visits to the bai. It would thus appear that solitary males are the most frequent users *and* receivers of splash displays: in other words, they target each other more than any other age/sex dyad. This does appear slightly puzzling. Firstly, the four solitary males known to exhibit splash displays at Mbeli encountered groups in the bai 50% more often than they did other solitary males (mean of 1.5 times more likely to encounter a group). Secondly, while it can be argued that solitary males, having no females to lose during agonistic encounter, might potentially be more reckless and aggressive adversaries (Harcourt, 1978a; Sicotte, 1993) (unlike group silverbacks, for whom the potential for losing females may provide a disincentive to interaction), they also have no possibility of directly attracting females by displaying at each other. In the majority of cases when solitary males displayed at one another, no females were even within sight of the interaction. Reasons for raised levels of agonism between lone males have been mentioned in previous chapters, and include the following:

a) Displays given in order to intimidate a potential competitor for females may incur benefits to reproductive success in the long-term. This would be a viable proposition if solitary males were found, unlike group males, to be defending their presence in areas of high group-use (i.e., access to females) such as bais.
b) Rates of solitary male agonism may be raised due to a heightened sense of tension (e.g., corticoid levels) possibly resulting from the frustration and increased vulnerability (to predators and possibly conspecific attack) of solitary life.
c) It has been shown among captive male gorillas that an increase in androgen levels occurs between 14 to 20 years, and that androgen levels and aggressive behaviour are significantly higher in young adult males than in sub-adult and fully adult males (Stoinski et al., 2002).

An alternative explanation for the observed bias in display dyads may be that solitary males are deterred from displaying at groups, especially where visibility is not compromised, by the threat of violent defence by a group's leading silverback. In other words, a latent tendency to aggression naturally occurring in solitary males finds a less dangerous outlet, especially in an open habitat, through display at like individuals. Data on wounding among silverbacks presented in Chapter 6 were inconclusive as they showed higher levels of wounding sustained by solitaries than group silverbacks; an effect that could still be caused by better fighting skills in group silverbacks, or higher levels of fighting between solitaries.

How widespread is the display-use of water in gorillas?
Researchers at Maya Bai, in the Odzala National Park (180 km from Mbeli) report seeing displays incorporating water (Magliocca, pers.comm.); an unsurprising discovery given the similar conditions at the two sites. Splashing behaviour has also been noted in captive gorillas. In a compilation of ethograms for captive gorillas (Ogden & Schildraut, 1991) several recorded instances of subjects actively seeking contact with water for reasons other than feeding are cited (e.g., duBois et al. observed wading and splashing during self-play, Goerke records playing with water by a juvenile gorilla, while Gould describes swishing/splashing, sitting, standing or running through water). During the same study, grimacing at water spray was also noted. Brown (1988) reported adolescents, juveniles and even silverbacks playing with water, including splash and slapping behaviour. No 'social play' was recorded for silverbacks in Brown's study, but 'object play' mostly involved the use of water. The only report suggesting splashing as a distinct display form that has come to my notice is by Golding (1975) who describes western lowland gorillas leaping and generating splash displays at their keepers in a shallow area of the moat surrounding their enclosure at the University of Ibadan Zoo, Nigeria.

Anecdotal evidence suggests that wild gorillas are aware of the properties of splashed water. At Lopé, in Gabon, one western lowland silverback was observed, while crossing a shallow stream, splashing water over his shoulder onto his back (pers. obs). However C.E.G. Tutin (pers. comm.) also at Lopé, relates that on startling a silverback feeding in a swamp, the gorilla first waded out of the mud and water before giving a terrestrial display on hard ground. Williamson (pers. comm.) reports seeing an 8yr old female mountain gorilla at Karisoke, sitting next to a rock pool, waving her arm back and forth in the water. However, years of intensive study from the Karisoke Research Centre have failed to reveal splash display as an element in the behavioural repertoire of mountain gorillas, and a similar picture apparently applies to eastern lowland gorillas though there have been comparatively few studies on this sub-species.

Although only one other field site for western lowland gorilla research has witnessed the apparently communicative use of water, it should be borne in mind that observation conditions at Mbeli and at Maya are optimum, and several other behaviours previously unseen in this species have been recorded at these sites. What then is the likelihood that other populations of western lowland gorillas utilise the display?

A prime factor limiting the distribution of splash displays, inevitably, is access to an aquatic substrate. Most, if not all gorillas, including those found in uplands will have some access to flowing streams, although a limited exposure to water, both from a developmental standpoint and in a daily temporal sense could easily restrict the emergence or occurrence of the form. In addition, for the behaviour to find its inter-group, agonistic (adult) setting requires independent social units to encounter each other in an aquatic environment. In dryer forests, this is likely to be an extremely rare event. Therefore it is not unreasonable to suggest that habitual use of splash displays may be limited to individuals from populations ranging at moderate to high densities in forests containing either sizeable areas, or smaller but much sought after, patches of wetland. Thus, swampy bais, which appear to attract many gorilla groups into a relatively tiny area (despite extensive surrounding wetlands), may represent the optimum environment in which one might predict the exhibition of splash displays.

However, if splash displays are relatively uncomplicated adaptations of ground-slap and charge displays, individuals from less than optimum areas might be predicted to be capable of either performing such displays whenever necessity dictates and substrate allows, or failing that, of developing them with relative ease and rapidity. In other words, splash displays, stemming as they do from what are likely to be innate behaviours, may appear almost spontaneously in individuals not benefiting from extended periods of exposure to the display. Splash displaying as a basic behaviour is unlikely to be a candidate for cultural variation in gorillas, though the use of particular styles might prove a more fruitful area of inquiry.

Other Species

It is hardly surprising that some aquatic or semi-aquatic mammals use water to achieve communicative goals. Beavers (*Castor spp.*) produce a sonic display by slapping the surface of water with their tails. Some otters (*Lutra spp.*) also communicate alarm by diving noisily into water, despite their ability to do so soundlessly in other circumstances. Among largely terrestrial mammals however, examples are few and far between. Elephants (*Loxodonta africana*) have been seen to splash water towards a threat, including crocodiles (pers. obs.). The North American black bear (*Ursus americanus*) has been observed generating splashes during display charges (L. Rogers, pers. comm.) but there is some doubt as to whether the splashing is an intentional element of the display or merely an accidental bi-product.

Of wild primates, only a few individual chimpanzees in a community inhabiting the Mahale Mountains site, Tanzania, have been seen to utilise water in a similar manner. Nishida (1993) reports several adult male chimpanzees selecting rocks near a stream and throwing them into the water, apparently with the express aim of creating an intimidating splash. This is a fascinating observation, coming as it does from another highly intelligent primate, though one better known for its ingenuity and abilities in tool-use. Unlike gorillas, most chimpanzees appear to have a genuine intolerance for getting wet, which may be linked to dietary requirements. While chimpanzee social structure shows considerable flexibility in order to cope with periods of low fruit availability (fission-fusion structure), gorilla groups characteristically remain more stable. When fruit is in short supply, gorillas, with their ability to subsist on a diet largely composed of leaves, shoots, and piths, are more likely to be drawn towards swamps, as areas abundant in nutritious herb foods. Differences in social structure and corresponding dietary requirements may underpin the observed dichotomy in these two ape species tolerances for contact with water. The stone throwing chimpanzees of Mahale, then, appear to have discovered the display qualities of water, as have the gorillas of Mbeli. By using rocks as tools, however, they have achieved a similar result without having to enter the water.

Part II

The importance of eye-gaze and head orientation in gorilla interaction, and the role of pelage in social signalling.

Introduction

Eye-gaze in gorillas and other primates

The face offers an important source of information on many characteristics important to human and nonhuman primates alike including an individual's species, age, gender, and potentially its mental state or intentions (van Hooff, 1967; Fujita, 1987; Ellis & Young, 1988, p 87; Perrett & Mistlin, 1990; Nahm et al., 1997). Within face perception, the role of the eyes and the eye region as a visual stimulus is of particular importance, and primates have been shown to fixate preferentially upon the eye region when presented with test faces during laboratory experimentation (e.g., Keating & Keating, 1982; Kyes & Candland, 1987). Interestingly, eye morphology in most primates (in contrast to those of humans) suggests that gaze direction is camouflaged. The large exposed sclera in humans allows gaze direction to be determined easily, however very little of this area is visible in other primates, including the apes (Kobayashi & Koshima, 2001). It has been suggested that cryptic eye coloration may hide gaze direction so as to enable individuals to avoid agonistic interactions with conspecifics that may be precipitated by direct eye contact (Perrett & Mistlin, 1990).

Such interpretations seem somewhat at odds with the overwhelming body of evidence supporting eye gaze as a highly important communicative signal in nonhuman primates (e.g., Emery, 2000). In particular, the role of direct and sustained eye contact (staring) during threatening behaviour is evident in many species and may be the most ubiquitous such element in the primate order (e.g., Hinde & Rowell, 1962; Redican, 1975). Variation exists however: both in terms of the response to a threatening stare (Redican, 1975), and in the function of the original staring behaviour: for instance, eye contact is implicated in sexual arousal in stumptailed macaques (*Macaca arctoides* – Linnankoshi, Grönroos & Pertovaara, 1993), and among chimpanzees staring may be observed as part of threat behaviour, but also during affiliative interactions including reconciliation and courtship (Goodall, 1986; de Waal, 1989).

Schaller (1963, p209) notes that in disturbing situations, in which the anger of a mountain gorilla is aroused, "The eyes are hard and usually fixed on the animal causing the anger". Whether this can be considered in any way analogous to a 'display' of eye gaze is uncertain. He also notes that a brief stare may be all that is required of a silverback in order to supplant a group member (Schaller, 1965). In Yamagiwa's (1992) study of social staring in an all-male group of mountain gorillas, a strict definition was employed such that only examples of one individual looking into another's face for at least 5 seconds from a distance of less than 30cm were considered acts of staring. Using this exclusive criteria, Yamagiwa found staring to occur in the following contexts: *Social Play* – often when more vigorous forms of play solicitation failed to elicit a response, staring was used (mostly by younger toward older gorillas) as a highly successful means of eliciting play: *Homosexual behaviour* – younger individuals in particular used staring to elicit homosexual mounting from older gorillas, especially when other means had failed to provoke a response: *'Slow' supplantation* – once again, this seemed to be a tactic primarily of younger males in achieving the displacement of older individuals. Displacement was not immediate, but followed after a period during which the younger male stared in turn at the elder's face and hands as he fed. *Pre-conflict staring* – staring was used successfully in preventing anticipated conflicts during interventions primarily by younger individuals (in all cases, 'younger' includes blackbacks, and is used relative to silverbacks): *Post-conflict staring* – following fights or periods of heightened social tension, staring was occasionally used between participants and onlookers, possibly as a means of reducing tension: *Greeting* – of the lesser used contexts, staring occasionally occurred following a separation of an hour or more; younger individuals stared at each other, while silverbacks never stared in such cases, but were the targets of staring. Although supplantation could be seen as an agonistic behaviour, in this context the behaviour had more in common with begging behaviour; thus in each of the examples described by Yamagiwa (1992), staring was used in solicitous, tension reducing or otherwise affiliative situations. It should be remembered, however, that by focusing only on such close-range uses of gaze, agonistic examples may have been omitted from the sample.

Gomez (1992, cited in Gomez 1996), in a study of four hand-reared western lowland gorillas, found that the young apes utilised a wide variety of techniques solely in order to gain eye contact with him, which, once established, would lead to them making a non-verbal request. This he cites as evidence towards gorillas as having some form of 'ostensive' function in eye gaze behaviour (ostensive behaviour [Sperber & Wilson, 1986] is defined as that capable of expressing and assessing communicative intent).

While direct gaze has been widely shown to represent a threat, gaze aversion is a common response to threatening stimuli. It is suggested that overt avoidance of gaze may lower arousal levels in the targeted subject and reduce the chances of agonistic interaction both by precluding it from the obligation to respond (Chance, 1962; Altmann, 1967; Kaufman & Rosenblum, 1966) and by altering the motivational state of the aggressor (Redican, 1975). Many species show patterns of behaviour consistent with this, e.g., *Lemur catta* (Jolly, 1966), *Macaca arctiodes* (Bertrand, 1969), *Presbytis entellus* (Jay, 1965), *Microcebus murinus* (Coss, 1978). Kingdon (1988) goes further to suggest that ritualised gaze avoidance, particularly in sub-species of the *Cercopithecus cephus* group has developed with distinctive facial markings into an alternative behavioural form of 'head-flagging' (Kingdon, 1988).

Schaller (1963) reports a rare and unusual behaviour in mountain gorillas in which the head is shaken fairly rapidly back and forth in response (deemed submissive or appeasing) to his presence. More importantly with regard to the current study, he describes 'head turning', in which gaze is avoided by turning the head away from the threatening stare of another gorilla, or the presence of a human observer. Schaller suggests that the behaviour shows submissiveness, and indicates that '.. aggression is not intended' (p292). He also describes stare avoidance during situations of low-intensity alarm or uneasiness: at such times the gorilla's lips were also noted to be drawn inwards with the mouth tightly compressed. This 'tight-lipped' expression is also described by Dixson (1981, p131) as being similar in both appearance and context, to nervous lip-biting in humans, and he cites R.D. Nadler as reporting that the expression was mostly produced in conjunction with '.. a marked shifting of the animal's gaze away from the receiver of the display'. Elsewhere, Schaller (1963, p235) describes the 'strutting walk', a display between gorillas or at an observer, in which the arms are rotated outwards at the elbow, accentuating the size of the forearms: the body appears stiff and the head is turned obliquely away from the observer. Schaller notes, however, that although the head position was averted, gorillas would still watch him out of the corner of the eye.

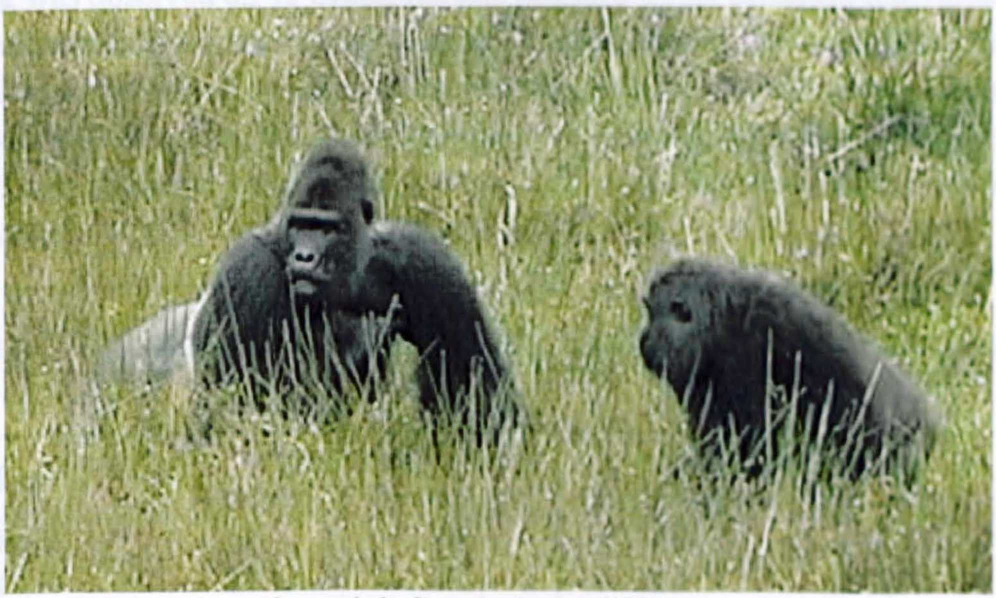
Various combinations and single examples of the 'strutting' or stiff walk, head-turning, staring and the tight-lipped face are noted in captive groups of gorillas. Notably, the tight-lipped face, strut walk/stance, and head-turning/stare avoidance appear primarily in agonistic display contexts (Bennett & Fried [*head-divert*]; duBois, Mead & Cox [*"lips are tightly compressed and the head diverges from side to side"*]; Gould [*stiff posture, head diverted to the side, tight-lipped face*]; Lockard [*refrains from direct stare, mouth tightly compressed, head turned to side*]; Maple & Hoff [*stiff walk; lips compressed together; head diverted away from object being threatened*]; Meder [*tense lips*]; Woods [*stiff walk; lips compressed together*]; all cited in Ogden & Shildkraut, 1991). Among these records from captive western lowland gorillas is the suggestion that head-turning and the tight-lipped face may be used in display circumstances, although, despite inferences, it is not always clear if the displaying animal is the initiator or target of the behaviour. Thus some confusion appears evident. A tight-lipped face has been linked in the wild to unease, tension and nervousness, while in captivity it appears strongly allied to aggressive displays, and head-turning has been linked with gaze aversion and even submission in the wild, but a version of this also appears in some captive populations in connection with aggressive displays. Could gorillas be incorporating a submissive or aggression limiting device (stare avoidance) into an otherwise agonistic and threatening encounter? Is there evidence to suggest that stare avoidance is only performed by the recipient of threatening acts?

This section will use observational data from Mbeli to examine the context and possible function of staring, head-turning (or stare-avoidance), and the tight-lipped face, and offer alternative interpretations to some previously suggested, and potentially clarify areas in which definitions may have led to confusion. Crucial to this endeavour is an acknowledgement of the importance of morphological characteristics shaped by sexual selection including body shape and pelage, and the ways in which these features are utilised in communication or signalling through the manipulation of body posture.

Methods

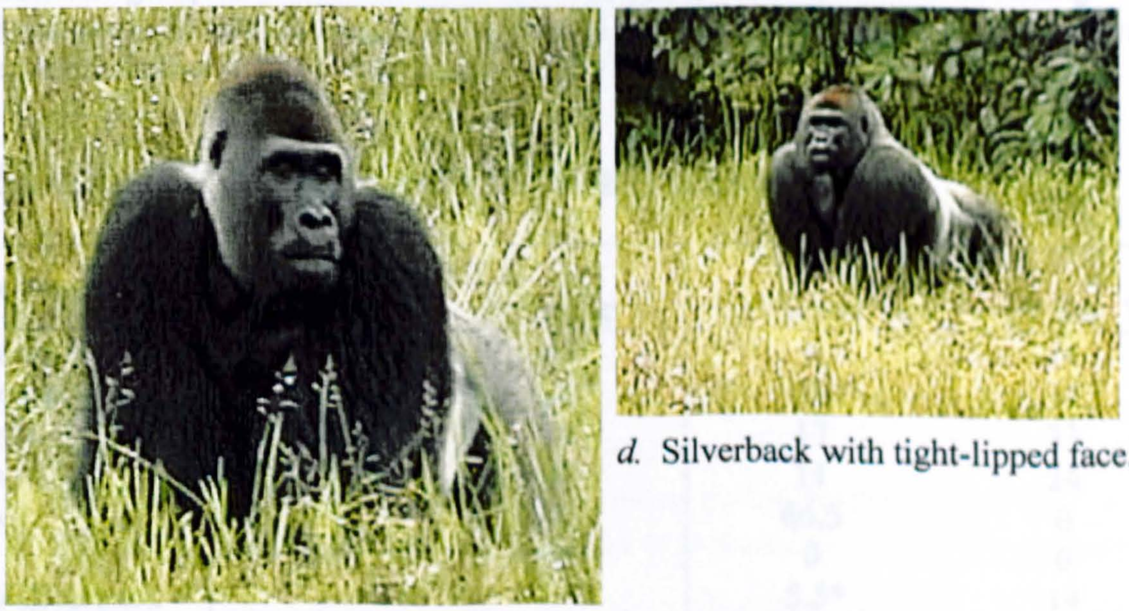
Initial analyses, however, proceed under the paradigm of gaze and gaze aversion as primarily signals of visual attention as described above. In this analysis, '*staring*' is loosely defined as any behaviour in which a gorilla appears to affix direct eye gaze at another in a concentrated manner (in contrast to simple looking as part of general scanning or vigilance behaviour). In order to retain some degree of homogeneity with Yamagiwa's (1992) definition, an intra-dyad distance threshold of 10 metres is applied, with all examples of staring at or within this distance considered, and all those outside it discarded (the object of a gorilla's stare cannot be judged with confidence at greater distances). At Mbeli, *head-turning* refers to the distinctive pattern described by Schaller (1963), R.D. Nadler (cited in Dixson, 1981, p131) and several authors in Ogden & Schildkraut (1991), in which a gorilla involved in a social interaction markedly turns the head laterally away from another individual, and in particular during the 'strutting walk' or stiff stance. Plate A7.2 shows examples of head-turning and the tight-lipped face in silverbacks at Mbeli.

Plate A7.2 Examples of head-turning and the tight-lipped face at Mbeli



a. The herding of an adult female (note differences in gaze direction).

b. Two silverbacks in agonistic interaction.



d. Silverback with tight-lipped face.

c. One participant in a silverback-silverback interaction.

Results

Staring behaviour

Staring was observed on 45 occasions and initiated by 24 different individuals in inter-unit contexts, and on 39 occasions by 19 individuals in intra-group contexts. Table A7.14 gives a breakdown of staring by major interaction type-classes. Judgement of these classes was unavoidably subjective, but as staring was seldom exhibited without other less ambiguous behavioural elements, error is likely to be slight; less clear cases were classed as 'unknown'.

Table A7.14 Frequency of interaction types in which staring behaviour was witnessed

Type	Intra-group		Inter-unit	
	Number	Percentage	Percentage	Number
Agonistic	18	46	49	22
Affiliative	11	28	38	17
Play agonistic	2	5	11	5
Unknown	8	21	2	1
TOTAL	39	-	-	45

The table shows remarkable homogeneity in the proportion of stares given in agonistic encounters: similarities would probably be greater for affiliative encounters also, but for a large proportion of 'unknown' types during intra-group interaction. Three of these unknown-type encounters were directed at adult females by silverbacks and may have been in some way coercive. However the other five, though cryptic in terms of function, were clearly not agonistic. Despite some similarities in frequency, very different social processes may be responsible for the observed distribution. As Table A7.15 illustrates, the number of initiating individuals per age/sex-class responsible for these figures varies depending on whether the encounter was within or between units. Immature gorillas initiate most affiliative staring in both intra-group and inter-unit settings. Group silverbacks never stared affiliatively in either setting, but stared agonistically considerably more within the group than between units: this was due to the frequent use of staring during intra-group female herding, and the general disinclination of silverbacks to interact with members of other units at close ranges.

Table A7.15 Percentage of stare encounters per age/sex-class

Age/sex-class	Intra-group		Inter-unit	
	Affiliative %	Agonistic %	Affiliative %	Agonistic %
Silverback	0	47	0	14
Adult female	0	29	0	15
Blackback (incl.ysb)	27	18	17	33
Sub-adult	0	0	11	24
Juvenile	36	6	66.5	0
Infant	36	0	0	0
Solitary silverback	-	-	5.5*	14
N=	11	17	18	39

* The only example of inter-unit affiliative staring involving a silverback was a solitary male manoeuvring close to an adult female: As such the label 'affiliative' may be misleading.

Table A7.16 gives the actual number of individuals in each age/sex-class staring and being targeted with staring. No attempt has been made here to control for the number of individuals per class in the population, as the most pertinent message of the data comes from a comparison of values within each class, rather than between classes.

Table A7.16 Number of individuals of each age/sex-class staring and targeted with staring

Age/sex-class	Intra-group		Inter-unit	
	Staring	Targeted	Staring	Targeted
Silverback	11	2	3	2
Adult female	9	23	3	4
Blackback (incl.ysb)	8	5	15	15
Sub-adult	1	3	9	10
Juvenile	6	4	12	11
Infant	4	2	0	0
Solitary silverback	-	-	3	3

Group silverbacks seldom stared in an inter-group context, but were relatively prolific within their groups (especially considering the ratio of these to other group members). While employing stares more than any other class, they were only targeted with staring twice in each of the two social settings. In inter-group encounters, adult staring was rare and roughly egalitarian in terms of use and reception of the behaviour, but immatures showed increased levels when interacting with members of other groups, both in use and receipt: this probably reflects a heightened interest in interacting affiliatively with novel or less frequently seen partners.

In many cases, the exact role of the stare within an interaction was not clear, and it was not possible to list many of the occasions witnessed within well-defined contextual boundaries as defined by Yamagiwa (1992). During agonistic encounters, staring often followed other display behaviours such as charges, but seemed to heighten the sense of discomfort felt by the target. Some retreats were elicited by staring alone, but feeding displacements accounted for only one of 21 agonistic interactions between members of different groups and one of 17 within groups. Silverbacks employed staring as part of their herding behaviour towards their own adult females (especially new immigrants) in 7 of 17 interactions, and the behaviour was also used by resident females against new immigrants. Just under half of all inter-unit agonistic stare incidents were classed simply as 'intimidation' or 'proximity intolerance'. Two of eleven intra-group affiliative staring occasions were during immature play bouts, three were in greeting following brief separation, and two were by infants while trying to gain suckling access with their mothers. During intra-group affiliative encounters, 7 of 17 staring occasions occurred when immatures (mostly juveniles and sub-adults) greeted immatures from other groups, and six were during bouts of play.

Of the 45 stare initiations in an inter-unit context, 18 provoked stares at some point during the targeted individual's response; eight times during affiliative encounters, nine times when returning aggression, and once during submission. During intra-group occasions, staring was only returned on four of 17 agonistic encounters, and never during affiliative use.

Finally, considering the other behavioural elements mentioned in the Introduction, Table A7.17 shows the frequency that head-turning, the tight-lipped face, and a stiff-limbed walk or stance were used during exchanges involving staring.

Table A7.17 Inclusion of other behavioural elements in staring behaviour

Behaviour accompanying staring	Intra-group Number	%	Inter-unit Number	%
HT + TL + SL	6	15	8	18
HT + TL	0	0	2	4
SL + TL	1	3	2	4
HT	1	3	1	2
TL	1	3	3	7
SL	4	10	2	4
Stare only	26	67	27	60
TOTAL	39	-	45	-

HT - head-turning, TL - tight-lipped face, SL - stiff-limbed walk or stance

In the intra-group context, a third of all encounters involving staring also included one or more of the other elements considered. During inter-unit encounters, this level rose to 40% of the sample. In agonistic encounters only, 68% of inter-unit stare-use involved one of the other elements, while 53% did so in intra-group encounters.

Head-turning behaviour

Table A7.18 shows the number and percentage of occasions in which head-turning was witnessed in each major interaction type. As is clearly seen, agonism far outweighed any other type as a context for exhibition of the behaviour. The few occasions of head-turning during affiliative encounters were during mock-fights by immatures during play. The importance of this behaviour during agonism is also suggested by the difference in overall frequencies of expression between intra- and inter-unit conditions.

Table A7.18 Frequency of interaction types in which head-turning was witnessed

Type	Intra-group Number	Intra-group Percentage	Inter-unit Percentage	Inter-unit Number
Agonistic	12	92	91	51
Affiliative	1	8	2	1
Play agonistic	0	0	7	4
Unknown	0	0		
TOTAL	13	-	-	56

Crucially, the values in Table A7.18 represent not only the overall character of each dyadic encounter, but the behavioural state of the initiator of the contact who was also the individual responsible for the initial expression of head-turning; thus it can be seen that on 91% of occasions, head-turning was used by the initiator of an agonistic interaction. However, the data do not specify that head-turning was the initial element used when making an agonistic approach. Therefore it is still conceivable that use of this element was made in the context of a response to the behaviour of the targeted individual *after* the initial approach. From the data in its current state it is difficult to be precise about how exactly the behaviour is used within the context of the agonism observed, but evidence suggesting that it is in fact a directed *aggressive* display comes from the observation that during inter-unit encounters, of the 56 head-turning occasions, the targeted individual head-turned in response on 30; four of these led to eventual submission, but the rest were during acts of reciprocal aggression.

In Table A7.19, it can be seen that while silverbacks were the most frequent users of head-turning during intra-group exchanges, they were never targeted with the behaviour. Almost the opposite effect was observed for adult females, who were targeted much in excess of their use of the behaviour (eight of the nine occasions of adult female receipt of the behaviour were initiated by the group's silverback). Plate A7.2 (*a*) shows head-turning as employed by a silverback during the agonistic herding of a new immigrant female. In contrast to a more traditional interpretation of eye-gaze, this shows the dominant silverback apparently with his gaze averted, and the crouching, submissive female staring straight at the male.

Table A7.19 Number of individuals of each age/sex-class head-turning and targeted with head-turning

Age/sex-class	Intra-group		Inter-unit	
	Head-turning	Targeted	Head-turning	Targeted
Silverback	9	0	13	11
Adult female	2	9	0	1
Blackback (incl.ysb)	1	0	22	21
Sub-adult	0	2	4	9
Juvenile	1	1	2	1
Infant	0	1	0	0
Solitary silverback	-	-	15	13

Head-turning was a rare behaviour for non-silverback members within the group, but a more frequent element between groups, especially so for blackbacks, who mostly targeted other immatures (predominantly other males) with the behaviour. Group silverbacks displayed head-turning during inter-unit encounters well in excess of their rate of staring. This is likely to be due to the distance limit imposed on staring behaviour – both in the methodology for this analysis (10m) and in the actual distance at which the two behavioural elements can be clearly seen by a recipient. If head-turning has a communicative value, it is likely to have the capacity to function over a wider distance range that staring. Despite there being approximately four times more group silverbacks than solitaries in the population, solitary silverbacks were noted to display head-turning more than their group leading counterparts during inter-unit encounters, potentially indicating a heightened importance of the behaviour for these individuals.

Table A7.20 shows the frequency with which the other behavioural elements under consideration in this analysis were included in encounters involving head-turning. Little can be said regarding intra-group behaviour due to the small sample size. For inter-unit encounters, it can be seen that very few occasions of head-turning alone were observed, and that head-turning with only staring was also rare (95% of head-turning occasions also contained either a stiff-limbed stance and/or a tight-lipped face).

Table A7.20 Inclusion of other behavioural elements exhibited during behaviour containing head-turning

Other behaviours	Intra-group		Inter-unit	
	Number	%	Number	%
ST + TL + SL	6	46	8	14
ST + TL	0	0	2	4
SL + TL	3	23	33	59
ST	1	8	1	2
TL	1	8	7	13
SL	0	0	3	5
Head-turning only	2	15	2	4
TOTAL	13	-	56	-

ST - staring, TL - tight-lipped face, SL - stiff-limbed walk or stance

Once again, it was difficult to be precise with regard to the context of these predominantly agonistic encounters. In the intra-group context, eight occasions of head-turning were during the herding or harassment of immigrant females by silverbacks or resident females. No examples were during feeding displacements or supplantations. In head-turning bouts during inter-unit encounters, three-quarters of occasions were listed as either in 'intimidation' or 'proximity intolerance', and in only two cases was feeding displacement or supplantation considered the motive of the behaviour.

Before going on to discuss these findings, it may be helpful to consider staring and head-turning behaviour within the context of all affiliative or agonistic encounters. Of 115 initiations of agonistic inter-unit dyadic interaction, 31 included the tight-lipped face, 13 included head-turning, 19 included staring, and in 35 the initiator's stance or walk/charge was stiff-limbed. Sixty-five agonistic initiations contained none of these elements. Only seven of 54 successful or attempted supplantations (feeding or otherwise) involved use of these elements by either party, while 27 involved the use of 'cough-grunt' vocalisations. In 102 affiliative dyadic initiations between members of different units, 11 contained staring, but only two involved the tight-lipped face or stiff-limbed stance, and only one involved head-turning.

During 122 intra-group agonistic initiations of dyadic interaction, 85 involved the tight-lipped face, 50 head-turning, 21 staring, and 78 a stiff-limbed stance. Eleven contained none of these elements. Of 51 affiliative initiations, 16 involved staring, five the tight-lipped face, four a stiff-limbed posture, and one head-turning. Twenty eight contained none of these. There were 51 cases of supplantation within groups, only four of which involved use of one or more of the described elements, although 27 cases involved the use of cough-grunts.

Discussion

Observations from Mbeli suggest that much staring behaviour fulfils a similar function to that for the mountain gorillas studied by Yamagiwa (1992). In an affiliative context, staring was primarily between younger immatures, and served to capture the attention of a second party, as a greeting, as an invitation to play, and in soliciting suckling. Particularly with regard to solicitous contexts, the behaviour resembles the 'ostensive' function discussed by Gomez (1996) in which direct eye to eye gaze is sought as a prerequisite for a further request or action. Notably during inter-unit affiliative gaze use, eight cases involved the staring individual imposing his or her face in front of the target at a distance of less than a metre, thus 'demanding' that the gaze be met or acknowledged rather than simply looking hard in another's direction. The distance threshold of 30cm imposed by Yamagiwa (1992) almost certainly excluded any agonistic use of eye gaze. The wider threshold used at Mbeli permitted many such examples to be considered, though it appeared that distance may have remained a factor, in that silverbacks, who generally avoided close-range agonism with each other, used staring in this manner much less than immatures for whom contact aggression was largely in a non-serious context.

There is frequently a danger when comparing rates of a given behaviour between populations, that a detail of the behaviour's performance has been omitted or missed, such that comparisons do not actually relate to the same behaviour. This may be case with head-turning as most definitions are vague at best. At Mbeli, no behaviours resembling Schaller's (1963) head-shaking were observed, but head-turning was an easily recognisable and apparently ritualised behaviour that was seen on a regular basis. Typically, individuals involved in an agonistic display, would adopt a stiff-limbed stance, with a tight-lipped expression. The head would then be turned to one side such that the face pointed at roughly 90° to the position of the opponent. At such times, the body was, as Schaller (1963, p235) describes for the 'strutting walk' often positioned so as to display the side of the body. At times when the body was to a greater degree facing the opponent, the head was frequently turned to one side for several seconds, then turned to the other. This alternated turning could be repeated several times.

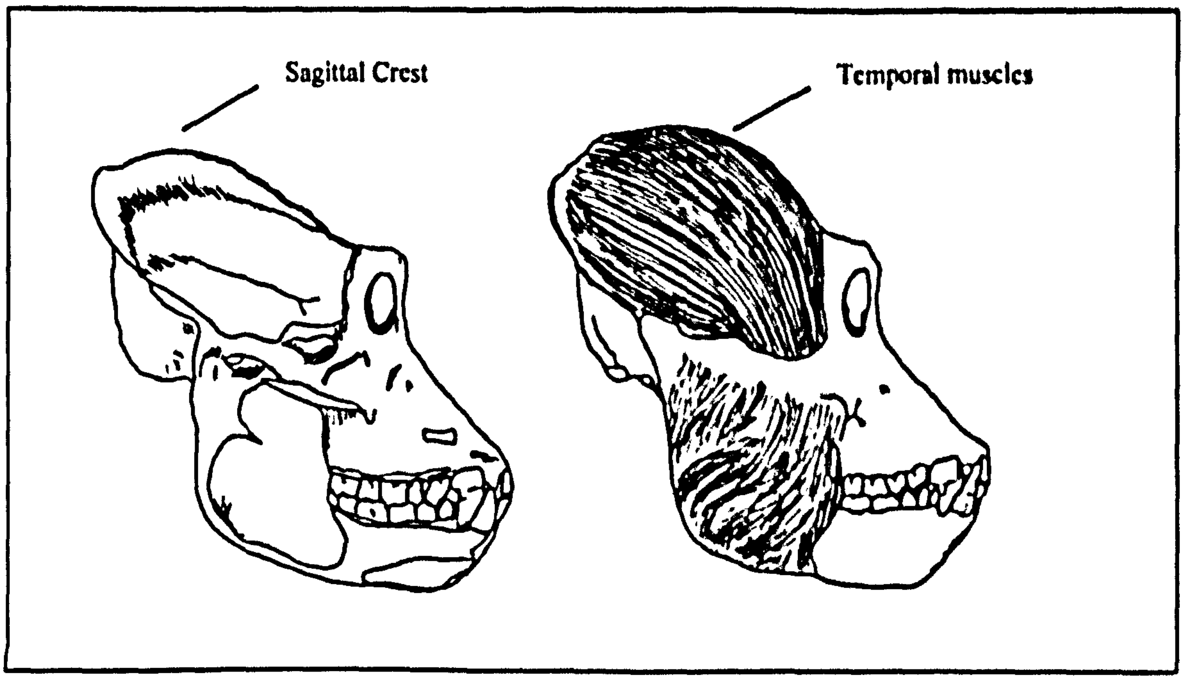
In comparison to staring, the general context of head-turning was overwhelmingly agonistic. As mentioned in the Results, however, the lack of sequential ordering in the data may mask the precise nature of the action's exhibition. In other words, even though a gorilla may have initiated an agonistic encounter, his or her use of head-turning may have been a submissive or aggression limiting response to the actions of the individual targeted. It might be suggested that despite the other aggressive behaviours displayed, the ritualised display of gaze aversion somehow prevented a dangerous escalation towards physical contact. The value of the 'cut-off' effect of gaze aversion has been suggested for both subordinate animals during agonistic encounters, and for dominant males when making courtship approaches to females (Kindgon, 1980). He notes that when both interacting individuals employ these behaviours, aggression may be dampened. Kingdon (1988), describes how 'cut-off' gestures may be employed even *during agonistic* inter-group encounters in some *Cercopithcus* species, presumably as aggression limiters. These are compelling reports, and given the potential costs of fighting between silverbacks, the value of some form of ritualised 'checking' behaviour could be considerable. On balance, however, the evidence for head-turning at Mbeli points away from a submissive or aggression limiting function. Firstly, in 69% of intra-group and 20% of inter-unit encounters involving head-turning, staring was also employed by the initiator. Mixed use of eye-gaze *and* eye-gaze aversion may be unlikely as it confuses signals in an atmosphere where ambiguity may be particularly costly. Secondly, key examples, such as silverbacks exhibiting head-turning during agonistic herding of their own females suggest that the behaviour displays dominance rather than submissiveness (it is hard to imagine why a silverback would require an aggression limiting gesture in such a circumstance). The use of head-turning by silverbacks in any agonistic intra-group interaction should rule out any submissive function due the dominant status of the adult male within the group. Indeed, in all resolved cases involving silverback use of head-turning against other group members, the silverback was dominant in the interaction.

On several occasions, unmistakable non-ritualised gaze-avoidance was witnessed. Mostly during agonistic dyadic interaction and always performed by the more submissive partner, such gaze aversion involved the target of a close-range approach looking up, left, right or down in a distracted manner, as if unable to retreat, but wishing to escape or ignore the scrutiny of the other. This action was not accompanied by a tight-lipped face or stiff-limbed stance.

The tight-lipped face was overwhelmingly seen in situations of display between two individuals, but there was little suggestion that it betrayed nervousness in gorillas. 88% of inter-unit cases of tight-lipped face-use were in agonistic initiations and accompanied other aggressive display forms, all of which can be interpreted as signals for intimidating an opponent. How this facial gesture may have evolved is unclear. It may be the coincidental consequence of a clenched jaw and generally tensed musculature, or less likely, may exaggerate the apparent size of the canines beneath the lips. In either case, this gesture appeared almost universally connected with mutual aggression, and with a stiff-limbed stance or walk, and accompanied 95% of head-turning cases.

If, as the data suggest, head-turning is a ritualised component of aggressive display, then what psychological state does it betray or what morphological characteristic is it designed to mask or display? The hypothesis proposed on the basis of observations at Mbeli is that of 'crest-display'. Gorillas have relatively large robust jaws, which are particularly massive in the adult male. In order to provide sufficient surface area for attachment of the large temporal muscles necessary to power the jaws, the silverback skull develops a sagittal crest; large nuchal areas and occipital crests also permit attachment of the large muscles needed to support the weight of the head on the neck (Raven, 1950; Dixson, 1981). The sagittal crest and large temporal muscles give the frontal section of the silverback's skull-cap a convex appearance, but it is a common misconception that the mitre-like crest rising at the rear of the head is also a part of this skelto-muscular structure (*see* Plate A7.3).

Plate A7.3 Side views of the silverback skull showing the sagittal crest and the position and height of the temporal muscles.



Redrawn from Raven (1950)

Rather, the domed appearance of the head is caused by a pad of fibrous, fatty tissue above the rear portion of the sagittal crest (Dixson, 1998), which begins to be noticeable in males at around 13 years, and is not fully formed until approximately 15-16 years (pers. obs.). This area is absent in adult females at Mbeli, although some individuals have a slight ridge visible. In many captive females however, large crests may be present, giving them a superficial resemblance to adult males; an observation that suggests that this area may be particularly susceptible to fat deposition in response to abundant and rich food (pers.obs.).

If it proves to be the case that large head-crests indicate high food intake in an individual, then the development of the feature as a permanent male indicator trait can be predicted to have followed a Fisherian self-reinforcing selection mechanism. If males with large head-crests have higher survival rates and longer reproductive tenures, and if the offspring of females with a genetic tendency to mate with such males have higher survival rates, then the seeds of an evolutionary feedback process can be discerned wherein females increasingly choose males with higher crests, and crest size becomes ever larger even if costs are incurred or the structure ceases to be a 'genuine' reflection of the original phylogenetic indicator trait. In addition to a feeding/health signal, the proximity of the head-crest to the sagittal crest and temporal muscles, may mean that a well-developed crest area could also advertise fighting prowess (biting is a ubiquitous feature of serious male-male aggression). Again, such display would serve to intimidate rival males, and advertise the male's ability to protect females from predators, and their offspring from infanticidal attacks from extra-group males. Fossey (1983, p55) notes that during inter-silverback displays, pilo-erection may occur on the crest, further exaggerating its size, while at Mbeli the crests of elderly silverbacks have been noted to appear somewhat 'deflated', both by atrophy of the temporal muscles and a reduction in the size of the head-crest. In western lowland gorillas, the whole front of a silverback's head, including the temporal area and the mitre is usually a rich chestnut colour, in contract to the rest of the body. Red hair continues over the top of the head-crest and extends somewhat onto the nape in most silverbacks, but no other areas show this coloration. A remnant and probably intensification of juvenile pelage, such coloration is likely to have become a distinct adult male trait under selection pressure for any feature that draws attention to and highlights the crest area.

It is suggested that if the top of the silverback's head does serve as an 'indicator' of general condition and/or fighting prowess, the most effective manner of displaying it is in side profile. The images in Plate A7.4 are not ideal in that they illustrate the crests of three different silverbacks, the centre one of which was only approximately 15 years old, however both left-hand and centre images show how a frontal view lacks depth, and fails to highlight the size of the head-crest. However the right-hand image, with the head in side profile, clearly shows the full size and conformation of the crest. It is suggested therefore that head-turning during agonistic interaction serves primarily to optimise the display the head-crest, both to intimidate rivals and occasionally group members, and to advertise to females of other units the potential to protect against predators and infanticidal extra-group males.

Plate A7.4 Head-crest perception from front and side elevation

Although lacking any crest development, immatures and adult females are likely to have learnt head-turning behaviour from observing interactions, much as chest-beats and other adult display forms are frequently used during play between immatures (adult females and immatures often chest-beat despite lacking the greatly enlarged laryngeal saccules that facilitate the resonant sound of the silverback chest-beat [Dixson, 1981]).

Areas for future research

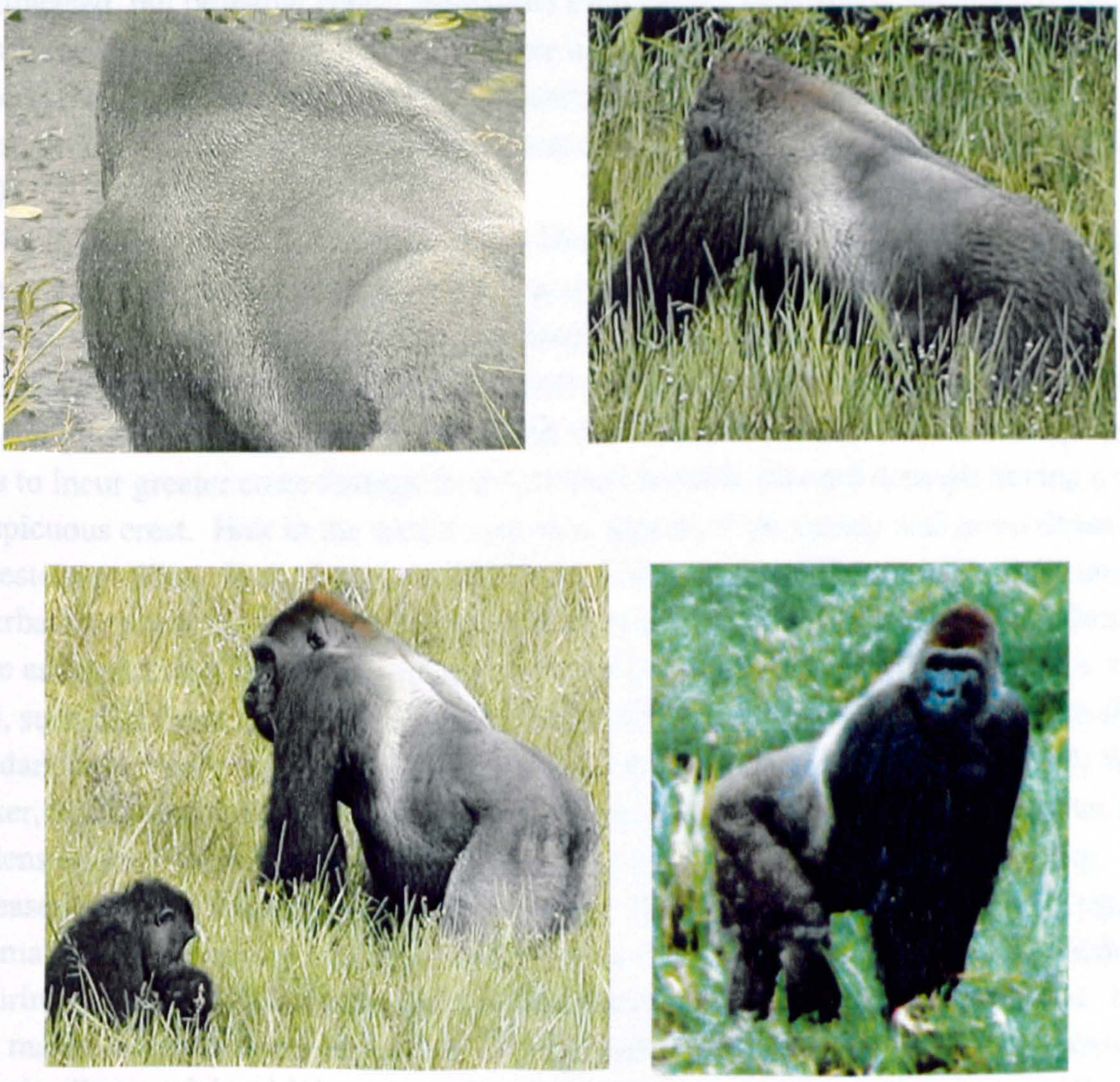
The role of the head-crest as a secondary sexual characteristic has not yet been investigated in a controlled, captive environment. It remains plausible that head-turning is a ritualised signal of gaze-aversion used to limit aggression. However, most other species noted to employ such behaviours lack any cranial specialisation analogous to the gorilla head-crest. A conspicuous exception is the crowned guenon (*Cercopithecus pogonias*), which sports a 'mohican-style' sagittal crest of black hair against a white crown. Tilting of the head and other lateral movements draw attention to the crown in this species, though Kingdon (1988) notes that presentation of the side profile corresponds with the 'cut-off' phase of a threat display sequence. As a means of testing for a socio-sexual signalling function for the crest, it would be of considerable interest to present digitally manipulated images of silverback gorilla crests to captive subjects. Both size and colour should be considered as variables to be examined, as should the visual plane (front view or side profile) displayed to subjects. Ideally, test presentation of altered images would be carried out to measure attention-span and gaze in both adult male and adult female subjects. Although care would be required to note the reproductive status of female subjects, such a test procedure could be carried out with a minimum of disruption in any facility where males can be temporarily separated from females. This said, any inhibitory effects of male or female presence on the behaviour of test subjects would also be of interest. Adult females would be predicted to pay more attention to males with larger and more brightly coloured crests, as might silverbacks, though potentially with very different reactions.

Other characteristics of body shape and pelage pertaining to social signalling

Many primate species combine secondary sexual coloration with ritualised movements to create distinctive visual displays (e.g., *Papio hamadryas ursinus,* van Hooff, 1969; *Cercopithecus aethiops* spp., Henzi, 1985; Gerald, 2001; *C. pogonias, C. neglectus*, and *C. cephus*, Kingdon, 1988). While postural modification (head-turning or head-flagging) combined with conspicuous coloration or markings may draw attention to the head region to facilitate social signalling in gorillas and other primate species, and colourful sexual skin or pelage draw attention to the genitalia, in some species similar patterns may draw attention to other parts of the body (Andersson, 1994, p345). The silverback gorilla may represent a striking example of the interplay of costs and benefits, not only of sexual dimorphism in size, but also in secondary sexual characteristics such as pelage. In the western lowland gorilla, the significance of the pelage has received surprisingly little comment. This may in part be due to the rarity of wild encounters of a kind permitting many silverbacks to be seen clearly over a short period, such that a less isolated view of specific traits can be perceived. At Mbeli, excellent observation conditions and the ability to record the physical characteristics of many individuals permits a re-evaluation of somewhat overlooked traits that may offer intriguing new avenues for future research. Descriptions of mountain gorillas usually identify two main features of the pelage: long black hair covering most of the body (except the chest and face), and in the silverback, much shorter, white/grey hair in the lower back 'saddle' region, sometimes extending over the thighs with advancing age (e.g., Schaller, 1963; Dixson, 1981). It is generally accepted that the longer, denser hair of the mountain gorilla in contrast to the western lowland species is an adaptation to a colder climate resulting from greater altitude (e.g., Schaller, 1963; Dixson, 1981). I have been unable to discover any systematic attempts to provide a thorough explanation for the function of the silver saddle in males, though it is often accepted that the coloration allows other gorillas to spot the male easily in the forest: males transformed, as Kingdon (1988, p231) suggests for other species "..into social beacons". While this function may be served, another is strongly suggested by observations at Mbeli. Plate 3.4 in Chapter 3, and Plate A7.5 clearly show the saddle region rendered dark grey or black when dry and viewed from the rear (Plate A7.5, bottom left) or from any angle when damp (top left and right). This is due to the black skin becoming more visible in certain light conditions or when the sparse, fine saddle hair is flattened against the skin.

While the saddle area in Mbeli silverbacks may be virtually hairless, it is notable, especially on the two right hand images, that a fringe of longer white hair remains highly visible, running from the nape, behind the shoulder and ending towards the lower abdomen. It is suggested that this fringe, whether backed up by a silver saddle or not, has resulted from sexual selection pressure to exaggerate the size of the arms and shoulders. In addition to the teeth, the arms represent the other major fighting 'weapons' at the male gorilla's disposal, and notably have the longest, darkest, and most dense hair on the gorilla's body: a feature that exaggerates their size, and may have a slight effect in reducing the depth of laceration or puncture injuries during fights. This dense, dark hair continues onto the torso behind the shoulder, such that the white fringe-hair creates a false outline, suggesting a much larger arm and shoulder than is actually present (*also see* Plate 2.8*h*, Chapter 2).

Plate A7.5 The effect of dampening or viewing from the rear on perception of saddle coloration



A behavioural correlate to the identification of this area as a secondary sexual display trait is the observation in mountain gorillas, at Mbeli, and at captive gorilla holding institutions that silverbacks primarily make sideways charges and characteristically stand side-on to their opponents during displays (Schaller, 1963, p235: pers. obs.). It is possible that the grey 'whiskers' frequently found below a silverback's ears may also have evolved in order to offer slightly improved definition to the line of the fore-shoulder.

If the white fringe of hair permanently visible in the western lowland silverback is effective in exaggerating the size and power of the arms and upper torso, why should the entire lower back be white as well. While it may serve as an effective 'beacon' to group members and potentially transferring females in the dark conditions of the forest floor, another issue may be of some relevance. It has already been noted that the longer, denser and darker black hair of the mountain gorilla is probably a response to the much cooler climate of the Virungas. In western lowland gorillas, hair appears to be finer, less dense, and generally shorter. Few changes occur in either pelage length, distribution or colour between the juvenile age-class and adulthood in females, suggesting that the coat type exhibited by these individuals is to some extent, optimal for homeostasis in individuals of this size under given environmental conditions. Not only are gorillas the largest living apes, but sexual dimorphism in body size is extreme, with silverbacks weighing twice as much as adult females. Reasons for such extreme dimorphism are complex and multifaceted, but probably centre around the influence of folivory on speeding female growth (and indirectly by reducing the value of female-female size differential due to reduced feeding competition), an early cessation of female growth, and prolonged maturation in males in response to sexual selection pressures (Leigh & Shea, 1995; Taylor, 1997).

In the Virungas, dense, dark hair is likely to be selected for its insulation properties in an environment where the temperature rarely rises above 20°C and occasionally nears freezing. Mountain gorillas, though occasionally showing a small degree of crown redness, lack the striking head-crest coloration of western lowland gorillas (as do eastern lowland gorillas), and it is possible that such hair types would reduce insulation properties so as to incur greater costs through heat-loss than benefits accrued through having a more conspicuous crest. Hair in the saddle area also appears to be thicker and more dense than in western gorillas. In the hot, humid habitat of the western lowland gorilla by contrast, silverbacks may actually incur costs from thick pelage as a result of heat stress. Being twice as large as the female, silverbacks will have a greatly reduced surface area to volume ratio, such that thermo-regulation may be more critical. Furthermore, studies have shown that dark coat colour may increase heat load in other species (Acharya et al., 1995; West & Packer, 2002), and the dense black hair of the arms and shoulders may place further heat burdens on the silverback. Heat stress can be deleterious in several ways including increases in sperm abnormality (West & Packer, 2002). West and Packer (2002) report that male lions (*Panthera leo*) have darker manes during cooler months and that males maturing during particularly hot months have shorter manes throughout their lives. Long, dark manes were shown to increase body temperature and incur costs from heat stress. Life-size lion models with longer, darker manes were avoided by other males, while models with shorter lighter manes were approached and attacked more, suggesting that mane colour and length provides information to other males regarding condition and fighting prowess (lions may lose their manes following injuries). Females, by contrast, approached dark-maned males more than light ones, implying that males able to withstand the extra stresses of carrying dark manes would be genetically of superior quality, and physically better able to protect cubs from infanticide resulting from take-over bids by other males.

It is hypothesised that the sparse, fine hair of the silverback's lower back area increases heat dissipation in an animal pushed toward the limits of homeostasis by extreme selection pressure for large body size and a pelage that further exaggerates strength and fighting ability. Future research should address how hair type and colour are influenced by endocrinological and other metabolic processes, and whether the fine white hair of the silverback is produced through something akin to a premature ageing process (remembering that this area turns red during early adolescence in many males). Is the white coloration of the male a characteristic first and foremost of a mechanism to regulate body temperature, or is social signalling its primary function? It would be of value to first measure heat-loss from different areas of silverback and adult female bodies in order to test the heat dissipation signatures of the saddle area and head. Hair from all areas of the body should be collected from captive silverbacks during routine annual health checks and measured for width, length, pigmentation, and type. Such a study may assist in describing the phylogenetic evolution an animal whose entire body, with the exception of the rump and legs, appears to encapsulate the extremes of primate male sexual selection together with some of the costs it incurs. Findings from such a study might also offer insights valuable to the debate regarding speciation and the current distribution of the genus.