This version of the thesis excludes 2 photographs of local people, since the author was unable to get their permission to make the photographs public.

Appendix 6 – Published material by the author

McLennan, M. (2010) *Chimpanzee ecology and interactions with people in an unprotected human-dominated landscape at Bulindi, Western Uganda.* PhD thesis. Oxford Brookes University.

Chimpanzee Ecology and Interactions with People in an Unprotected Human-Dominated Landscape at Bulindi, Western Uganda

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*

ABSTRACT

As humans continue to modify natural habitats in Africa, particularly outside of protected areas, the survival of many chimpanzee (*Pan troglodytes*) populations is dependant on their ability to adapt to human-dominated landscapes, and the willingness of local people to share their environment and resources with these large mammals. Unless hunted, chimpanzees may persist in anthropogenically-modified habitats including forest–farm mosaics, but competition and conflict can characterise their relationship with people. Conservation strategies are needed to facilitate successful coexistence. However, few studies have examined human–ape sympatry in detail. This thesis explores the ecological and behavioural adaptation of a previously unstudied chimpanzee community to an increasingly 'agriculturalised' landscape at Bulindi, Uganda. These chimpanzees live in exceptionally close proximity to farmers that exert unsustainable pressure on small unprotected forests. Research was conducted during 21 months between February 2006 and January 2008. Quantitative ecological methods were used to characterise the apes' habitat and measure seasonal food availability. Indirect methods (e.g. faecal analysis and nest mapping) were employed to investigate chimpanzee diet and range use, supplemented by opportunistic behavioural observations. Riverine forests at Bulindi are rich in chimpanzee foods, but are rapidly being destroyed by people. Important foods in the apes' diet include both wild and cultivated items; chimpanzees increased consumption of cultivars during the low forest fruiting season. Unique among studied populations in Uganda, Bulindi chimpanzees use tools to dig up subterranean bee nests for honey. Interviews were conducted to survey residents' attitudes towards chimpanzees and forests. Chimpanzee behaviour is widely perceived by residents to have undergone recent negative changes, including increased crop-raiding and ranging into village areas, which correspond to major land-use changes (i.e. commercial logging and agricultural intensification). Further, adult males exhibit frequent human-directed aggression, apparently in response to harassment and intensifying competition with humans. Most residents fear chimpanzees. Because of poverty, insecure land tenure, inadequate law and policy enforcement, and corruption, local people currently have little incentive to maintain forest on their land. The study concludes that, under present conditions, chimpanzees will not survive at Bulindi or in similar unprotected forest–farm landscapes regionally without immediate, effective intervention. Recommendations for the conservation and management of chimpanzees in human-dominated landscapes are provided.

To Dad

ACKNOWLEDGMENTS

Many people helped in a myriad of ways during fieldwork and in the preparation of this thesis, and it would be impossible to name them all but I'd like to thank the following in particular. First of all, thanks to my supervisor Kate Hill for encouraging me to do this research, for her advice, support, and wise words throughout, and for allowing me the freedom to do the study I wanted to do. I'd also like to acknowledge the enduring support of Simon Bearder and Anna Nekaris at Oxford Brookes who, along with Kate, gave me inspiration and confidence to pursue a PhD in the first place. My family have always been unfailing in their support and in encouraging me to follow my interests, even though it seemed I might forever be the eternal student. I'm sure Dad would have been proud to see this thesis completed.

I'm grateful to the Economic and Social Research Council and the National Environment Research Council for funding this PhD. A Leverhulme Trust to Kate Hill and Katherine Homewood helped with additional field costs. Permission to conduct my research in Uganda was granted by the President's Office, the Uganda National Council for Science and Technology, and the Uganda Wildlife Authority.

Research at Bulindi would have been impossible were it not for the enthusiasm, dedication, good humour and camaraderie of my research team: the late Dan Balemesa, Gerald Sunday Mayanda, Tom Sabiiti, Moses Ssemahunge and Jane Stokoe. I cannot emphasise enough how much this study benefitted from the insight and local knowledge of Dan, Gerald, Moses and Tom. We had countless truly memorable moments during fieldwork. I was extremely lucky to work with you. For assistance during a pilot study, I'm grateful to Issa Katwesige and Style Deogratius. Thanks to Karen Hiser for friendship and company over ice cold beers and Tilapia in Hoima's Millennium Hotel. And thanks to Dalson for cooking fantastic food; and to Paul, Robert, Medius, Teddy and Betty for being great neighbours.

The success of the project depended on the tolerance, assistance and participation of numerous residents of Bulindi Parish. Special thanks to Boniface Byakagaba, Jovan Kabuzi, Yosamu Gamusegere and Beatrice Kabangungu for help and friendship. Assistance in Hoima District was provided by many individuals and organisations,

particularly Joseline Nyangoma (the District Environment Officer), the District Chairman, the Kyabigambire Subcounty Chief and Chairman, and staff of the district offices of the Uganda Wildlife Authority, the National Forest Authority, and the District Forestry Services.

For support in Uganda I thank Fred Babweteera (Budongo Conservation Field Station), Mnason Tweheyo (Makerere University), Debby Cox (Jane Goodall Institute), Lilly Ajarova (Chimpanzee Sanctuary and Wildlife Conservation Trust) and Andy Plumptre (Wildlife Conservation Society). Fred Babweteera gave permission for me to visit the Sonso field site in the Budongo Forest. Meteorological records were generously provided by the Bulindi Agricultural Research and Development Centre; thanks in particular to Mr Tom Karwemera who collected the data. Plants were identified by Dr Paul Ssegawa, Ben Kirunda and Protase Rwaburindore at Makerere University Herbarium, and with assistance from David Goyder at the Royal Botanic Gardens, Kew. Insects were identified by Allan Lugoloobi at the National Agricultural Research Organisation, Kampala, and by Barry Bolton and David Notton at the Department of Entomology, The Natural History Museum, London. Access to Landsat imagery was kindly provided by Nadine Laporte of the Woods Hole Research Center's Africa Program (Protected Area Watch Project) and WCS-Kampala. Andy Plumptre generously allowed me to use his unpublished data on tree densities in Budongo.

Back in the UK, Nicola McHugh showed me how to create maps using ArcGIS; Wakefield Carter gave advice on PCA analysis; Andrew Lack and Giuseppe Donati offered insightful comments on Chapters 3 and 4, and Giuseppe helped with statistics; Anna Nekaris gave instructive comments on all chapters; and Stewart Thompson read the full final draft.

Lastly, studying chimpanzees at Bulindi provided some of the most exhilarating, nerve-wracking, fulfilling and poignant experiences of my life. The tolerance shown towards us by the adult males at the study's end was a great privilege, and remarkable given the chimpanzees' deteriorating relationship with people. Unfortunately the future for these amazing individuals is not bright, but I very much hope this study makes a positive contribution to conservation efforts at Bulindi and elsewhere in the region.

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LIST OF ABBREVIATIONS & ACRONYMS

ANOVA – Analysis of variance

BA – Basal area

CAR – Central African Republic

DBH – Diameter at breast height

DRC – Democratic Republic of Congo

FAI – Food (or Fruit) Availability Index

FAO – Food and Agriculture Organization of the United Nations

FR – Forest Reserve

GIS – Geographic Information System

GLFs – Green leaf fragments

GPS – Global Positioning System

IUCN – International Union for Conservation of Nature

IV – Independent variable

JGI – Jane Goodall Institute

MCP – Minimum convex polygon

MWLE – Ministry of Water, Lands and Environment

NFA – National Forestry Authority

NGO – Non-Governmental Organisation

NP – National Park

PCA – Principal component analysis

SD – Standard Deviation

SE – Standard Error

SPSS – Statistical Package for the Social Sciences

THV – Terrestrial herbaceous vegetation

UBOS – Uganda Bureau of Statistics

UWA – Uganda Wildlife Authority

WCS – Wildlife Conservation Society

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CHAPTER 1 – GENERAL INTRODUCTION

Chimpanzees (*Pan troglodytes*) are one of the world's most widely studied mammals. In habitats ranging from dense lowland rainforest to arid savanna-woodland, the species has been the focus of research projects in more than 15 countries across its range in tropical Africa. The setting for this research is a forest–farm mosaic in western Uganda, where a previously unstudied population of wild chimpanzees live amidst a human farming community. Why is it important to study chimpanzees in a human-dominated landscape? As with all great ape taxa, chimpanzees are classified as Endangered by the International Union for Conservation of Nature (IUCN) (Oates et al. 2008). In East, West and Central Africa chimpanzee populations are disappearing because of widespread habitat loss, commercial hunting and epidemic disease (Butynski 2001; Walsh et al. 2003; Caldecott and Miles 2005; Campbell et al. 2008; Greengrass 2009). Where they are not hunted for meat, human population growth, habitat fragmentation and forest clearance for agriculture has meant chimpanzees are coming into ever-closer contact with rural human communities (McLennan 2008; Hockings and Humle 2009; Plumptre et al. 2010). From a conservation perspective, this begs the question: is coexistence between chimpanzees and people in shared landscapes possible?

Until recently, great apes outside of protected areas or on the fringes of major habitats were often ignored by research and conservation. But since humans are an inescapable feature of many environments inhabited by great apes today, for example around the edges of parks and reserves (Reynolds 2005; Goldman et al. 2008), the importance of human-dominated landscapes for the survival of some populations is increasingly recognised.[1] Accordingly, the ecology and behaviour of apes and their relationship with people in shared habitats is gaining increased attention from fieldworkers (Yamakoshi 2005; Goldsmith et al. 2006; Hockings 2009). Chimpanzees seem able to adapt to anthropogenic landscapes such as forest–farm ecotones, abandoned settlements and secondary vegetation, particularly where human population densities are relatively low (Leciak et al. 2005; Duvall 2008a; Brugiere et al. 2009). But where people and

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[1] This introduction focuses on great apes, but this situation equally applies to other nonhuman primates (Isabirye-Basuta and Lwanga 2008; Lee 2010) and, indeed, to wildlife generally (e.g. Graham et al. 2009).

chimpanzees encounter one another frequently and utilise the same resources, competition and conflict are an inevitable outcome of this interaction (Reynolds et al. 2003; McLennan 2008; Hockings 2009). In common with a variety of nonhuman primates (hereafter 'primates') great apes have adapted to the 'agriculturalisation' of their habitats by incorporating human foods into their diets (Hill 2005). But crop-raiding is only one facet of human–great ape conflict. Apes are large-bodied, potentially very dangerous, and are often feared by local people (Madden 2006; Campbell-Smith et al. 2010; Hockings et al. 2010). This calls for urgent conservation strategies that reduce conflict and facilitate sustainable coexistence between people and apes (Hockings and Humle 2009).

1.1. Chimpanzees in Uganda

In Uganda, the eastern subspecies of chimpanzee (*P. t. schweinfurthii*) occurs in forests along the eastern edge of the Rift valley in the west and southwest of the country (Plumptre et al. 2003b).[2] (An exception is a small relic population in the north on the Sudanese border; Davenport et al. 2001). Chimpanzees have been well-studied in Uganda: research is ongoing at Kibale National Park (NP), Budongo Forest Reserve (FR) and, more recently, Toro-Semliki Wildlife Reserve, in mid-western Uganda (see Wrangham et al. 1996; Reynolds 2005; Hunt and McGrew 2002, respectively). Long-term studies have also been conducted in Kalinzu FR (Furuichi et al. 2001a) and Bwindi-Impenetrable NP (Stanford 2008), in the southwest of the country.

Habitat loss, degradation and fragmentation are the principle threats facing Uganda's chimpanzees (Plumptre et al. 2003b, 2010). The annual deforestation rate in Uganda is one of the highest in Africa (2.2% in 2000–2005; FAO 2007), and most chimpanzee habitat outside of main parks and reserves has been cleared for farming. But in some regions chimpanzees persist in small outlying forests, typically along watercourses, on private or communal land or in minor forest reserves (Reynolds et al. 2003; Isabirye-

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[2] Based on craniometric analysis, Groves (2005) proposed that eastern chimpanzees can be divided into two subspecies and that populations in Rwanda, Burundi, Tanzania and western Uganda should be reassigned to a new (fifth) subspecies *P. t. marungensis*. However, this nomenclature has yet to be widely accepted and I use the conventional name *P. t. schweinfurthii* to refer to Ugandan populations.

Basuta 2004; McLennan 2008).[3] It is here – outside the main gazetted areas – where most deforestation is currently taking place (MWLE 2002). In part, this reflects recent government initiatives to reduce rural poverty that promote cash cropping over subsistence farming.[4] But with 90% of Ugandans reliant on wood fuels as their primary energy source (MWLE 2002), fuelwood production – in particular charcoal manufacture – is also a major contributor to deforestation on unprotected land (Naughton-Treves et al. 2007). Thus, remaining chimpanzee habitat outside of major reserves and parks is severely threatened. Since primates are not traditionally eaten in Uganda, unlike in many West and Central African countries (Caldecott and Miles 2005), a situation has emerged where chimpanzees persist in shrinking forests surrounded by people and amid expanding agricultural land-use systems. It is against this backdrop that this study was conceived.

1.2. Study Aims

The aims of this research were both theoretical and applied. I wanted to (i) examine the ecological adaptation of chimpanzees to a dynamic, increasingly human-modified landscape and compare this with reports from other, less disturbed sites. This aspect of the research was conducted from the ‘perspective’ of the apes and is concerned with the behavioural and ecological plasticity of this species. At the same time, I followed previous studies of human–wildlife interactions by considering (ii) the attitudes of local people to living alongside these large mammals with an emphasis on perceived costs (e.g. Hill 2004; Chalise and Johnson 2005; Paterson 2005). In this respect, the research goes beyond most previous work by examining a potential conflict situation from ‘both sides of the coin’. Understanding the impact that humans and great apes can have on each other in shared environments is important for developing effective conservation and management strategies where conflict occurs. But such data can also be used to predict problems likely to arise at other sites where people–ape interactions are set to increase as a result of human activities, and thus to inform appropriate preventative measures.

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[3] The current or intended land use in many smaller forest reserves is industrial tree planting to meet future timber and fuelwood demands, mainly using fast-growing exotic species (e.g. *Pinus* and *Eucalyptus*). Note that these small ‘forest’ reserves comprise a range of vegetation types, which may or may not include tropical high forest (MWLE 2002).

[4] See, for example, the Plan for the Modernisation of Agriculture (MAAIF/MFPED 2000).

The study complements recent research at Bossou in Republic of Guinea, where chimpanzees and humans live in close proximity (Hockings 2009; Hockings et al. 2009, 2010). An important distinction between these studies is that, unlike at Bossou, this research was conducted in a region where local people do not revere apes as ancestors and where forests are privately-owned and wholly unprotected. As such, it is the first detailed ecological study of chimpanzees in a dynamic human-dominated landscape at the 'frontline' of agricultural expansion. A second difference is that whereas chimpanzees at Bossou have been studied for three decades (Sugiyama 2004), this research was conducted with unhabituated animals among a human population unused to research projects.

1.3. Thesis Structure

The following chapter (Chapter 2) provides a qualitative description of the study site at Bulindi, located in the Hoima District of western Uganda. Information about climate and the region's human population are also presented. Thereafter the thesis is divided into two main parts. Part one focuses on chimpanzee ecology, beginning with the results of a quantitative tree survey in forest fragments utilised by chimpanzees (Chapter 3). Since no previous research had been done at Bulindi it was important to characterise the chimpanzees' habitat in terms of forest structure, composition and plant resources available. The impact of recent human disturbance on these forests is also considered. Chapter 4 presents data on forest phenology at Bulindi and assesses seasonal patterns of food availability for chimpanzees. The following chapters (Chapters 5 and 6) describe the apes' dietary repertoire and examine feeding ecology in relation to food availability. Whereas Chapter 5 concentrates on plant foods, animal foods are the focus of Chapter 6. Home range size and seasonal patterns of ranging and grouping are the subjects of Chapter 7. Throughout these chapters the data are contextualised with reference to the chimpanzees' human-modified forest–farm environment, and there is a strong emphasis on inter-site comparisons.

Part two focuses on the relationship between humans and chimpanzees at Bulindi. In Chapter 8 the behavioural responses of chimpanzees during encounters with the research team are described and examined in the context of interactions between apes and local people. Chapter 9 presents the results of a survey of residents' attitudes towards chimpanzees. Local perceptions regarding the value of forests are also investigated, and socio-economic and political factors influencing accelerating rates of forest clearance in this region are discussed. The final chapter considers the conservation implications of the study findings. Recommendations for the conservation and management of chimpanzees at Bulindi, and elsewhere where humans and great apes share a landscape and resources, are provided.

1.4. Overview of Methods

The study was conducted over 21 months in February–July 2006 (pilot study) and October 2006–January 2008 (main study). Methods employed for each research component are outlined in detail in the relevant chapter. Here, I provide only a brief summary. Despite the study's atypical setting – small forest fragments in an agricultural landscape – I followed methods used to study great ape ecology in less disturbed habitats (e.g. Malenky et al. 1993; Tutin and Fernandez 1993a; White and Edwards 2000). Quantitative techniques were employed to survey vegetation and measure forest food availability. Chimpanzees at Bulindi were unhabituated and I therefore relied heavily on indirect methods to study diet (primarily faecal analysis) and range use (e.g. locations of night nests). No systematic attempt was made to habituate chimpanzees because of the very close proximity between the apes and local people. Nevertheless, behavioural data were collected *ad libitum* during opportunistic or chance encounters with the apes. I used a geographic information system (ArcGIS) to map the study site and analyse chimpanzee home range and ranging patterns. Garmin Map 76 and Magellan Meridian Platinum global positioning system (GPS) receivers were used in the field to record locations of interest (e.g. nests, dungs, sightings). Residents' perceptions and experiences of chimpanzees, and their use of forests, were explored through interviews. The research attracted considerable attention locally, thus informal discussion with villagers was a daily aspect of fieldwork, providing valuable supporting information. I also draw upon qualitative observations when discussing land-use patterns and human–chimpanzee interactions. The study had full ethical approval of Oxford Brookes University Research Ethics Committee.

Field Assistance

A pilot study was carried out with the assistance of a Ugandan forestry graduate and a former forest surveyor. For the main study, the research team included myself, a second forestry graduate, native to Hoima District, a female European volunteer, and three local men (subsistence farmers). It was appropriate to employ men from villages associated with particular forests to assist during initial vegetation surveys. The three men subsequently trained as full-time field assistants demonstrated a particular interest in the chimpanzees and an aptitude and enthusiasm for the research.

CHAPTER 2 – STUDY SITE:
BULINDI IN HOIMA DISTRICT

2.1. Hoima District

The location of this study is Hoima District in the Bunyoro Kingdom in mid-western Uganda. The northern part of the district lies between two major forest blocks separated by approximately 50 km: Bugoma Forest Reserve (FR) in the south and Budongo FR in the north, in neighbouring Masindi District (Figure 2.1). The intervening region is settled and cultivated, but small forests occur patchily along watercourses. Hoima District was identified in an unpublished report by the Jane Goodall Institute and Uganda Wildlife Authority as a region of growing conflict between chimpanzees and local farming communities (JGI/UWA 2002), making it an ideal setting for this study. According to this report, which investigated conflict at several localities, fragmentation and clearance of unprotected forests for agriculture and timber has created a problem of crop-raiding by chimpanzees, particularly with regards to cash crops such as cocoa (*Theobroma cacao*). As a result, local intolerance towards chimpanzees was reportedly increasing (JGI/UWA 2002).

While Budongo Forest has a long history of chimpanzee research (Reynolds and Reynolds 1965; Reynolds 2005), the status and distribution of chimpanzees south of Budongo in northern Hoima District was poorly known prior to this study.[1] Nevertheless, the presence of chimpanzees at several localities was confirmed in the JGI/UWA (2002) report. This part of Hoima has considerable conservation value, for it falls within a proposed biodiversity 'corridor' linking main forests in western Uganda via smaller FRs and riverine forests (Plumptre et al. 2010).

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[1] Forest patches in northern Hoima were not surveyed in the nationwide chimpanzee survey conducted in 1999–2002. Based on density estimates for larger outliers around Bugoma, an overall population of ~70 individuals was estimated for the region separating Budongo and Bugoma (Plumptre et al. 2003b).

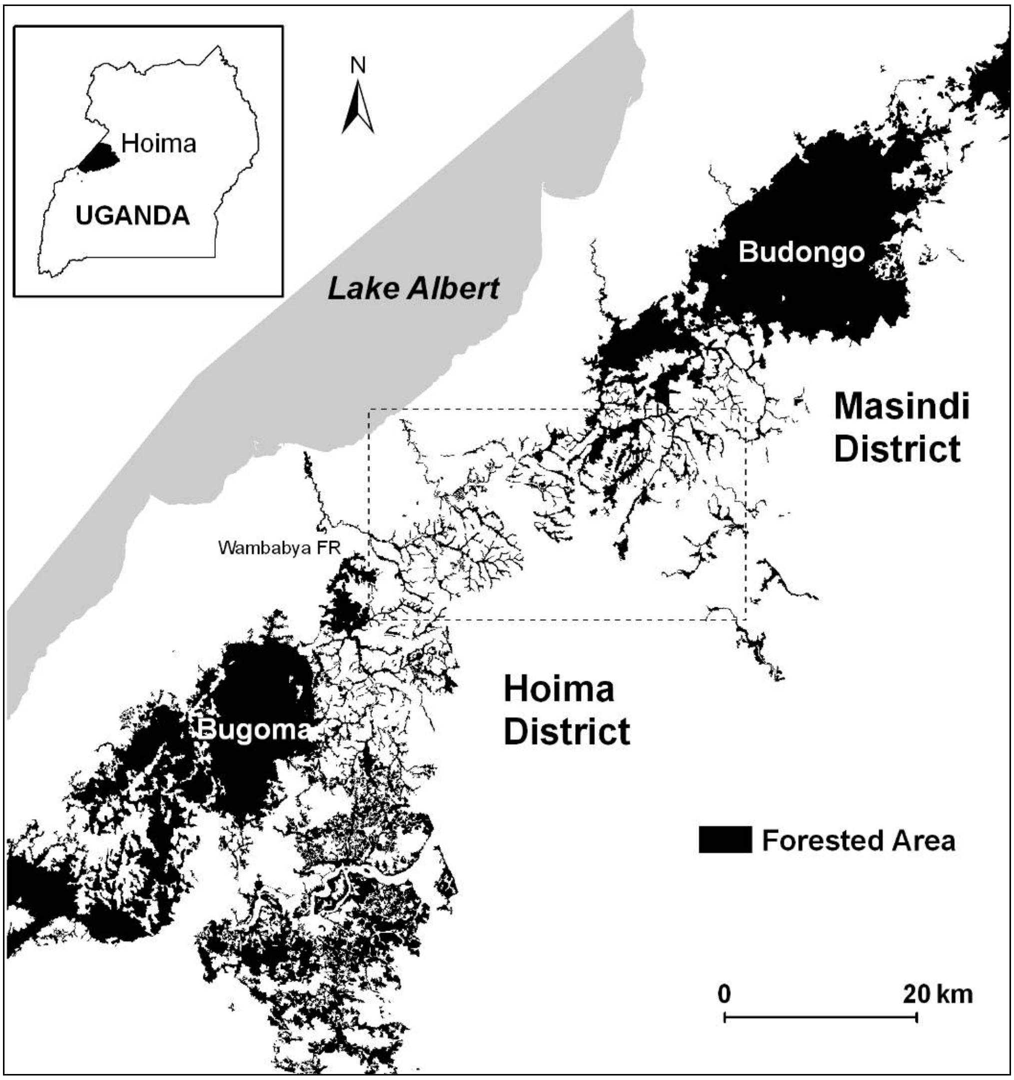

Figure 2.1. Map showing main forest blocks in the Bunyoro Kingdom of western Uganda: Bugoma (in Hoima District) and Budongo (in Masindi District). The dashed rectangle indicates the part of northern Hoima surveyed for chimpanzees for this study.

Geographical Description

Hoima District is bounded by Masindi District in the north, Kiboga District in the east, and Kibale and Bundibugyo districts in the south. To the west, it is flanked by Lake Albert, across which lies the Democratic Republic of Congo. At an elevation of 620 m the lake is virtually the lowest and hottest area in Uganda (*Atlas of Uganda* 1967). East of the lake, the topography in northern Hoima and neighbouring Masindi District is weathered and undulating, characterised by broad hills and valleys. Elevations average 1100 m above sea level but reach 1400 m on hilltops. Most of Hoima's tropical high forest occurs in the south and southwest, in Bugoma and its outliers. The small forests in the northern half of the district occur mainly in swampy valleys along the Waki, Wambabya and Hoima rivers and their tributaries flowing west to Lake Albert, and along tributaries of River Kafu, which flows east to join the Nile. For details of the geology, soils and drainage of the region see *Atlas of Uganda* (1967), Groves (1934) and Eggeling (1947). Meteorological data and a description of the vegetation at the study site at Bulindi are presented below.

Hoima's Human Population

In 2002 human population density in the district was 95.4 people per km^2 (UBOS 2007). Over 90% of the population live in rural areas, of which 74% depend on subsistence agriculture for their livelihoods. The dominant language is Lunyoro, the traditional Banyoro dialect, but migration to the district has meant a variety of tribal languages are encountered; English is also widely spoken. While only 11% of the population had completed primary school in 2002, the literacy rate was 67% (UBOS 2007).

2.1.1. Chimpanzee Status Survey

During February–May 2006 field surveys were undertaken in Hoima to obtain information on chimpanzee distribution and to identify a suitable site for research. Surveys focused on the northern half of the district, spanning the region northeast of Wambabya FR, a major outlier of Bugoma, across to the east and northeast up to the district border with Masindi (Figure 2.1). The survey area covered 400 km^2 between 1°26'–1°37'N and 31°09'–31°32'E. Within this region, forests were identified using 1:50,000 topographic maps published by the Department of Land and Surveys in 1966, and with assistance from local government forestry personnel. Surveyed forests occurred within small government reserves as well as on private and customary land,[2] and ranged in size from less than ten hectares to several square kilometres.

At each locality the following information was sought from local people, including pitsawyers and distillers encountered inside the forest: a) chimpanzee presence/absence, b) frequency of sightings and/or calls (i.e., regular, seasonal or infrequent), c) most

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[2] Customary tenure is a traditional system whereby land is controlled by clans who allocate plots to members; once settled and cultivated the land is inherited patrilineally. It is the most prevalent land tenure system in Uganda (Place and Otsuka 2000).

recent sightings/vocalisations, d) numbers seen, and e) chimpanzee movements (for example, if chimpanzees are transient visitors, from which direction(s) do they travel to and from?). Forests were searched opportunistically for evidence of chimpanzees, especially nests. Understorey vegetation in many forest patches was dense, but no transects were cut. Observations were made on the size and status of forested areas, and local opinions about chimpanzees were noted.

The results of this survey are reported elsewhere (McLennan 2008; Appendix 6). In brief, the presence of chimpanzees was demonstrated across the surveyed area, including six localities where the apes were resident (i.e. seen regularly and throughout the year). At least five separate groups (known as 'communities') are believed to occupy the survey area. The findings suggest that chimpanzees are more numerous and more widely distributed between Budongo and Bugoma than previously recognised (Plumptre et al. 2003b). However, evident during surveys was the extent of recent, ongoing and seemingly unregulated forest clearance across northern Hoima. Chimpanzees were widely reported to eat agricultural foods, particularly cocoa, sugarcane (*Saccharum officinarum*) and mango (*Mangifera indica*). Several recent instances of chimpanzees attacking people were also reported. Some local people claimed chimpanzees had been killed, or caught in steel traps set to deter crop-raiding animals.

2.2. Study Site – Bulindi

Further to providing new data on the status and distribution of chimpanzees in this region of Uganda, surveys allowed assessment of the suitability of particular localities as a research site for the main study. Bulindi was chosen because it met the following criteria: (1) forests comprised multiple fragments (or 'patches') on non-government land; (2) chimpanzees were reportedly present year-round, suggesting these forests were habitually used by at least one community of chimpanzees; in addition, Bulindi was one of only three sites where chimpanzees were observed during surveys, and was also where the largest group of fresh nests was found; (3) the habitat matrix was a mosaic of farm and forest; (4) chimpanzees reportedly raided crops; and (5) the site was readily accessible, located 12 km from Hoima town on the main Hoima–Masindi road.

Prior to this study, no research focusing on wildlife or forests, either by nationals or non-nationals, had been conducted in the Bulindi area. However, previous exploratory visits to Bulindi were made by staff from government and non-government organisations in response to reports of conflict between people and chimpanzees (JGI/UWA 2002).

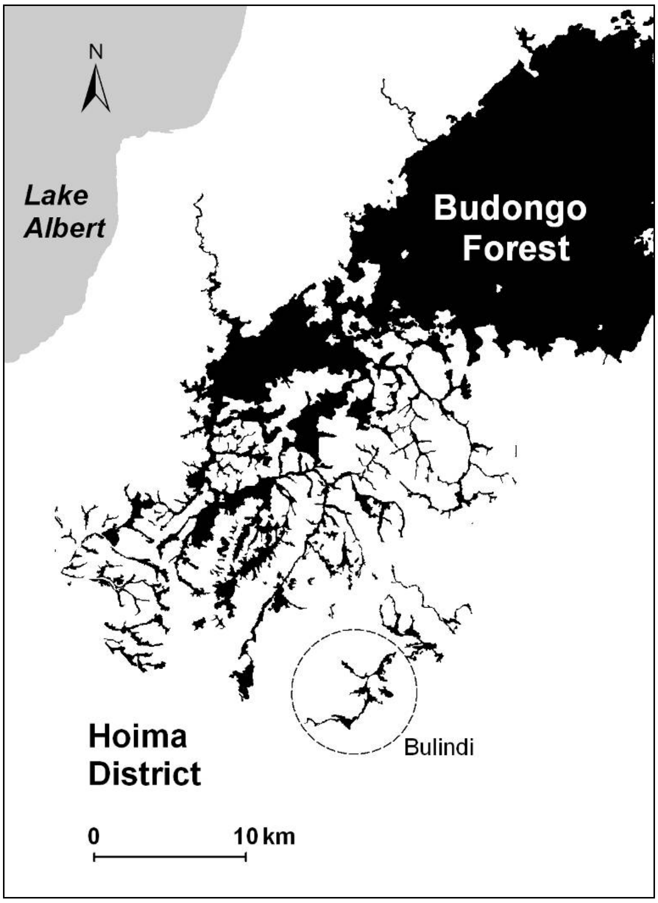

Figure 2.2. Map showing the main Budongo Forest block and outlying riverine forests to the south and southwest. The study site at Bulindi in Hoima District is encircled.

2.2.1. The Physical Landscape at Bulindi

Bulindi is located in the northeast corner of Hoima District, in Kyabigambire Sub-county, close to the border with Masindi District (Figure 2.2). Situated between the region's main forests, it lies 25 km south of the southernmost fringe of Budongo and 45 km northeast of Bugoma. The study area is approximately 40 km^2, situated between

1°27′–1°30′ N and 31°26′–31°30′ E. The name ‘Bulindi’, used here with reference to the research site and its chimpanzees, is that of the parish – an administrative division above village but below Sub-county level – to which most villages in the study area belong. Bulindi is also the name of the parish main trading centre.

Climate

The climate of Hoima District varies from hot and dry in the Western Rift Valley to a more moderate temperature and rainfall pattern further east above the escarpment. Situated 30 km east of Lake Albert, Bulindi falls within this latter region. Meteorological data for the study area are available for the period 2001–7 from the Bulindi Agricultural Research & Development Centre (under the management of the National Agricultural Research Organisation), located 2 km east of the study area. Data were collected by the same staff member throughout the seven years. Mean annual precipitation was 1461 mm (range: 1319–1636 mm), indicating Bulindi is somewhat drier than nearby Budongo Forest where annual rainfall averages 1600 mm (Reynolds 2005). Though rain falls throughout the year at Bulindi – the region experiences no truly dry months – its distribution follows a typical East African bimodal pattern (Conway et al. 2005) with wetter months (mean rainfall >100 mm) occurring during March–May and July–November (Figure 2.3). In general, rainfall is higher during the second rainy season. A 3-month main dry season (mean rainfall <50 mm per month) occurs between December–February, during which many trees shed their leaves, and a second, transient dry period is apparent in June (<100 mm rain).[3] Some inter-annual variation is also apparent. In particular, the rainfall distribution in 2007 – when most project data were collected – diverged somewhat from the pattern observed in 2001–6. For example, April was relatively dry and June relatively wet (Figure 2.4). Additionally, annual rainfall at Bulindi in 2007 was moderately less than in the previous six years (mean in 2001–6: 1484.9 mm; 2007 = 1319.4 mm). In contrast, unusually heavy rainfall occurred elsewhere in Uganda and other parts of East Africa leading to widespread flooding. Regional weather patterns during 2007 may have been affected by the occurrence of La Niña (*New Vision* 2007), a less frequent counterpart to El Niño characterised by a cooling of sea surface temperatures of the eastern tropical Pacific. Marked inter-annual variability in rainfall patterns is not unusual in the region (Conway et al. 2005). For

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[3] Thus, according to definitions in Richards (1996), Bulindi experiences four dry months per year (<100 mm rainfall), including three successive ‘drought months’ (<50 mm rainfall).

example, long-term records from Kibale National Park (140 km south of Bulindi) demonstrate considerable monthly and annual variation in precipitation, attributable in some years to the effects of El Niño (Struhsaker 1997).

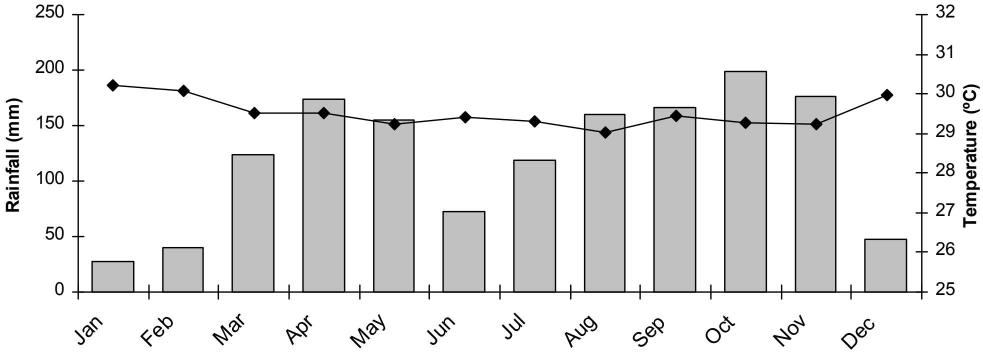

Figure 2.3. Mean monthly rainfall (bars) and mean monthly maximum temperature (line) at Bulindi, 2001–7. Minimum temperature data were unavailable.

Mean monthly maximum (shade) temperature was 29.5°C, remaining fairly constant year-round. Highest temperatures occur in the dry months of December–February (Figure 2.3). Although minimum temperature data were unavailable, night-time temperatures are markedly cooler than during the day-time. The monthly mean minimum temperature 25 km north at Budongo was 20.9°C (1993–2001; Tweheyo et al. 2005).

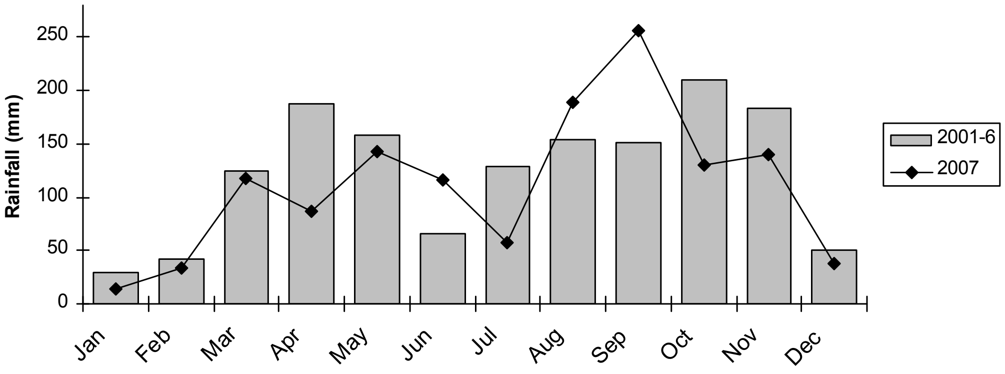

Figure 2.4. Monthly rainfall (mm) during 2007 (line) plotted against mean monthly rainfall in 2001–6 (grey bars).

Topography and Vegetation

The topography at Bulindi is undulating as is typical of the region (*Atlas of Uganda* 1967). The study site is bound to the east and southeast by a crescent shaped ridge of rocky hills that rise to 1400 m in elevation. These hills form part of the 26 km^2 Kandanda–Ngobya FR, a wooded grassland reserved by the National Forest Authority (NFA) for future industrial production of pine (*Pinus* spp.). Smaller hills occur to the north. The resulting watersheds drain into small permanent watercourses and papyrus (*Cyperus papyrus*) swamps in the valley bottoms, around which riverine forests occur at elevations of 1100–1150 m (Plate 1). For much of the year the rivers and streams at Bulindi are shallow and less than 5 m wide, though after heavy rain they become deeper and wider, flooding areas of swampy forest.

Broadly speaking, the vegetation of the study area is a mosaic of riverine forest, wooded grassland, and papyrus swamp, intermixed with cultivated fields and bush fallow. Vegetation surveys were conducted in main forest patches to reveal the composition and densities of tree species in the chimpanzees' habitat. Characteristic species in the riverine forests are the date palm *Phoenix reclinata* and the trees *Trilepisium madagascariensis* and *Antiaris toxicaria* (Moraceae). The results of tree surveys are presented in detail in the following chapter.

Ground vegetation in riverine forest is dense, dominated by herbaceous shrubs in the families Zingiberaceae (e.g. *Aframomum* spp.), Marantaceae (*Marantochloa leucantha*), Commelinaceae (e.g. *Palisota schweinfurthii* and *Pollia condensate*), Tiliaceae (*Triumfetta* spp.) and Euphorbiaceae (*Acalypha* spp.). The spreading shrub *Alchornea cordifolia* forms dense tangles around swamps and streams. On drier ground along forest margins stands of elephant grass (*Pennisetum purpureum*) and *Acanthus pubescens* occur. At the time of the study, forest vegetation at Bulindi was undergoing rapid alteration and reduction, a consequence of intensive timber harvesting coupled with agricultural expansion. Gaps created by logging are invaded by a dense cover of climbers (e.g. *Momordica foetida*). In heavily disturbed areas the invasive shrub *Lantana camara* forms impenetrable thickets. Consequently, visibility at ground-level rarely exceeds 5 m in forest.

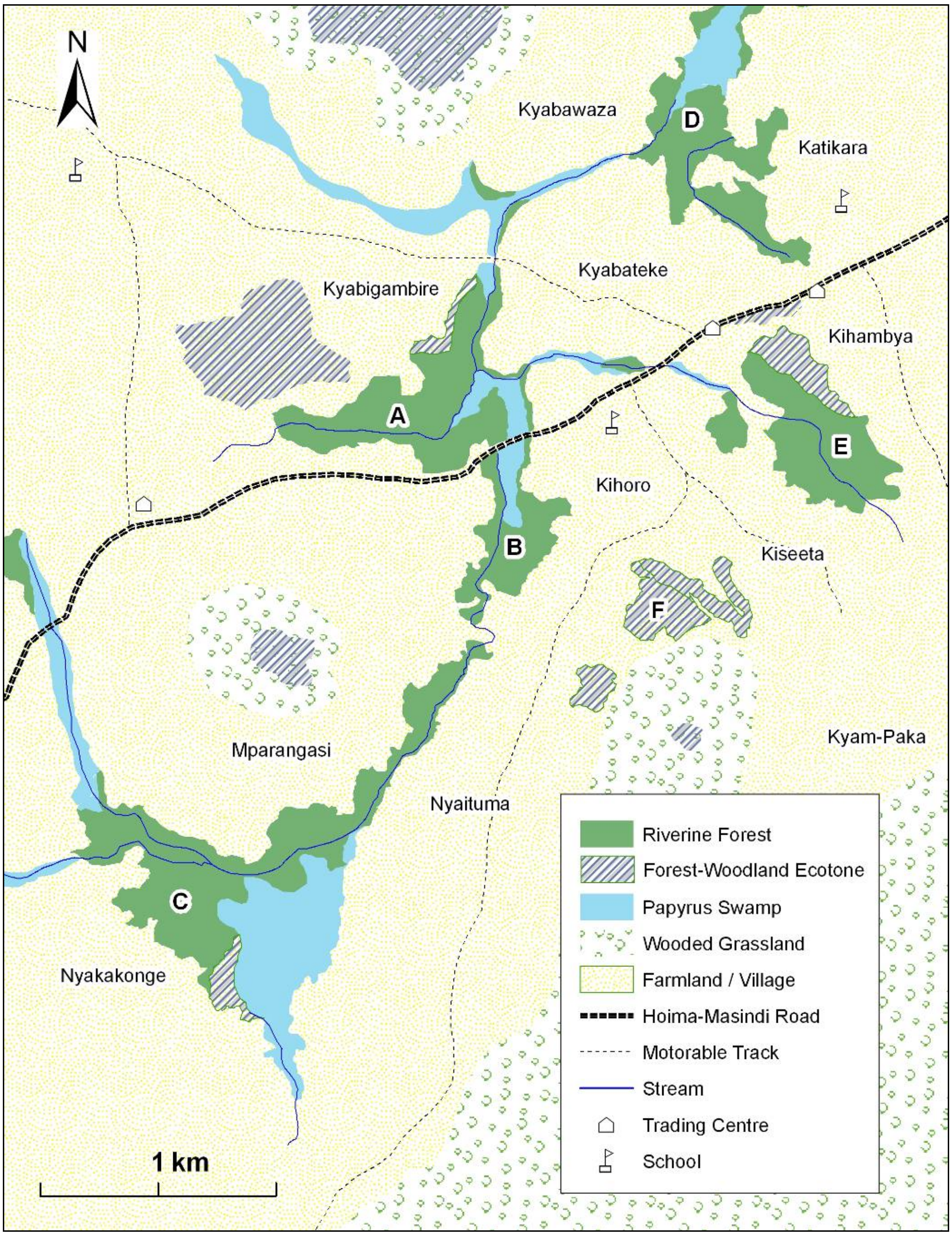

Figure 2.5. Map of study area at Bulindi showing forest patches and the locations of 11 villages. The main forests used by chimpanzees are indicated by capitalised letters: A = Kyamalera, B = Kyamusoga, C = Mparangasi–Nyakakonge, D = Kaawango, E = Kiseeta, F = Katigiro. The surrounding matrix is dominated by farmland and village areas but wooded grassland occurs on hillsides to the east and southeast in Kandanda–Ngobya Central Forest Reserve. The chimpanzees occasionally range outside of the area shown into the hills of Kandanda–Ngobya.

Wooded grassland characterises the vegetation on hill slopes, including much of Kandanda–Ngobya FR in the east of the study site. While systematic sampling was not conducted, trees commonly encountered in this habitat are *Combretum* spp., *Terminalia* sp., *Erythrina abyssinica*, *Albizia* spp., *Annona senegalensis* and *Vitex doniana*. Grass of the genus *Hyparrhenia* is typically associated with such a community (Langdale-Brown et al. 1964). Grassland at Bulindi is heavily grazed and subject to burning in drier months. Consequently, this broad vegetation type may represent a fire-climax community (Ibid.). Dense formations comprising a mixture of savanna-woodland and forest tree species occur patchily on lower slopes (1150–1200 m elevation), and sometimes at the drier edges of riverine forest, where expansion is restricted by cultivation and burning. Such 'ecotone' forest–thickets also occur in steep hill-side valleys at elevations of up to 1350 m. Around the valley swamps and forests, and on lower hill slopes, the matrix is dominated by cultivated (or abandoned) gardens, with scattered homesteads and, occasionally, small stands of exotic pine or eucalyptus (*Eucalyptus* spp.) trees.

Figure 2.5 shows a map of the study area at Bulindi. The site is intersected by the main Hoima–Masindi road, along which several trading centres are situated, as well as numerous tracks and footpaths. There are 11 permanent villages situated around main forest patches. Other village areas include schools and churches.

Forest Patches at Bulindi

The research revealed that Bulindi is home to a single community of ≥25 chimpanzees that range within the vicinity of the 11 villages. Details regarding the composition of this community are given in Chapter 8. During the study the chimpanzees' utilised five main riverine forests. These are 'Kyamalera', 'Kyamusoga', 'Kiseeta', 'Kaawango' and 'Mparangasi–Nyakakonge' (Figure 2.5). Note that while some of these names are used locally with reference to a *portion* of a particular forest (e.g. the part associated with a particular village or a particular well), local people do not generally refer by name to forest patches in their entirety. Forests on opposite sides of a stream or swamp are usually regarded as distinct, even if they comprise a continuous stretch of vegetation. Likewise a 'forest' can locally refer to the part growing on a particular individual's land. For research purposes entire forest patches – those with boundaries that could be clearly defined – were regarded as primary habitat units, accepting that discrete vegetation types within these forests may be more important to the chimpanzees themselves. Even so, in the case of Mparangasi–Nyakakonge it was useful to distinguish two parts to the forest for some analyses. This forest comprises a 2 km stretch of gallery forest bordering Mparangasi village, which opens out in the southwest of the study site to a wider area of dense swamp forest, bounded on one side by Nyakakonge village and on the other by an expanse of papyrus swamp (Figure 2.5). Where the two parts meet, the forest is permanently waterlogged and crisscrossed by a network of streams, making the Nyakakonge sector difficult to access from Mparangasi. Further, to access Nyakakonge forest from its village side required a detour of several kilometres. Consequently, data were collected less frequently in the Nyakakonge sector compared to Mparangasi and other main forest patches, even though Nyakakonge was much utilised by chimpanzees. Where appropriate, the two sectors – which together form a continuous forest patch – are differentiated.

Individual forest patches are small (≤50 ha). While it is apparent that considerable forest clearance at Bulindi has occurred recently, the historical extent of the forests is uncertain. Comparison of recent Landsat data in conjunction with GPS field data and a 1:50,000 Department of Land and Surveys map published in 1966 indicates that since that time perhaps 50% of the forest has been cleared for cultivation.[4] Nevertheless, local reports suggest that significant deforestation is a relatively new phenomenon (Chapter 9). Thus, at least in the recent past, the forests were probably restricted to the riverine valleys and were never especially extensive. Langdale-Brown et al. (1964: 42) note that true gallery forest is found in dry areas where it is confined to a river's banks and that "the intervening country, if protected from fire, would either remain savanna or develop into woodland, thicket or a drier type of forest". Although the Hoima region receives moderate rainfall, as shown above, it is unclear if forests at Bulindi – and throughout northern Hoima generally – would expand significantly away from the streams and swamps were it not for the activities of people.

With regards to the spatial arrangement of forest fragments, in the central and western half of the research area Kyamalera, Kyamusoga and Mparangasi–Nyakakonge form an arc of near-contiguous forest, broken only by short stretches (<100 m) of recently

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[4] Access to satellite imagery is courtesy of Nadine Laporte of the Woods Hole Research Center and WCS-Kampala.

cleared forest and, in the case of Kyamalera and Kyamusoga, by the 20 m wide Hoima–Masindi road (Figure 2.5). To the east, Kiseeta forest is isolated from its nearest neighbour Kaawango, in the northeast, by ~300 m that includes the Hoima–Masindi road and also the main Bulindi trading centre, thereby posing a particular challenge to chimpanzees crossing from one forest to the other. While Kiseeta and Kaawango are separated from other forests to the west by up to 650 m of farmland and homesteads, in the past they probably connected to Kyamalera via gallery forest along streams that still flow between patches. Little tree cover remains along these streams, which are today intersected by roads and tracks, though chimpanzees often follow these watercourses, taking advantage of the moderate cover when crossing between patches. Thus all riverine valley forests at Bulindi were probably formerly interconnected, with Kyamalera linking patches in the east with those in the west.

In addition to riverine forest the chimpanzees utilise small thickets on higher ground, transitional in floral composition between forest and woodland. Most noteworthy of these is 'Katigiro', an area comprising two such thickets 350 m east of Kyamusoga. The gently rising farmland separating Kyamusoga from Katigiro was cleared for cultivation only recently, as evidenced by the many tree stumps still visible (Plate 1).

Sympatric Primates

Chimpanzees at Bulindi are sympatric with four other species of diurnal primate, including one colobine and three cercopithecines: Black and white colobus (*Colobus guereza occidentalis*), tantalus monkey (*Chlorocebus tantalus budetti*),[5] blue monkey (*Cercopithecus mitis stuhlmanni*) and olive baboon (*Papio anubis*). In May 2007 the body of an adult male red-tailed monkey (*Cercopithecus ascanius schmidti*) was found in Kaawango forest. Local field assistants claimed this monkey had ranged alone for several years. While its death may represent the local extinction of this species in the Bulindi area, red-tail monkeys might conceivably occur in unexplored forest adjoining Kaawango in the northeast (Kyabatumbya and Katatahwa forests). An alternative explanation is that this individual was a released pet. The uncertainty surrounding red-tail monkeys notwithstanding, forests in the Bulindi area may thus support the full

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[5] These monkeys are commonly referred to as vervets. The 'true' vervet *Chlorocebus pygerythrus* only occurs in southwest Uganda. The two species are parapatric in Uganda and hybridise where their distributions converge (Groves 2006).

complement of diurnal primates found in this part of Uganda (Groves 2006).[6] The diversity of nocturnal primate species in the area is unknown; however, a dead galago (Galagidae) – almost certainly *Galagoides thomasi* (S. Bearder, pers. comm. 2010) – was seen in Kiseeta forest in 2006.

The local distributions of monkeys warrant mention. *Colobus guereza* are ubiquitous and resident in all riverine forests, and also occur in woodland thickets. Though considered savanna-dwelling monkeys (Kingdon and Gippoliti 2008), tantalus monkeys at Bulindi are commonly seen in forest. Perhaps 2–3 groups were present during the study; mobile, they travel between patches. Blue monkeys occur at very low densities and were only seen in Kaawango forest. The occurrence and distribution of baboons is especially noteworthy. Across the study area residents claimed that baboons are a recent arrival at Bulindi, apparently having migrated from the direction of Kyabatumbya and Katatahwa forests to the northeast of Kaawango, not long before this study's commencement (i.e. since 2000). If so, a possible explanation is displacement due to logging and forest clearance, and/or baboon hunts or 'drives' by farmers in those areas (e.g. in the Kinyara sugarcane outgrowing region in Masindi). One local man in his thirties, born in Mparangasi, said that he and his siblings grew up "not knowing what a baboon looked like." Nevertheless, an elderly man from Kiseeta claimed that when he came to Bulindi in the late 1920s there were many baboons; the Subcounty Chief subsequently embarked on a shooting campaign that eradicated baboons from the area. What is certain is that when I began work at Bulindi in May 2006 baboons were present in Kyamalera and Kaawango forests north of the Hoima–Masindi road. They began ranging into Kyamusoga and Mparangasi forests and as far south as Nyakakonge, for the first time in recent memory in mid-2007 (although they did not reach Kiseeta); local residents had previously claimed that the presence of chimpanzees kept baboons away from these forests. This influx of baboons caused widespread consternation, and in late 2007 village representatives were coordinating plans to hunt them from Bulindi. There were 1–2 troops ranging within the study area in 2006–8.

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[6] The gray-cheeked mangabey *Lophocebus albigena johnstoni*, common in Bugoma, does not occur in Budongo. It is not present at Bulindi and we did not see it in any northern Hoima forest during surveys; thus Bugoma and its outliers to the east – where it was seen – probably represent the northerly limit of the species in Uganda.

2.2.2. The Human Landscape at Bulindi

Demography

The human population of Bulindi parish in 2002 totalled 6394 (UBOS 2007), though the figure may have been closer to 8000 during the study period assuming an average annual growth rate equivalent to that of the District as a whole (4.7%). Average household size in Bulindi was 4.8 persons in 2002. The overwhelming majority of local residents are native Banyoro. Though relevant population statistics at the Parish-level are lacking, only 9 of 134 (6.7%) interviewed residents were from non-Banyoro tribes (see Chapter 9). For Hoima District as a whole, Banyoro comprised 60% of the population in 2002 (UBOS 2007). Evidently, Bulindi has not experienced the degree of immigration apparent in some other parts of Hoima and neighbouring Masindi District. For example, the human population around the southern edge of Budongo Forest is ethnically diverse – a consequence of repeated migrations of people escaping civil unrest in northern Uganda, eastern Congo and the Sudan (Marriott 1999; Paterson 2005), and by those seeking land or employment opportunities as provided by the Budongo sawmills during the 1950s and 1960s and, more recently, the Kinyara sugar estate (Reynolds 2005). In contrast, the only recent settlement by non-Banyoro at Bulindi is that of a small community of Alur from north-western Uganda. The Alur have settled and cultivated an area adjoining Kyam-Paka village, on the lower hill slopes of Kandanda–Ngobya in the far east of the study site. They appeared to occupy a marginal position in the wider community. Aside from the Alur, other notable non-Banyoro at Bulindi are migrant pitsawyers hired to cut timber in the forests. During the study these were mainly Bakiga men from southwest Uganda, who have a reputation as skilled and enthusiastic pitsawyers. Although these men were a permanent presence in forests throughout the research, they are transient workers without familial or land ties in the area. They build temporary camps inside the forest in the immediate vicinity of trees to be converted to timber, moving to other forests once the job is complete and/or all suitable trees are harvested (pers. obs.).

Agriculture

The majority of local people at Bulindi are smallholder farmers and agriculture is the main economic activity. Farming is generally accomplished by hand using hoes and *pangas* (machetes). Though many crops are grown for household consumption, surplus produce is sold at local markets and cash crops are also widely farmed. Considerable inter-annual and inter-household variation exists in crops grown but major food crops are maize, cassava, potato, beans, ground-nuts and millet. Other crops grown include peas, sorghum, cabbage, rice, pumpkin, tomato, onion, yams and sugarcane (pers. obs.). Banana and coffee – formerly important cash crops – are also farmed, but less intensively than in previous years; yields of both have declined as a result of bacterial wilt diseases currently affecting coffee and banana crops across Uganda (Tushemereirwe et al. 2006; Serani et al. 2007). Currently, the major cash crop grown at Bulindi is tobacco. Many farmers cleared forest during the study to maximise the area under production and to establish nurseries for seedlings alongside streams. A former cash crop, not currently harvested for market but deserving mention here, is cocoa. During the 1960s cocoa gardens (*shambas*) were planted within forests at Bulindi, as elsewhere in Hoima, but were abandoned when the cocoa market declined during the 1970s and 1980s (Kayobyo et al. 2001). Today, only a handful of households maintain *shambas* for household consumption, and these are outside the forest. With regard to livestock, few households can afford to keep cattle but chickens, pigs and to a lesser extent goats are common around homesteads. All households within the study area rely on locally gathered firewood for cooking and heat.

Hunting

Aside from diurnal primates, medium-sized mammals were rarely encountered. Local hunters confirm that most prey species (e.g. duiker, porcupine and bush pig) are nowadays scarce in forest, presumably as a consequence of habitat conversion and/or previous over-hunting. In Mparangasi–Nyakakonge the large holes of decades-old pit-traps were still evident. Apparently, these were intended to catch large antelope that formerly occurred in the area. Several local households engage in hunting and local men were periodically encountered hunting in forests; for example, on one occasion they caught a cane rat (*Thyronomys* sp.). Men from the Alur village hunt in the hills in and around Kandanda–Ngobya, where prey species are more common. The Banyoro do not traditionally eat primate meat and thus local hunters do not target chimpanzees. There was also no evidence that non-Banyoro hunters killed chimpanzees for meat during this study, though some hunting of apes reportedly occurs elsewhere in the region, both for meat and traditional medicine (McLennan 2008). Both groups of men hunt with nets and dogs, and no snares were seen in Bulindi forests. Thus the chimpanzees seem to be spared the snare-related injuries that afflict chimpanzees elsewhere in Uganda (Hashimoto 1999; Muller 2000; Reynolds 2005). Nevertheless, chimpanzees do occasionally get caught in large steel traps set to protect crops (Chapter 8). With regards to other primates, baboons and tantalus monkeys are classified as vermin and can legally be trapped or shot. Colobus monkeys are not classed as vermin but are also sometimes hunted or trapped. Besides humans, chimpanzees at Bulindi have no natural predators. Leopards occurred in the past – Kaawango broadly translates as 'place of leopards' – and are thus assumed to have been sympatric with chimpanzees.

Forest Ownership at Bulindi

While the home range of chimpanzees at Bulindi includes a variety of vegetation types, it is the low-lying forests growing around valley streams and swamps that constitute their core habitat, providing many of their most important foods and nesting sites (Chapter 7). These forest fragments are unprotected and privately owned, in most cases by households with land bordering the forest; land boundaries are often demarcated by the streams and swamps along which the forests occur. Generally, ownership is based on customary tenure and few households have formally registered land (or 'land titles'). Access rights to forests and forest resources is complex, but neighbours and kin are generally free to harvest firewood, forest foods, medicines, and so on (pers. obs.). More significant forms of extraction, such as harvesting small trees for fencing or building, timber cutting or charcoal burning, require permission from the owner. As such, forests at Bulindi are not 'open access', a characteristic commonly applied to customary-owned forests in Uganda (MWLE 2002). Even so, many owners evidently do not enter their forests regularly and extractive activities may occur in the absence of owner consent. For example, owners occasionally complained that poles were cut without permission or, more seriously, that pitsawyers harvested trees surreptitiously or in addition to those paid for.

Forest patches at Bulindi have multiple owners. Land boundaries divide a forest into portions of varying size, each belonging to a different individual or household. For example, Kiseeta forest (27 ha) has approximately 25 different owners, about half of which are former cocoa farmers who established small *shambas* in the forest in the 1960s. In contrast, Kyamalera (38 ha) has fewer than half that number of owners because the bulk of the forest is owned by a single family. Within a given forest, owners include some that are related (e.g. brothers), but many who are not, and owners on opposite sides of a forest typically live in different villages.

Permission to Work at Bulindi

Before fieldwork could begin at Bulindi, consent was required from local leaders. An introductory letter from the Subcounty Chief was delivered to the Chairman of each village (within the chimpanzees' known range at that time)[7] to whom I explained the nature of the research, its intention and duration. Permission to work in the area was granted in each case, and village meetings were arranged so that I could introduce myself to local residents and describe the research. In order to work in the forests, however, I also needed permission from individual forest owners.

Establishing number of owners per forest patch and determining which part belonged to which owner proved to be time-consuming and problematic. Partly, this was because local informants provided incomplete information on ownership, but confusion also arose because some individuals falsely claimed ownership or otherwise exaggerated the size of their section of forest. In addition, land boundaries inside forest were sometimes vaguely defined, and several owners were not resident at Bulindi. By the end of the 18-month study the matter of forest ownership had not been conclusively resolved, and 'new' owners continued to emerge throughout the research. Thus the precise number of individual forest owners within the range of the Bulindi chimpanzees is unknown, but the figure certainly exceeds 50. Although no forest owner refused permission for the study to be conducted on their land, some residents were uneasy about the research and suspicious of its purpose. This issue is returned to in Chapter 9.

Summary

1. A field survey was made in northern Hoima District to gain information on chimpanzee distribution in small forest fragments south of the Budongo Forest, and to identify a suitable site for this study.

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[7] As the study progressed introductions were subsequently made with Chairmen of additional villages, as improved knowledge of chimpanzees' ranging necessitated extension of the area covered by research activities.

2. The chosen site, Bulindi, is a mosaic of small riverine forests, papyrus swamps and wooded grassland, intermixed with farmland and villages. Agriculture is the main economic activity of local residents.
3. Forests at Bulindi occur on private land and are unprotected. Land boundaries divide forests into multiple portions; numerous local households claim ownership of parts of forest utilised by chimpanzees.

CHAPTER 3 – THE FOREST TREE COMMUNITY AT BULINDI: STRUCTURE, DIVERSITY, COMPOSITION & DISTURBANCE

3.1. Introduction

The Bunyoro forests are located in the north of the Albertine Rift, a belt of diverse habitats stretching from above Lake Albert to the southernmost point of Lake Tanganyika on either side of the rift valley (Plumptre et al. 2003a, 2007). The ecological diversity of the Albertine Rift reflects its complex topography and altitudinal range (from ~600 m at the base of the rift valley to 5100 m on the highest peaks of Uganda's Rwenzori Mountains), and its location as a meeting point for East African savanna and West African rainforest communities. Consequently, the vegetation of the Rift forms an overlap zone for a number of distinct floras (or phytochoria; White 1983), and exhibits relatively high plant species richness and endemism (Plumptre et al. 2003a, 2007).

Ugandan forests can be divided into highland and lowland types, with the transition occurring between ~1500–2000 m (Hamilton 1974). The main forests in Bunyoro – Budongo and Bugoma – are of the lowland variety (Eggeling 1947), but are classified as medium-altitude forests (Langdale-Brown et al. 1964). In compositional terms, the lowland forests of western Uganda are drier, floristically impoverished outliers of the main Guineo–Congolean rainforest phytochorion (Hamilton 1974; White 1983; Poulsen et al. 2005). Even so, Budongo Forest has the most recorded tree species of 22 sites surveyed within the Albertine Rift (Plumptre et al. 2003a, 2007). The flora and ecology of Budongo is well documented (Eggeling 1947; Synnott 1985; Howard 1991; Lwanga 1996a; Plumptre 1996; Nangendo et al. 2006). Bugoma has been the focus of fewer studies but seems to support a less diverse flora (Howard 1991; Lwanga 1996b; Plumptre et al. 2003a). Both forests fall within the *Cynometra–Celtis* forest zone that borders the rift valley (Langdale-Brown et al. 1964; Hamilton 1974). For Budongo, Eggeling (1947) identified four forest types: he proposed that three (colonising, mixed and *Cynometra*-dominated forest) belong to a single sere, with *Cynometra* forest representing the climax stage. The fourth type, swamp forest, is an edaphic climax but is relatively unimportant in terms of area, accounting for just 2% of forest (Eggeling

1947). More recently, Plumptre (1996) showed that mixed forest in Budongo has increased at the expense of *Cynometra* forest following selective logging, mainly of mahoganies (Meliaceae), and arboricide treatment of non-marketable ‘weed’ species (including *Cynometra*).

These studies at Budongo, and to a lesser extent Bugoma, provide important data on structure, composition and ecology of forests in this part of western Uganda. But comparable data for riverine forests that occur throughout the intervening region in northern Hoima, including at Bulindi, are not available. For wide-ranging mammals such as chimpanzees, these outlying patches constitute a much smaller area of forest available for foraging relative to main forest blocks. Since the riverine forests are principally edaphic formations, associated with permanent swamps and riverine valleys, they are expected to differ floristically too. Intensive use of small unprotected or poorly managed forests by people may also exert a major influence on forest structure and species composition (Wilder et al. 1998; Moinde-Fockler et al. 2007; Turyahabwe et al. 2008), with important implications for chimpanzees and other animals (e.g. through its influence on density, abundance and availability of foods). As a result of habitat differences, chimpanzee ecology at Bulindi may diverge considerably from that of populations inhabiting nearby forest blocks, such as Budongo.

A necessary first step in any ecologically-oriented study is to gain an understanding of the plant resources available within the study animals’ habitat. A main objective of the ecological aspect of this research was to quantify wild food availability in forest fragments (Chapter 4) and relate the temporal–spatial distribution of forest foods to chimpanzee diet (Chapter 5), and ranging patterns (Chapter 7). Accordingly, the first component of research at Bulindi sought to:

1. Inventory tree species in forest fragments utilised by chimpanzees.
2. Characterise the forest habitat in terms of physiognomic forest types, structure, diversity (species richness), species densities and dominance.
3. Assess the impact of human disturbance in forests through analysis of the size, density and species of trees harvested, with particular focus on commercial timber extraction.

3.2. Methods

3.2.1. Sampling Trees

Systematic methods for sampling vegetation in studies of African ape ecology vary considerably among sites and studies, depending on factors that include: research objectives; size of area to be sampled; time and resources available for vegetation sampling; existence of previous surveys conducted in the area (and their scope and methods); as well as habitat and topographic variables. A common method is to cut long narrow 'belt' transects, typically several kilometres in length and perpendicular to drainage lines in order to pass through a variety of vegetation types. Trees occurring within a specified distance (e.g. 5–10 m) on either side of the transect line, and above a specified diameter at breast height (DBH) (usually ≥10 cm), are measured and identified (e.g. Hashimoto et al. 1999; Anderson et al. 2002; Hohmann et al. 2006; Yamagiwa and Basabose 2006a). Since apes have large home ranges (Chapter 7), belt transects – essentially, long thin vegetation plots – are useful because they enable rapid sampling across a wide expanse of habitat (White and Edwards 2000). In some studies a series of shorter transects are used, sometimes within an existing trail grid system (e.g. Chapman et al. 1997). In others, the sampling area comprises multiple plots (or 'quadrats') spaced uniformly or randomly along transects (e.g. Boubli et al. 2004; Nkurunungi et al. 2004; Moscovice et al. 2007).

Accelerating forest fragmentation in the tropics has led to increased interest in the conservation value of fragmented landscapes for wildlife (Bierregaard et al. 1992; Marsh 2003; Anderson et al. 2007; Chapman et al. 2007; Boyle and Smith 2010). Studies of habitat type and quality for primates inhabiting small fragments (i.e. ≤100 ha) involve modifications to survey methods appropriate for larger expanses of forest. For example, short (≤100 m) belt transects running perpendicular from the river to the forest edge were used to sample trees in riverine patches along the Tana River, Kenya (Mbora and Meikle 2004). Onderdonk and Chapman (2000) assessed tree composition in patches around Kibale NP along 50 m transects placed in areas considered representative of each patch. A subsequent study of the same patches involved total counts of all trees >10 cm DBH (Chapman et al. 2007). At Bossou, Republic of Guinea, belt transects were used to survey vegetation in three hill forests utilised by chimpanzees (Hockings 2007). For this study, establishment of plots placed randomly along a network of transects was considered the most appropriate method for sampling trees in forest patches at Bulindi, for reasons outlined below. Complete enumeration of trees was not feasible at Bulindi where patches are larger (averaging 25 ha) than those in the Kibale study (<10 ha in all but one case), though smaller than at Bossou (≤100 ha).

In addition to their use in vegetation surveys, transects at Bulindi were intended to facilitate rapid straight line travel through patches (i.e. for phenological sampling) and provide access to areas with near-impenetrable undergrowth such as dense *Lantana camara* thickets and vine tangles. Prior to cutting transects, the perimeters of forest patches were traversed on foot utilising the track function of a handheld GPS to map the shape of a patch and calculate its area. Following mapping, 'baseline' transects were cut, oriented to run the furthest distance possible within each patch (range: 175–835 m). In most instances two baselines were cut due to the fragment's irregular shape. In addition, transects were positioned to avoid swamps, small cultivated gardens within forest, and areas of regular human activity such as forest wells and distilleries (small-scale enterprises for distilling alcohol, situated on stream banks to facilitate the distilling process; Plate 2). The positions of transect lines are shown in Figure 3.1. Since riverine forests at Bulindi are confined to areas either side of waterbodies, baseline transects tended to run parallel to streams or swamp edges. However, tree species composition changes along a gradient from swampy valley centres to better drained soils at forest edges. Furthermore, small forest patches of irregular shape, such as those at Bulindi, have a low area to perimeter ratio (i.e. a high proportion of forest edge). Thus if sampling was restricted to either side of baseline transects (i.e. the belt transect method), edge habitat would be underrepresented. To circumvent this problem shorter 'secondary' transects were placed at 100 m intervals perpendicular to baselines, on alternate sides where possible and running to the forest edge (Figure 3.1). Vegetation plots were then established randomly along both baseline and secondary transects, ensuring that different vegetation types were adequately sampled. The main drawback to this method was the additional time required to cut secondary transects and position the many plots.

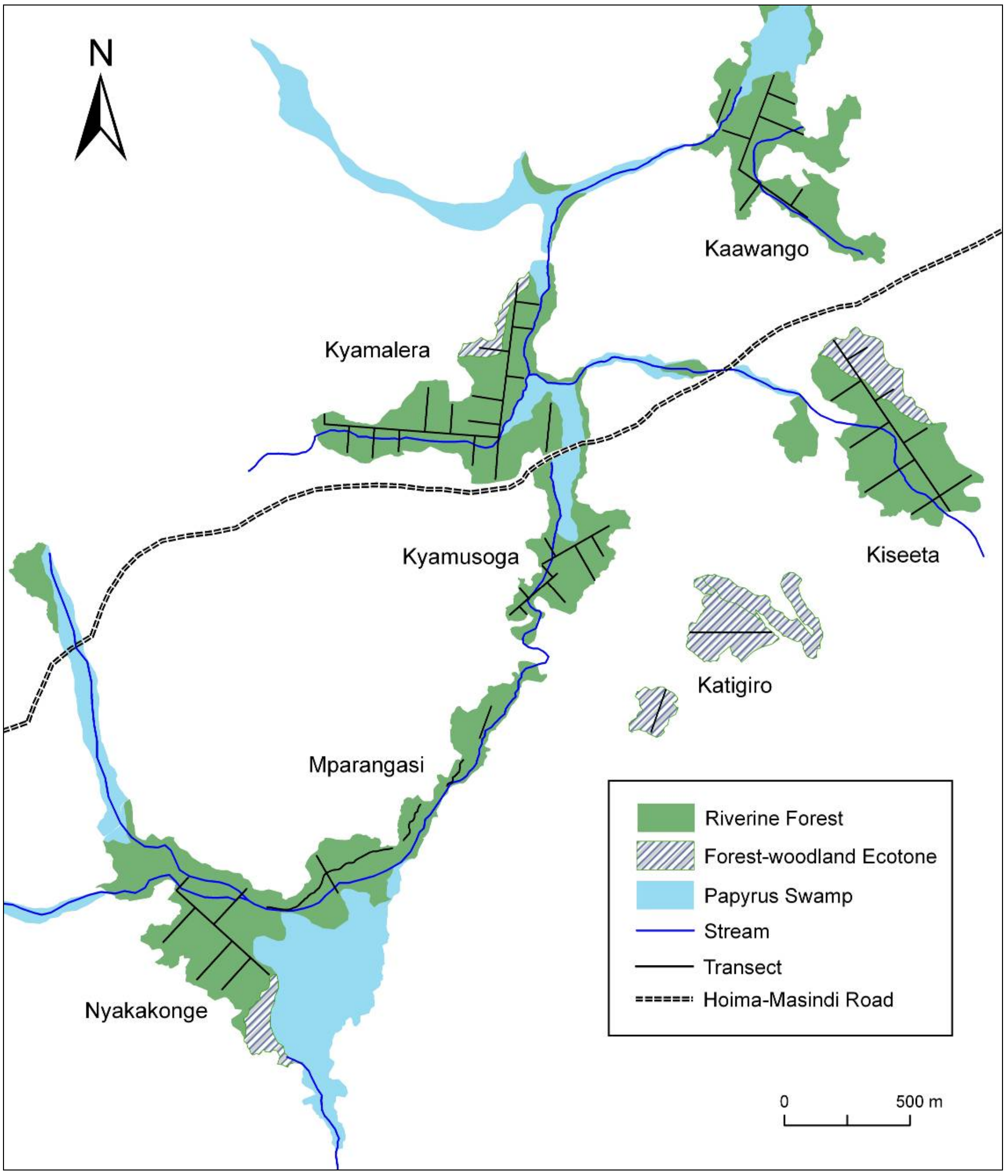

Figure 3.1. Map showing position of transects in main forest fragments at Bulindi in relation to major drainage features. Kyamalera, Kaawango, Kyamusoga, Kiseeta and Mparangasi–Nyakakonge are low-lying riverine forests, whereas Katigiro is a forest–woodland ecotone on well-drained soil. Mparangasi–Nyakakonge comprises two sectors: gallery forest (Mparangasi) and waterlogged swamp forest (Nyakakonge). The non-linear transect lines in the Mparangasi sector are existing trails.

Table 3.1. Forest fragment characteristics, sampling effort and proportion of sample plots in different forest types in five riverine fragments and a hillside forest–thicket at Bulindi. Forest types: Swamp (Swp), Mixed (Mix), Cocoa (Co) and Ecotone (Eco).

Forest Fragment	**Fragment Type**	**Elevation (m)** [1]	**Area (ha)** [2]	**Transect Length (m)**	**No. Plots**	**Sample Area (ha)**	**% Plots in Each Forest Type** [3]			
							Swp	**Mix**	**Co**	**Eco**
Kyamalera	Riverine	1129	37.8*	2620	47	0.94	36%	60%	2%	2%
Kyamusoga	Riverine	1131	16.3*	960	21	0.42	43%	33%	24%	0%
Kiseeta	Riverine	1156	26.6	1775	32	0.64	6%	34%	34%	25%
Kaawango	Riverine	1123	24.1*	1340	28	0.56	32%	64%	0%	4%
Mparangasi–Nyakakonge	Riverine	1135	49.9	2305	47	0.94	54%	43%	0%	2%
(Mparangasi sector)		–	–	(1135)	(25)	(0.50)	(28%)	(68%)	(0%)	(4%)
(Nyakakonge sector)		–	–	(1170)	(22)	(0.44)	(86%)	(14%)	(0%)	(0%)
Katigiro	Hillside	1171	–	475	10	0.20	0%	0%	0%	100%
(Patch #1)		–	11.5	(300)	(6)	(0.12)	–	–	–	–
(Patch #2)		–	2.6	(175)	(4)	(0.08)	–	–	–	–
Total:	–	–	168.8	9475	185	3.70	33.7%	45.7%	9.2%	11.4%

[1] Elevation is calculated as the mean elevation of GPS track points generated from mapping forest perimeters;

[2] Area estimates for patches marked with an asterisk include small areas of papyrus swamp. The Kiseeta area estimate excludes an adjoining 2.8 ha patch, not included in the vegetation survey;

[3] For some forest fragments combined percentages do not equal 100% due to rounding.

Transects followed a fixed compass bearing; a series of poles arranged in a straight line helped maintain precision. Care was taken to cut as little vegetation as possible to minimise forest disturbance, and beginning and end points were concealed to discourage use by local people. (This measure was largely in vain, however, because parts of some transects became widely used by people collecting firewood or cutting poles, or by hunters and pitsawyers). Table 3.1 provides information on the characteristics of forest fragments included in the tree survey in terms of elevation, area, and proportion of plots assigned to different physiognomic forest types (see below), together with details of sampling effort. These forests were the main forest patches utilised by chimpanzees during the research period. The combined area of these forests, which include five riverine forests and an area of hillside forest–thicket, is 169 ha (= 1.7 km^2). Total transect length equalled 9475 m, of which 895 m comprised sections of an existing trail that ran parallel to a stream in narrow gallery forest at Mparangasi. This trail was used habitually by chimpanzees travelling between Nyakakonge and all other main forest patches, but pole cutters, hunters and pitsawyers also utilised it. Given the importance of this ‘corridor’ for the chimpanzees it was thought that to cut new transects would cause unnecessary disturbance to this already-degraded thin stretch of forest. Existing trails have also been employed as vegetation transects elsewhere (e.g. at Bwindi; Stanford 2008).

Flagging tape was used to mark distance along transects at 25 m intervals and plot corners were marked with red paint to aid relocation. I chose rectangular plots measuring 10 x 20 m (200 m^2 = 0.02 ha). Rectangular plots are generally recommended over square plots (Ganzhorn 2003). For example, they have been shown to capture more species relative to square plots of similar area (Laurance et al. 1998). Nevertheless, the selected plot size is relatively small for sampling tropical forest trees, though unavoidable since larger plots (e.g. 20 x 50 m), if established randomly along transects, would frequently have extended into cultivated areas or papyrus swamp, or across busy foot paths. As such, the plot size used was appropriate for sampling homogenous vegetation units in small disturbed forests of highly irregular shape.

One hundred and eighty-five plots were established, equivalent to one plot per 51 m of transect (Table 3.1). The total area sampled thus measured 3.70 ha (= 2% of the combined area of the sampled fragments). Plot position along transects was determined away from the field by randomly drawing numbers with the provision that a minimum of 10 m separate neighbouring plots; a toss of a coin decided on which side of the transect a plot was established. Within each plot, all trees ≥10 cm DBH (recorded at a height of 1.3 m) were measured, identified and enumerated with aluminium tags to aid relocation. Lianas were not recorded. For buttressed trees DBH was measured immediately above the buttresses where possible; for very large trees with tall buttresses DBH was estimated to the nearest 5 cm. In the case of strangling figs, the measure was taken around the central root structure, avoiding outlying roots that would erroneously inflate the DBH value. In recently logged forest the boles of small trees were sometimes broken by felled timber trees, but if such a tree was alive (i.e. coppicing) and its DBH measurable at 1.3 m, it was recorded. Tree height was measured using a rangefinder and clinometer.

Tree surveys were initiated in Kyamalera forest in June 2006. Following a 2-month hiatus, surveys were conducted between October 2006 and May 2007 in Kyamusoga, Kiseeta, Mparangasi, Nyakakonge and Kaawango forests. In mid-2007 three short additional transects were cut in Kyamalera, Kyamusoga and Kaawango in habitat judged to have been underrepresented in the original sampling effort (i.e. in cocoa forest at Kyamusoga, and in *Macaranga* swamp forest in Kyamalera and Kaawango). In January 2008, the final month of research, additional sampling was conducted in two small patches of hillside ecotone forest at Katigiro after chimpanzees shifted their foraging activity to this area in December 2007. Smaller areas of ecotone habitat were also sampled at the edges of riverine fragments.

Tree species were initially identified in the field with the assistance of an experienced forester and with reference to field guides (Eggeling and Dale 1951; Hamilton 1991; Katende et al. 1995). Voucher specimens were collected for reference and identifications were confirmed by botanists at Makerere University’s herbarium. Several specimens were identified at Kew Gardens Herbarium in April 2008.

Measuring Disturbance – Cut Stumps

At the time of vegetation surveys Bulindi forests were being heavily logged for marketable timber, a process beginning several years before this study. Trees are converted to timber either with handsaws (i.e. pitsawing) or by freehand milling using a chainsaw (or 'power saw') (Plate 3). In addition, local residents cut understorey or immature trees and saplings for construction and other purposes. In order to assess levels of disturbance and gain information on species, sizes and densities of trees harvested for timber, transects were walked in the five riverine forests in July–August 2007, and data were collected on stumps encountered within 5 m either side of the line. The length of transects walked was 7390 metres,[1] giving a sample area of 7.39 ha. Only stumps ≥10 cm DBH were recorded. Because trees are typically cut below the height that DBH is measured (1.3 m), it was not possible to precisely measure DBH in most cases. Therefore DBH was estimated to the nearest 1 cm (for small trees; 10–20 cm), 5 cm (medium-sized trees; 21–50 cm) or 10 cm (large trees; >50 cm), by examining the stump and, in the case of sawn specimens, leftover logs. Data were collected by the author and an experienced field assistant, both of whom had measured hundreds of stems during tree surveys and were thus familiar with diameter sizes. The estimated DBH of cut trees are therefore assumed to be accurate to within 1–10 cm, depending on tree size.

3.2.2. Data Analysis

Tree Species Richness

To evaluate the efficiency of the sampling effort for describing tree species richness (alpha diversity), and thus the potential range of resources available to chimpanzees at Bulindi, the freeware application *EstimateS* (Version 8; Colwell 2006) was used to generate species accumulation curves. Species accumulation curves plot the rate at which new species are found within a habitat or area as a function of sampling effort (Gotelli and Colwell 2001; Colwell et al. 2004).[2] When successive samples (i.e. vegetation plots) are pooled the species accumulation curve is rarely smooth due to spatial patchiness in species distribution. *EstimateS* smoothes the curve by computing expected species richness with 95% confidence intervals at different subsets from the pooled full sample, a method known as sample-based rarefaction (see Colwell et al.

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[1] The length of transects sampled represented 82% of the original transects established in riverine forests. Some sections of older lines were no longer open due to understorey regeneration.

[2] Where effort is measured in area, as here, such graphs are commonly referred to as species–area curves. Strictly speaking, however, the latter curves plot number of species in areas of different size and thus depict beta not alpha diversity (e.g. Gray et al. 2004).

2004). For comparison, a classic non-randomised curve based on the sequential order of plots was also calculated.

While the ability of the species accumulation curve to reach an asymptote is an indicator of sampling adequacy (Gotelli and Colwell 2001), in practice it is almost never possible to capture all species in a given habitat by sampling; thus true species richness will be underestimated. A number of richness estimator tests have been developed to predict total species richness from sample data. Of these, non-parametric estimators are advantageous since they require no assumptions regarding community structure (Chiarucci et al. 2003; Williams et al. 2007). I used the non-parametric Chao 2 and second-order Jackknife estimators to predict total tree species richness at Bulindi because both were shown to perform well in efficiency tests (Colwell and Coddington 1994; Chiarucci et al. 2003). For a comprehensive explanation of these estimators with relevant equations, see Colwell and Coddington (1994). Both estimators take into account the number of species of the total sample that occur in one plot only, and the number occurring in exactly two plots (Colwell and Coddington 1994). Reported values are the mean of 100 estimates based on 100 randomisations of the sample accumulation order, as computed by *EstimateS*.

Forest Structure and Taxonomic Composition

Structural composition of the forest tree community at Bulindi is shown by plotting the distribution of diameter and tree height classes, with data from all forests pooled. Taxonomic composition was quantified at family and species level, following Mori and Boom (1987) and Kessler et al. (2005). For each species and family the total number of stems, stems per hectare (ha $^{-1}$) and basal area (BA) ha $^{-}$ 1 were calculated.[3] Based on these totals the following values were calculated for family: *relative diversity* (the % species per family of the total number of species); *relative density* (the % stems per family of the total number of stems ha $^{-1}$); and *relative dominance* (the % BA per family of the total BA ha $^{-1}$). For species, the same values were generated except *relative frequency* replaces relative diversity. The relative frequency is the number of plots in which each species occurred as a % of the sum of occurrences of all species. Following Mori and Boom (1987), *Importance Values* (IV) for each species were

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[3] Basal area refers to the cross-sectional area of a tree trunk at breast height (1.3 m), here given in square metres.

calculated by summing the relative frequency (i.e. how often a species was encountered throughout the forest), relative density (its abundance) and relative dominance (an indicator of the relative size of individual stems), as a measure of the overall ecological importance of each species in the community. A *Family Importance Value* (FIV) was similarly calculated for each family except relative diversity substitutes for relative frequency.

Forest Types

While this study aimed to quantify tree structure and composition in forest fragments, qualitative characterisations of forest type are also useful and widely used in the literature (White and Edwards 2000). The small forests at Bulindi share a common flora comprising mainly riverine and swamp species. Nevertheless, four physiognomic forest types are recognisable:

1. *Swamp forest* – seasonally inundated or permanently waterlogged forest growing around papyrus swamps or alongside low-lying streams, dominated by aggregations of *Phoenix reclinata* palms. Stands of the understorey trees *Macaranga schweinfurthii* and *Neoboutonia melleri* are also common. *Pseudospondias microcarpa* is the most abundant large buttressed tree.
2. *Mixed forest* – this forest type grades from swamp forest where the ground rises away from low-lying streams and swamp. No single species dominates the stand but common medium to large trees are *Trilepisium madagascariensis*, *Antiaris toxicaria* and *Funtumia africana*. *Teclea nobilis* is a common understorey tree.
3. *Cocoa forest* – forest associated with abandoned cocoa *shambas* in both mixed and swamp forest.[4] When the *shambas* were established in the 1960s–1970s understorey vegetation was cleared but large trees were left standing for shade. Although long abandoned, the trees continue to produce pods and, today, cocoa (*Theobroma cacao*) remains the dominant understorey tree. Cocoa forest is an artificial variant of swamp and mixed forest.
4. *Ecotone Forest* – regenerating or colonising forest on well drained soil, comprising a mixture of savanna-woodland (e.g. *Combretum* spp., *Allophylus*

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[4] Forest *shambas* are here distinguished from cocoa gardens established outside of forest which typically utilise artificially planted shade trees.

spp.), forest (e.g. *Antiaris toxicaria*, *Trichilia* spp.) and pioneer species (e.g. *Albizia* spp. and *Margaritaria discoidea*). The canopy is closed but large, tall stems are scarce.

Whereas forest types 1–3 are confined to low-lying riverine forest, ecotone forest occurs along forest margins, where it grades from mixed forest, as well as on lower hill slopes – unsuitable for agriculture – where it forms dense thickets. Thus swamp, mixed and ecotone forest occur along an environmental gradient from swampy bottomland valleys to better drained soils at higher elevations (Plate 4).

Spatial variation in the distribution of forest types is expected to influence the foraging and ranging ecology of chimpanzees (Chapter 7). Individual plots were assigned to one of the four forest types according to species composition. An ordination method, principal components analysis (PCA), was performed to examine variation among plots with respect to species composition and abundance. PCA is used to reduce redundancy in complex multivariate datasets by transforming ecological variables into a smaller number of variables (principal components), which account for most of the variance in the data (McGarigal et al. 2000). The technique has been used in studies of great ape habitats to assess distinctiveness of habitat types, aid in the interpretation of habitat use, and facilitate construction of vegetation maps (Hashimoto et al. 1999; Boubli et al. 2004). The ten most common tree species, each with a density of >10 stems ha $^{-1}$, were selected as variables. The analysis was conducted on the square root transformation of the abundance of each species in 160 plots. Only plots assigned to the three riverine forest types (swamp, mixed and cocoa forest) were included because these common species were poorly represented in ecotone plots, which were confined to higher, drier ground and comprised a mix of forest, forest pioneer and grassland species; three riverine plots containing none of the selected species were also excluded. Swamp, mixed and cocoa forest types grade into one another over short spatial scales, owing to micro-variation in drainage conditions and the clumped distribution of cocoa *shambas*. Consequently, these forest types exhibit considerable homogeneity in tree species composition. PCA is a useful tool for assessing and depicting graphically the extent of ecological distinctiveness in closely related communities (McGarigal et al. 2000). Only principal components with eigenvalues greater than one were extracted, because these components explained a greater proportion of the variation in the data than expected by chance. Interpretation of the components was enhanced by employing the varimax rotation method, which increases the distinction between significant loading and non-loading original variables (i.e. tree species) on each component (Ibid.). For each component extracted, a one-way ANOVA was conducted to test for differences in mean component score of plots assigned to the three forest types, in order to assess the meaningfulness of this classification. Post-hoc comparisons were made with Newman–Keuls tests, calculated using the harmonic mean for unequal samples (Field 2005).

Forest types were compared in terms of structure (average DBH, stem density, BA ha $^{-1}$ and tree height), species richness and diversity. In the case of structural variables, nonparametric Kruskal–Wallis one-way ANOVAs were used because data were not normally distributed. For each variable tested, data were drawn from individual plots grouped by forest type. To compare species richness among forest types species accumulation (rarefaction) curves were generated, as described above, accept these were based on number of individuals sampled instead of plots to account for differences in tree density (Gotelli and Colwell 2001). Species diversity among forest types was assessed via the Shannon diversity index (H'), calculated from the equation:

$$H' = -\sum_{i=1}^{n} pi \ln pi$$

where p_i is the proportion of the sample that belongs to the ith species (Stiling 1999). The index takes into account the number of species (i.e. richness) and the evenness of species (i.e. the extent to which species are present in equal numbers in each forest type). A greater number of species and a more even distribution increase the diversity value (Stiling 1999).

Comparison of Forest Fragments

Because spatial variability in resources may be important for chimpanzees, I assessed compositional similarity between forest fragments (beta diversity) using the modified Morisita–Horn index (Wolda 1981). Unlike many other similarity indices Morisita–Horn is insensitive to unequal sample sizes, and uses information about the relative abundance of individuals of each species in addition to species composition when comparing assemblages. However, since it is very sensitive to changes in abundance of the most common species (Wolda 1981; Magurran 2004), abundance data were first square-root transformed (following Bonaldo et al. 2007). The index (MH) is calculated from the equation:

$$MH = 2 \sum (an_i \text{ x } bn_i) / (\mathrm{d}a + \mathrm{d}b) aN \text{ x } bN,$$

where an_i is the no. of individuals of the ith species at site a, bn_i is the no. of individuals of the ith species at site b, aN is the total no. of individuals at site a, and bN is the total no. of individuals at site b; da and db are calculated as:

$$\mathrm{d}a = \sum an_i^2 / aN^2,\ \mathrm{d}b = \sum bn_i^2 / bN^2.$$

Kruskal–Wallis one-way ANOVA tests were used to compare densities of the ten most common tree species among riverine forests. For each forest, samples comprised the density of each species per plot. The Shannon diversity and Morisita–Horn similarity indices were computed with *EstimateS*. Other analyses were performed using SPSS version 17. All statistical tests are two-tailed and significance was set at $P < 0.05$. Tree species nomenclature follows the *Flora of Tropical East Africa* (Polhill 1952 et seq.).

3.3. Results

3.3.1. Species Richness and Sampling Effort

A total of 1729 stems ≥10 cm DBH were recorded in the plots, comprising 79 species belonging to 61 genera and 27 families. The full species list with data on stem density ha $^{-1}$, BA ha $^{-1}$ and mean DBH, and density per individual forest patch, is presented in Appendix 1. There were no unidentified species. Tree species occurred at a density of 53 species ha $^{-1}$ (± 3.37 SD) based on the mean of 100 randomisations of the sample order.

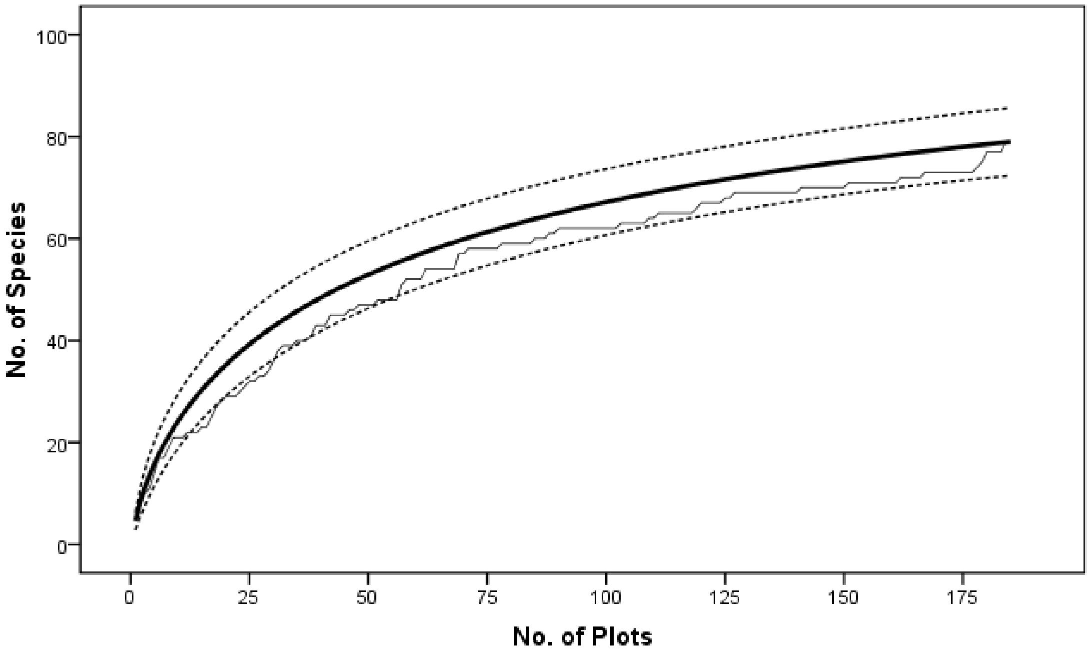

Figure 3.2. Species accumulation curves of trees ≥10 cm DBH showing: (1) expected species richness (sample-based rarefaction curve; solid smooth line) with 95% confidence intervals (dotted lines); and (2) species accumulation based on the sequential ordering of sample plots (thin jagged line). Each plot represents an area of 200 m^2 (0.02 ha) and 50 plots correspond to 1 ha.

Figure 3.2 shows two species accumulation curves: the sample-based rarefaction curve (or expected accumulation curve) with 95% confidence intervals, and the non-randomised accumulation curve. Although the rarefaction curve fails to reach an asymptote and is still rising, the curve's slope begins to level off after ~170 plots as the expected number of new species encountered decreases. In contrast, the non-randomised curve, which depicts the sequential ordering of samples, evens out after just ~130 plots but then rises again after 175 plots. This is because the final 10 plots were made in hillside ecotone forest at Katigiro where several new tree species were recorded; few new species were encountered in the riverine patches after 125 plots. Overall the curves suggest the sampling effort in riverine forest was satisfactory, but that further sampling of ecotone forest would increase observed species richness. This may explain the failure of the rarefaction curve to reach an asymptote.

Predicted total species richness differed between estimators. Chao 2 returned an estimate of 91 species whereas second-order Jackknife estimated 103 species. Based on these lower and upper bound values, vegetation surveys captured between 77 and 87% of tree species at Bulindi. In addition to the 79 recorded tree species, a further 19 identified tree species not encountered in plots were known to occur at very low densities either in riverine forest or ecotone forest–thicket at Bulindi, in some cases from single specimens. Thus the upper bound estimate of 103 species is the more accurate of the two estimators, but may still underestimate true species richness. The additional non-plot tree species are listed in Appendix 2.

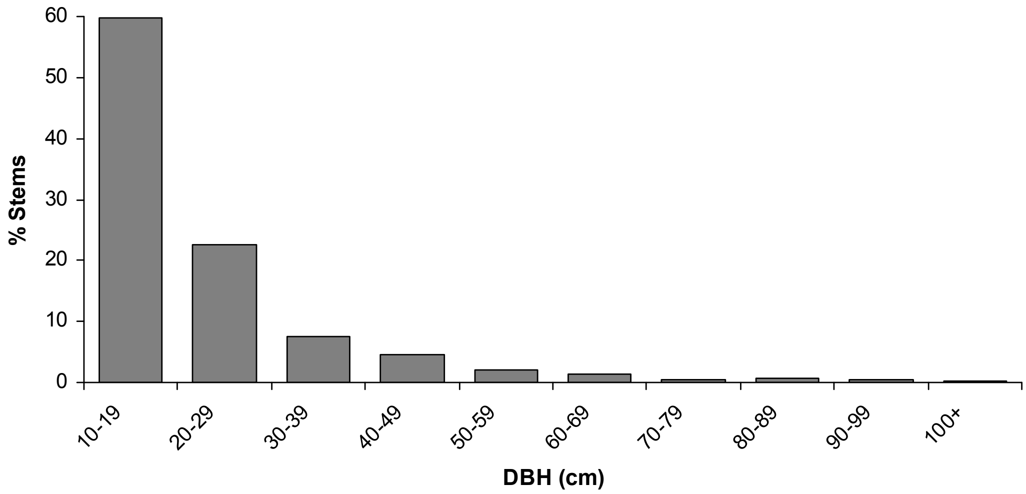

Figure 3.3. Diameter size class distribution of stems ≥10 cm DBH (*N* = 1729). Mean DBH is 22.4 cm.

3.3.2. Forest Structure

Total stem density (DBH ≥10 cm) was 467 individuals ha $^{-1}$ and total BA was 26.5 m^2 ha $^{-1}$. The distribution of stem size (diameter) classes is shown in Figure 3.3. Average DBH for all trees was 22.4 ± 14.8 cm (mean ± SD). Overall the distribution of stem size classes at Bulindi displays the typical inverse 'J-shape' or negative exponential curve characteristic of tropical forests (UNESCO 1978; Richards 1996). A majority (60%) of stems are in the smallest size class, and only 5.5% of stems are above 50 cm DBH. Nevertheless, these 5.5% represent 39% of the stand basal area. Very large stems were rare; only five individuals >100 cm DBH occur in the sample. The most commonly encountered large trees in plots, i.e. those represented by several individuals above 80 cm DBH, are *Pseudospondias microcarpa*, *Ficus* spp. (figs) and *Albizia* spp. With the exception of *Albizia coriaria* these trees were rarely targeted by timber cutters (see below). The largest plot tree – belonging to the uncommon timber species *Milicia excelsa* – measured 145.8 cm DBH, and was also the tallest at an estimated 58 m, but very large specimens of the figs *F. natalensis* and *F. variifolia* with diameters upwards of 200 cm occurred within the study area.

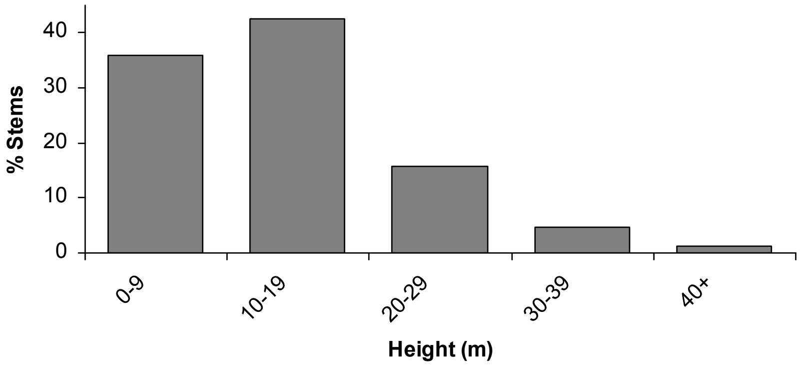

Figure 3.4. Height class distribution of stems ≥10 cm DBH (n = 1628). Mean tree height is 14.5 m.

Of the total sample of 1729 stems, 101 (6%) were excluded from analysis of tree height: 96 stems were artificially short (i.e. axe-cut or broken by felled timber trees, but with coppice growth and measurable at 1.3 m); four had fallen over but were alive; and one was missing data. Tree height distribution is shown in Figure 3.4. As the prevalence of trees in the smallest diameter class in the sample would predict, most stems (78%) were less than 20 m tall and only 6% of stems reached ≥30 m. Average tree height was 14.5 ± 8.4 m (mean ± SD). As expected, tree height was positively correlated with DBH (Spearman rank test: $r_s = 0.696$, $p < 0.001$), though considerable scatter is evident among the middle diameter classes (Figure 3.5). The most commonly encountered emergent trees (i.e. with heights above 40 m) are *Albizia* spp. and *Trilepisium madagascariensis*. Other tall, emergent trees occurring at lower densities are *Parkia filicoidea*, *Piptadeniastrum africanum*, *Sterculia dawei* and *Trichilia dregeana*.

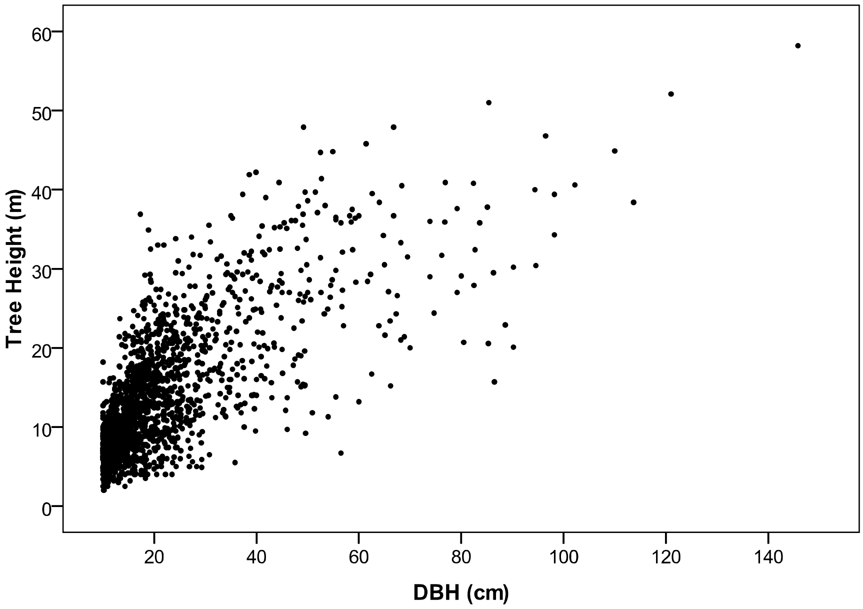

Figure 3.5. Relationship between DBH and height of forest trees (*n* = 1628).

Table 3.2. The ten most important tree families at Bulindi based on Family Importance Values (FIV). The FIV is the sum of the relative diversity (RDi), relative density (RD) and relative dominance (RDo) of each family. Also shown for each family is the total no. of species, the total no. of stems recorded (≥10 cm DBH), stem density ha $^{-1}$ and basal area (BA) ha $^{-1}$ (m^2).

Family	**No. Species**	**No. Stems**	**Density ha $^{-1}$**	**BA (m^2) ha $^{-1}$**	**RDi**	**RD**	**RDo**	**FIV**
1. Moraceae	11	429	116	8.4	13.9	24.8	31.6	70.3
2. Arecaceae (Palmae)	2	395	107	2.9	2.5	22.8	10.9	36.3
3. Fabaceae (Leguminosae)	8	83	22	3.5	10.1	4.8	13.2	28.1
4. Euphorbiaceae	7	126	34	2.4	8.9	7.3	9.0	25.2
5. Meliaceae	8	105	28	1.3	10.1	6.1	5.0	21.2
6. Anacardiaceae	4	75	20	2.6	5.1	4.3	9.8	19.2
7. Sapindaceae	4	91	25	1.5	5.1	5.3	5.8	16.1
8. Sterculiaceae	3	126	34	0.9	3.8	7.3	3.6	14.7
9. Apocynaceae	2	106	29	1.4	2.5	6.1	5.3	14.0
10. Rubiaceae	7	32	9	0.1	8.9	1.9	0.6	11.3
Remaining Families (*n* = 17)	23	161	44	1.4	29.1	9.3	5.3	43.7
Total:	79	1729	467	26.5	100	100	100	300

3.3.3. Forest Composition

1. Families

Of the 27 families recorded in plots, the 10 families with the highest ranked Family Importance Value (FIV) are listed in Table 3.2. The dominant family in Bulindi forests is Moraceae (the figs and mulberries): it is the most species-rich family with 11 species (representing 14% of the 79 species encountered), has the highest stem density (116 stems ha^{-1}; 25% of all stems), and accounts for nearly one-third of the total BA ha^{-1}. By contrast, the second highest ranked family Arecaceae (the palm family) is represented by just two species of which the date palm *Phoenix reclinata* accounts for 97% of the family's BA ha^{-1} and all but one of its 395 recorded stems. For the third ranked family, Fabaceae *sensu latu*, 94% of stems are of the Mimosoideae subfamily (Appendix 1).

2. Species

The 20 most important species at Bulindi are listed in Table 3.3. The highest ranked species is the monocotyledon *Phoenix reclinata*. Although this palm exhibits a narrow range of trunk diameters compared to other trees (maximum diameter = 28 cm), it occurs at a density of 106 stems ha^{-1} (representing 23% of total stem density ha^{-1}) and was encountered in 46% of plots. The second and third highest ranked species, *Trilepisium madagascariensis* and *Antiaris toxicaria*, are particularly abundant in mixed forest but occurred in all forest types. *Trilepisium madagascariensis* has the highest BA ha^{-1} of any species and was recorded in 48% of plots. The small cocoa tree *Theobroma cacao* has the fourth highest stem density overall (31 stems ha^{-1}) but occurs in only 12% of plots and has a relatively low BA; its distribution is highly clumped and mainly confined to abandoned forest plantations in Kiseeta and Kyamusoga. With the exception of the most common figs, *Ficus natalensis* and *F. sur*, individual fig species are present at low densities (Appendix 1). However, the overall density of figs (16.8 individuals ha^{-1}) is considerably higher than in many tropical forests (e.g. Struhsaker 1997; Kinnaird et al. 1999 and references therein), including Budongo (5.9 stems ha^{-1}; A. Plumptre, unpubl. data). Altogether the six highest ranked species (representing 7.6% of the total species) account for 52% of the combined importance value of all species (156 of 300 IV points). Thus, when data from all forest types are pooled no single species emerges as dominant. Rather a small *group* of species dominates the forest tree community at

Bulindi. When viewed at the microhabitat level, however, the ecological importance of particular species becomes more apparent.

3.3.4. Forest Types

Principal component analysis of the abundance of the ten most common tree species in riverine forest plots yielded three components with eigenvalues above one. These account for 47.0% of the cumulative variance in the data, lower than the 70% 'ideal' cumulative percent variance for the first 1–3 components recommended by McGarigal et al. (2000). Component 1 mainly differentiates plots containing the swamp trees *Phoenix reclinata* and *Macaranga schweinfurthii* (high positive loadings) from plots with *Antiaris toxicaria* and *Trilepisium madagascariensis*, which are common in mixed forest (high negative loadings) (Table 3.4). Thus Component 1 seems to reflect the plot's degree of 'swampiness'. Component 2 defines a gradient with *Trilepisium madagascariensis* and *Lovoa trichilioides* associated at the positive end of the axis and *Theobroma cacao* (cocoa) at the negative end. This component seems linked to mixed forest and whether or not a plot occurs within an area formerly farmed for cocoa. The third component mainly differentiates plots containing the large swamp tree *Pseudospondias microcarpa* from those with *Teclea nobilis*, a common understorey tree in mixed forest.

One-way ANOVA revealed a significant difference among plots assigned to swamp, mixed and cocoa forest in mean score of Component's 1 ($F_{2,157} = 67.56$, $p < 0.001$) and 2 ($F_{2,157} = 91.17$, $p < 0.001$), indicating these first two components defined gradients in species composition and abundance that correspond to subjectively defined forest types. Post-hoc tests revealed that swamp forest plots had significantly higher scores on Component 1 ('swampiness') than both mixed forest and cocoa plots. All pair-wise comparisons were significant on Component 2 ('mixed forest away from cocoa'). Mixed plots had significantly higher scores than both swamp and cocoa plots, and swamp plots had significantly higher scores than cocoa plots ($p < 0.05$ for all significant differences).

Table 3.3. The 20 most important tree species at Bulindi based on Importance Values (IV) – the sum of the relative frequency (RF), relative density (RD) and relative dominance (RDo) of each species (see text). Also shown for each species are the total no. of stems recorded (≥10 cm DBH), the percentage of sample plots the species occurred in, stem density ha $^{-1}$ and BA (m ^{2}) ha $^{-1}$.

Species	**Family**	**No. Stems**	**% Plots**	**Density ha $^{-1}$**	**BA (m ^{2}) ha $^{-1}$**	**RF**	**RD**	**RDo**	**IV**
1. *Phoenix reclinata* Jacq.	Arecaceae (Palmae)	394	45.9	106	2.8	10.0	22.8	10.6	43.4
2. *Trilepisium madagascariensis* DC.	Moraceae	224	47.6	61	3.1	10.4	13.0	11.9	35.2
3. *Antiaris toxicaria* Leschen.	Moraceae	129	38.9	35	2.3	8.5	7.5	8.6	24.6
4. *Pseudospondias microcarpa* (A. Rich.) Engl.	Anacardiaceae	69	26.5	19	2.5	5.8	4.0	9.6	19.4
5. *Funtumia africana* (Benth.) Stapf	Apocynaceae	104	30.3	28	1.3	6.6	6.0	5.0	17.6
6. *Glenniea africana* (Radlk.) Leenh.	Sapindaceae	76	28.6	21	1.3	6.3	4.4	5.1	15.7
7. *Theobroma cacao* L.	Sterculiaceae	115	11.9	31	0.4	2.6	6.7	1.6	10.8
8. *Teclea nobilis* Del.	Rutaceae	64	16.8	17	0.6	3.7	3.7	2.2	9.6
9. *Macaranga schweinfurthii* Pax	Euphorbiaceae	58	10.3	16	0.9	2.2	3.4	3.2	8.8
10. *Lovoa trichilioides* Harms	Meliaceae	45	17.3	12	0.5	3.8	2.6	2.0	8.4
11. *Albizia coriaria* (Welm. ex) Oliv.	Fabaceae (subfam. Mimosoideae)	14	6.5	4	1.3	1.4	0.8	5.1	7.3
12. *Ficus natalensis* Hochst.	Moraceae	17	6.5	5	1.0	1.4	1.0	3.8	6.2
13. *Sapium ellipticum* (Krauss) Pax	Euphorbiaceae	16	7.6	4	0.9	1.7	0.9	3.2	5.8
14. *Trichilia dregeana* Sond.	Meliaceae	25	10.3	7	0.5	2.2	1.4	1.8	5.5
15. *Albizia zygia* (DC.) Macbr.	Fabaceae (subfam. Mimosoideae)	20	10.3	5	0.5	2.2	1.2	2.1	5.5
16. *Ficus sur* Forssk.	Moraceae	21	7.6	6	0.4	1.7	1.2	1.7	4.6
17. *Parkia filicoidea* (Welw. ex) Oliv.	Fabaceae (subfam. Mimosoideae)	15	7.0	4	0.4	1.5	0.9	1.5	3.9
18. *Piptadeniastrum africanum* (Hook. f.) Brenan	Fabaceae (subfam. Mimosoideae)	15	7.0	4	0.3	1.5	0.9	1.3	3.7
19. *Margaritaria discoidea* (Baill.) Webster	Euphorbiaceae	17	7.0	5	0.3	1.5	1.0	1.0	3.5
20. *Albizia glaberrima* (Schumach. & Thonn.) Benth.	Fabaceae (subfam. Mimosoideae)	12	4.9	3	0.4	1.1	0.7	1.7	3.4
Remaining Species (*n* = 59)	–	279	–	75	4.6	23.8	16.1	17.2	57.1
Total:	–	1729	–	467	26.5	100	100	100	300

Table 3.4. Tree species with high loadings (>0.5) on three components extracted from principal component analysis of the abundance of ten common species in riverine forest plots.

Component	**Tree Species**	**Loading**
1	*Phoenix reclinata*	.736
	Macaranga schweinfurthii	.654
	Antiaris toxicaria	-.575
	Trilepisium madagascariensis	-.507
2	*Trilepisium madagascariensis*	.585
	Lovoa trichilioides	.529
	Theobroma cacao	-.730
3	*Pseudospondias microcarpa*	.508
	Teclea nobilis	-.676

In Figure 3.6 individual plots assigned to the three riverine forest types are plotted along the axis defined by these first two components, which together account for 33.4% of the variance in the data. The plots clearly cluster according to forest type. Nevertheless, whereas plots in cocoa forest are well differentiated from both swamp and mixed forest plots, reflecting the clumped distribution of cocoa trees in abandoned *shambas*, considerable overlap exists between swamp and mixed plots. This is expected because trees common in mixed forest also occur at lower densities in swampy areas and, to a lesser extent, vice versa. Overall, despite the fact that two-thirds of the variance remains unexplained, these two components describe ‘readily interpretable and ecologically consistent gradients’ (McGarigal et al. 2000), justifying distinction of these riverine forest types. Conversely, there was no difference among plots of different forest types in the mean score of Component 3 ($F_{2,157} = 0.313$, $p = 0.73$). This suggests that the variance in the data associated with this component is caused by other factors that do not correspond closely to physiognomically defined forest type (possibly tree diameter size).

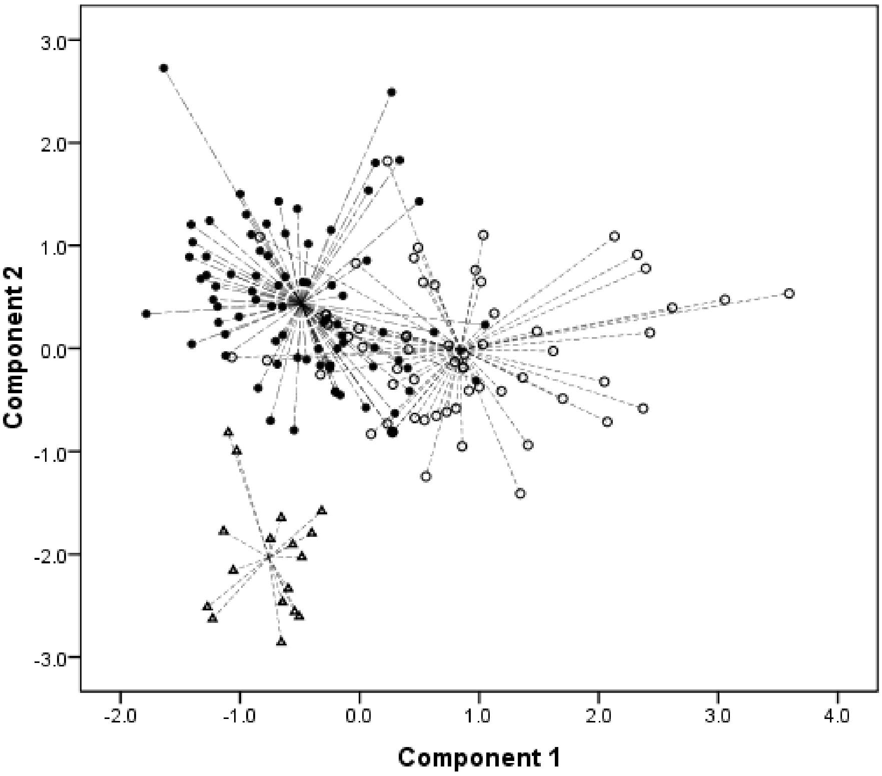

Figure 3.6. Principal component analysis of the abundance of ten common tree species in plots assigned to three riverine forest types (swamp, mixed and cocoa; *n* = 160). Component 1 represents a gradient from plots in *Phoenix*- and *Macaranga*-dominated swamp forest (positive loadings) to *Antiaris–Trilepisium* mixed forest (negative loadings). Component 2 represents a gradient from plots associated with *Trilepisium* and *Lovoa* mixed forest (positive loadings) to cocoa-dominated plots in formerly cultivated forest (negative loadings). Open circles = swamp forest plots, closed circles = mixed forest plots, and triangles = cocoa forest plots. Dashed lines are displayed from the centroid points of each forest type, defined as the average of the coordinates of all plots classified into each forest type.

Forest types were unevenly represented in the pooled sample plots. Mixed forest and swamp forest were encountered most frequently, accounting for 46% and 34% of plots, respectively. Ecotone and cocoa forest were comparatively minor habitats, accounting for 11% and 9% of plots, respectively (Table 3.5). This is likely an adequate representation of forest types within the chimpanzees' core range. However, the relative proportion of ecotone forest plots would increase if the sampling area was expanded to include little-used patches of forest–woodland (e.g. within Kandanda–Ngobya FR). Data from forest plots were used to produce a vegetation map of the study area showing the distribution of the four forest types in the chimpanzees' core range (Figure 3.7).

Table 3.5. Comparative structure, diversity and common tree species in four forest types at Bulindi. Values for stem density, DBH, BA and tree height are the mean ± SD per 0.02 ha plot; Kruskal–Wallis tests were used to test for differences in structural variables among forest types. Shannon diversity index values are denoted by *H′*. Only common species accounting for >5% of stems in each forest type are listed.

	Forest Type			
	Swamp	**Mixed**	**Cocoa**	**Ecotone**
No. plots (% of total)	62 (33.7%)	84 (45.7%)	17 (9.2%)	21 (11.4%)
Area sampled (ha)	1.24	1.68	0.34	0.42
No. stems recorded	731	692	156	150
Density (Stems ha^{-1}) **	589.5 ± 375.8	411.9 ± 190.2	458.8 ± 214.5	357.1 ± 220.4
DBH *	22.3 ± 7.0	24.5 ± 7.0	20.7 ± 5.4	20.4 ± 4.2
BA ha^{-1} (m^2) *	30.0 ± 22.9	27.3 ± 19.7	25.6 ± 17.4	15.2 ± 12.1
Tree height ***	14.0 ± 4.5	16.6 ± 4.8	11.7 ± 4.9	11.0 ± 3.4
H′	2.37	2.89	1.48	3.44
Common species (% stems)	*Phoenix reclinata* (45.0%) *Macaranga schweinfurthii* (7.9%) *Trilepisium madagascariensis* (7.0%) *Pseudospondias microcarpa* (5.6%) *Glenniea africana* (5.2%)	*Trilepisium madagascariensis* (23.4%) *Antiaris toxicaria* (12.9%) *Funtumia africana* (10.3%) *Phoenix reclinata* (7.8%) *Lovoa trichilioides* (5.6%) *Teclea nobilis* (5.5%)	*Theobroma cacao* (67.3%) *Antiaris toxicaria* (5.8%)	*Antiaris toxicaria* (9.3%) *Combretum collinum* (7.3%) *Margaritaria discoidea* (6.0%) *Albizia zygia* (5.3%) *Allophylus africanus* (5.3%) *Trichilia dregeana* (5.3%)

Kruskal–Wallis one-way ANOVA: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ ($df = 3$ in all tests)

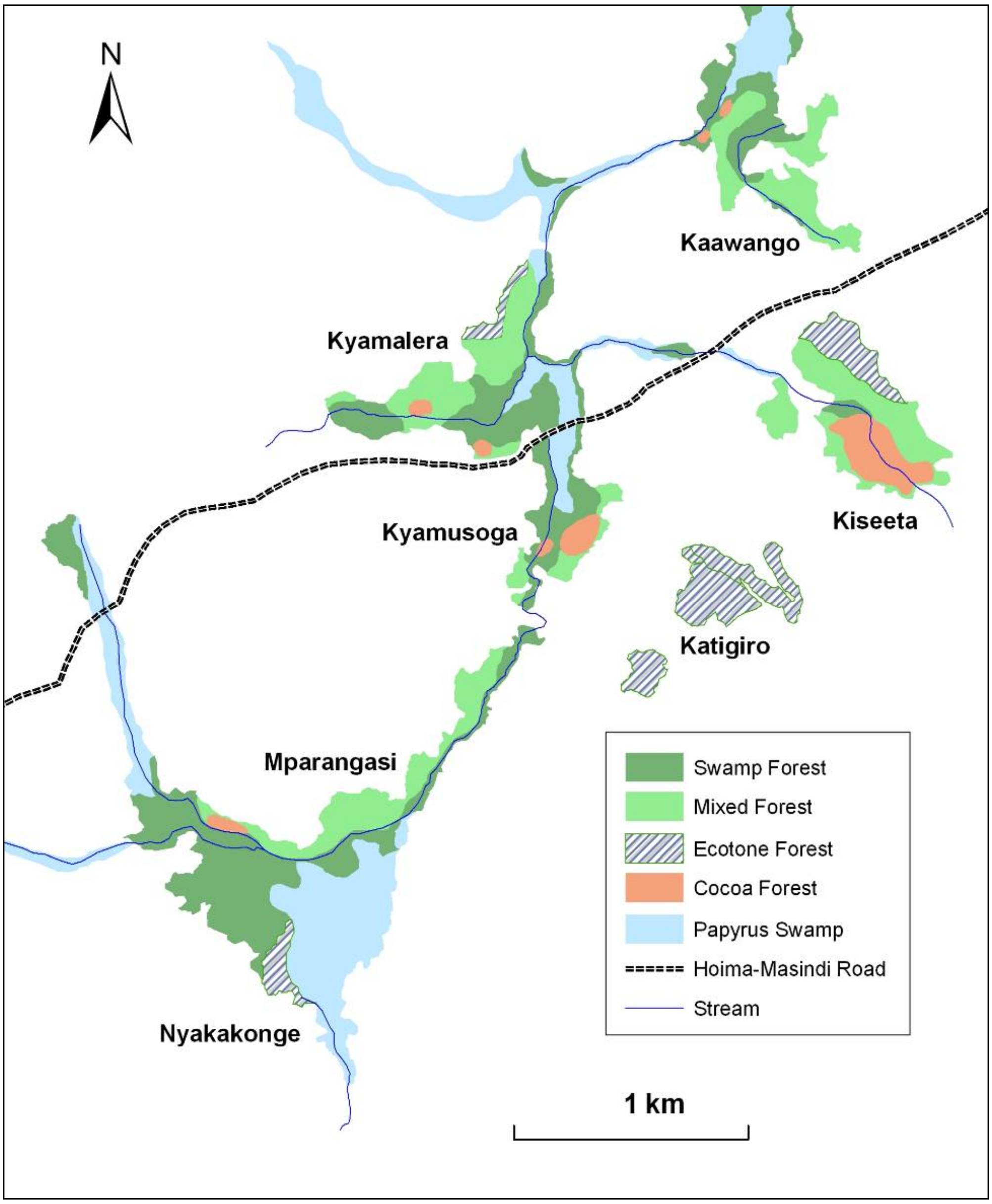

Figure 3.7. Vegetation map showing the distributions of four forest types (Swamp, Mixed, Cocoa and Ecotone) in main forest fragments utilised by chimpanzees. Mparangasi–Nyakakonge forest comprises two sections: gallery forest (Mparangasi) and waterlogged swamp forest (Nyakakonge).

There were significant differences among forest types in stem density, BA ha $^{-1}$, average DBH and average tree height (Table 3.5). Stem density was highest in swamp forest, reflecting the tendency of *Phoenix* palms to form dense clumps, and was lowest in ecotone forest. Although mixed forest plots had the highest average DBH, recent cutting of large specimens of several species (e.g. *Antiaris toxicaria* and *Lovoa trichilioides*) that occur at highest densities in mixed forest may have had the effect of reducing mean diameter sizes in mixed forest relative to other forest types. In fact, BA was highest in swamp forest that supports lower densities of most species targeted by loggers. BA was very low in ecotone forest, reflecting the low-density mix of small woodland species and early-successional forest pioneers, and paucity of mature forest trees. Highest average tree heights were recorded in mixed forest plots, followed by swamp plots; cocoa and ecotone forest plots had low average tree heights. The low average canopy of the abandoned cocoa *shambas* reflects not only the abundance of the understorey cocoa tree, but also the fact that large former shade trees were being harvested for timber.

Species Richness and Diversity

Figure 3.8 depicts species richness in the four forest types. None of the expected accumulation curves approach an asymptote, implying that with continued sampling further species would be encountered in all forest types. Although overall numbers of stems recorded in ecotone and cocoa forest are small relative to the more abundant swamp and mixed forest, clear differences in the steepness of the rising curves are evident. Species richness is lowest in cocoa forest, reflecting the artificial dominance of the cocoa tree. Ecotone forest is the most species rich habitat with 43 tree species encountered after 150 individuals are sampled; comparable richness is only reached in mixed and swamp forest after >360 and >470 individuals, respectively.

The most commonly encountered species in each forest type are listed in Table 3.5. The *Phoenix* palm dominates the stand in swamp forest, accounting for 45% of stems. Although mixed forest supports a number of common species, *Trilepisium madagascariensis* is the most abundant tree accounting for 23% of stems. As expected, the exotic understorey cocoa tree represents a large proportion of stems (67%) in former forest cocoa *shambas*. In contrast, no single species is especially common in ecotone forest. Accordingly, diversity is highest in ecotone forest (Shannon diversity index: $H' = 3.4$) and lowest in cocoa forest ($H' = 1.5$); diversity values for swamp and mixed forest are intermediate though mixed forest is more diverse than swamp forest (Table 3.5). The corresponding value for the total (community-wide) sample is $H' = 3.1$. Shannon diversity values typically fall between 1.5 and 3.5 (Stiling 1999).

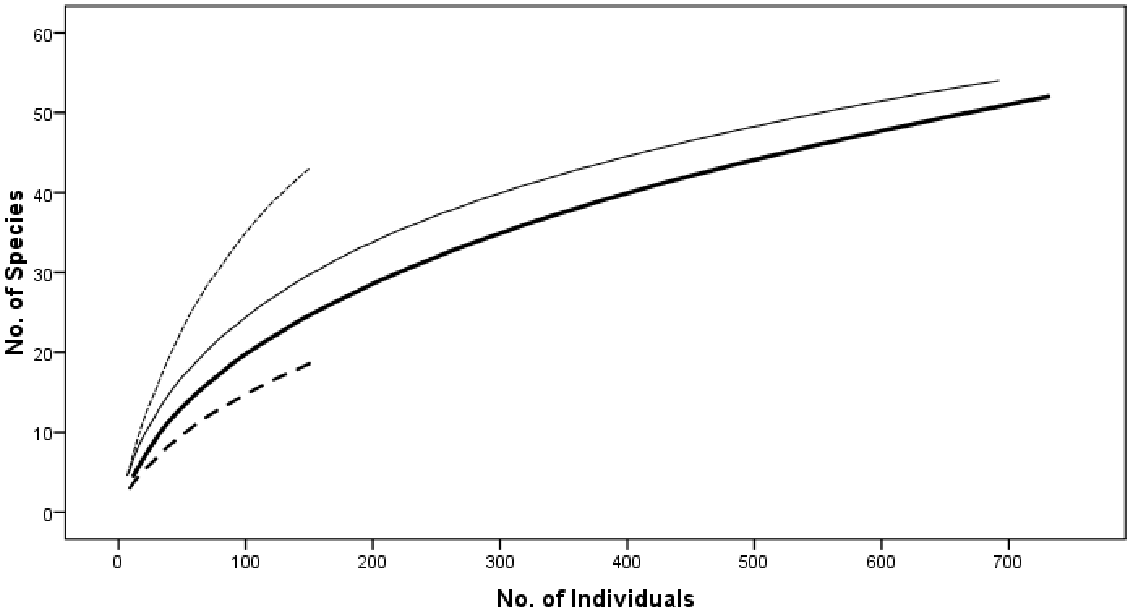

Figure 3.8. Expected species accumulation (rarefaction) curve of trees ≥10 cm DBH in four forest types: ecotone forest (upper dotted line); mixed forest (thin solid line); swamp forest (thick solid line); and cocoa forest (lower dashed line). 95% confidence intervals are not shown for readability.

3.3.5. Comparison Among Forest Fragments

Individual forest fragments differed in the relative proportion of plots assigned to each forest type (see Table 3.1). Because plots were well distributed throughout fragments this is assumed to reflect real differences in the relative representation of forest types in fragments. In Kyamalera and Kaawango mixed forest is the predominant forest type (roughly two-thirds of plots), though both also contain sizeable areas of swamp forest (Figure 3.7). Conversely, Kyamusoga and Mparangasi–Nyakakonge comprise a greater proportion of swamp relative to mixed forest. The greatest expanse of swamp forest is found in the Nyakakonge sector of Mparangasi–Nyakakonge, where it comprised 86% of sample plots. Kiseeta stands out among riverine patches in having little swamp habitat; it is the only riverine patch not bordering papyrus swamp. Kiseeta also contains the largest area of cocoa forest (34% of plots); during the 1960s many households around the forest participated in a cocoa growers association and converted sections of the forest for that purpose (Figure 3.7). Consequently, plots in waterlogged areas were usually classed as cocoa rather than swamp forest. Kyamusoga also contains significant areas of abandoned cocoa (24% of plots). Much smaller forest cocoa plantations also occur in Kyamalera, Kaawango and Mparangasi. Of the riverine forests, only Kiseeta –

which has a higher average elevation compared to other riverine patches (Table 3.1) – contains a sizable area of ecotone forest (25%). On the other hand, Katigiro – comprising two small patches of lower hillside forest – is 100% ecotone habitat (Figure 3.7).

Table 3.6. Results of Morisita–Horn pair-wise comparisons of compositional similarity of tree species between forest fragments. Low values (<0.5) indicating low overlap are shown in bold type; intermediate values (<0.7) are underlined. Fragments: KLA = Kyamalera, KGA = Kyamusoga, KTA = Kiseeta, KWG = Kaawango, MPA–NKE = Mparangasi–Nyakakonge, KGRO = Katigiro.

Fragment	**KLA**	**KGA**	**KTA**	**KWG**	**MPA –NKE**	**KGRO**
KLA	–	0.810	<u>0.639</u>	0.887	0.833	**0.365**
KGA		–	0.702	0.829	0.725	**0.297**
KTA			–	<u>0.659</u>	<u>0.538</u>	**0.448**
KWG				–	0.865	**0.384**
MPA–NKE					–	**0.306**
KGRO						–

Morisita–Horn similarity values for pairwise comparisons of individual forest patches are shown in Table 3.6. The Morisita–Horn index returns a value between 0 and 1.0, with higher values indicating greater similarity. Despite differences in the overall proportion of different forest types between fragments, the results point to a high degree of compositional homogeneity between four of the five riverine patches (Kyamalera, Kyamusoga, Kaawango and Mparangasi–Nyakakonge); for these bottomland forests, all pairwise values are greater than 0.7. As noted above, these fragments comprise mainly mixed and swamp forest in varying proportions, but few common trees occur exclusively in one or the other forest type. Pairwise similarity values between Kiseeta and the other riverine fragments are somewhat lower (between 0.5–0.7), for reasons already noted. The hillside ecotone forest at Katigiro is clearly distinct compositionally from all other forest patches (<0.5 for all pairwise comparisons), though most similar to Kiseeta.

Table 3.7. Densities (stems ha $^{-1}$) of ten most common tree species in riverine forests at Bulindi (KLA = Kyamalera, KGA = Kyamusoga, KTA = Kiseeta, KWG = Kaawango, MPA–NKE = Mparangasi–Nyakakonge). Species densities among forests are compared with Kruskal–Wallis tests and significant differences are indicated. Highest densities for each species are shown in bold. Species densities for the Mparangasi (*MPA*) and Nyakakonge (*NKE*) sectors of Mparangasi–Nyakakonge forest are individually shown, but values used in Kruskal–Wallis tests were for the forest in its entirety. A dash indicates that the species was not recorded in plots.

Species	**Density**							
	KLA	**KGA**	**KTA**	**KWG**	**MPA–NKE**	*(MPA)*	*(NKE)*	**All Forests**
1. *Phoenix reclinata* Jacq. ***	126.6	**161.9**	9.4	85.7	160.6	64.0	270.5	106.5
2. *Trilepisium madagascariensis* DC. *	**88.3**	81.0	39.1	44.6	60.6	100.0	15.9	60.5
3. *Antiaris toxicaria* Leschen. **	**66.0**	21.4	32.8	23.2	20.2	34.0	4.5	34.9
4. *Theobroma cacao* L. ***	4.3	95.2	**106.3**	5.4	–	–	–	31.1
5. *Funtumia africana* (Benth.) Stapf	28.7	**66.7**	18.8	35.7	16.0	24.0	6.8	28.1
6. *Glenniea africana* (Radlk.) Leenh. *	30.9	**33.3**	4.7	26.8	16.0	14.0	18.2	20.5
7. *Pseudospondias microcarpa* (A. Rich.) Engl.	12.8	**47.6**	10.9	16.1	22.3	34.0	9.1	18.6
8. *Teclea nobilis* Del. ***	10.6	–	1.6	16.1	**45.7**	40.0	52.3	17.3
9. *Macaranga schweinfurthii* Pax	14.9	19.0	–	23.2	**24.5**	12.0	38.6	15.7
10. *Lovoa trichilioides* Harms	**21.3**	9.5	4.7	10.7	11.7	18.0	4.5	12.2

Kruskal–Wallis one-way ANOVA: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ ($df = 4$ in all tests)

Densities of the ten most common species at Bulindi in each riverine forest patch are shown in Table 3.7. In spite of the overall similarity in species composition among these low-lying forests, densities of certain species differ widely among patches (see Appendix 1 for the full species list with densities for each forest fragment). For six species differences in densities between two or more forests are significant (e.g. *Phoenix reclinata* and cocoa).

Within individual fragments spatial heterogeneity in species composition was also apparent. As noted previously, Mparangasi–Nyakakonge can be divided into two sectors based on predominant forest type. The Mparangasi sector comprises a narrow 2-km stretch of gallery forest in which the majority of plots were classified as mixed forest. In contrast the Nyakakonge sector to the south is traversed by streams and borders a large papyrus swamp, and is permanently wet (Figure 3.7). Distinct differences in densities of some indicator species reflect this spatial variability. For example, *Phoenix* palms occur at an exceptionally high density in Nyakakonge (270 stems ha $^{-1}$), more than four times greater than in the contiguous Mparangasi sector (Table 3.7). Furthermore, several distinct microhabitats are unique to individual fragments: for example, *Raphia farinifera* swamp forest and *Zanha golungensis* mixed forest occur only in parts of Kyamalera, whereas another variant of swamp forest, in which the small tree *Maytenus heterophylla* is common in the understorey, is restricted to the western part of Nyakakonge.

3.3.6. Disturbance – Cut Stumps

A total of 616 artificially cut stumps (≥10 cm DBH) were recorded along transect lines, giving a density of 83.4 stumps ha $^{-1}$. This figure should be considered an underestimate. Gaps created by logging are typically invaded by a dense cover of vines, and it is likely that stumps were missed in heavily disturbed areas. Additionally, decaying stumps older than about 2–3 years were often not recorded because of difficulties establishing if they had been cut or had died naturally. Stumps were grouped into the following three diameter classes: small (10–20 cm), medium (21–50 cm) and large (>50 cm). Figure 3.9 compares the distribution of cut stumps in each diameter class with that of live stems recorded in plots. Although the two data sets are not strictly comparable since the diameters of most stumps had to be estimated, some broad patterns are apparent. While the majority of both living trees and stumps are small-sized, a greater proportion of stumps are in the small diameter class. The most important difference is that compared to live stems a relatively large proportion of stumps are in the large diameter class, and a lesser proportion of stumps are medium-sized (χ^2 = 123.49, *df* = 2, *p* <0.001). This reflects the observation that people mainly cut small trees for poles (for example, to construct tobacco drying barns), but also target large stems for timber.

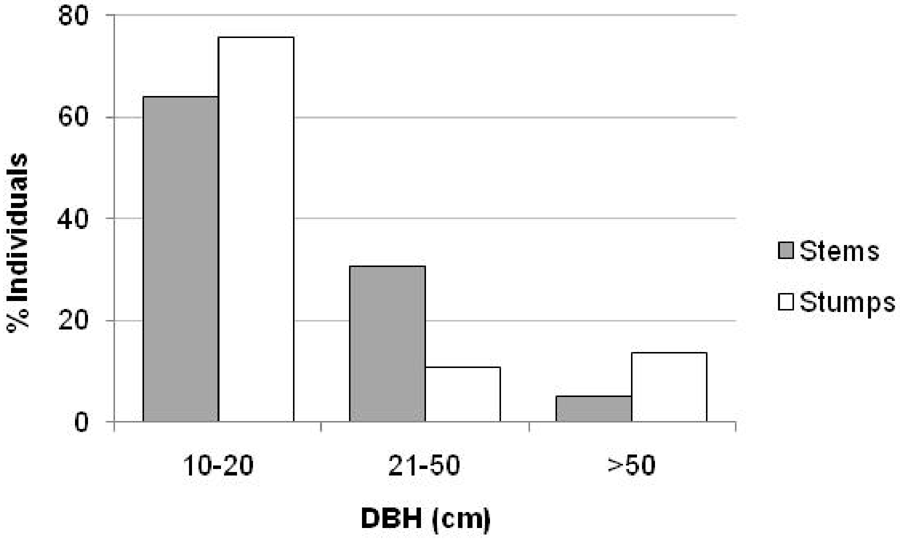

Figure 3.9. Distribution of live stems recorded in plots (*n* = 1769) and cut stumps recorded along transects (*n* = 616) in three diameter size classes: small (10–20 cm), medium (21–50 cm) and large (>50 cm).

Eighty percent of small trees harvested were of four species: *Antiaris toxicaria*, *Funtumia africana*, *Phoenix reclinata* and *Trilepisium madagascariensis*. These species represent four of the five most abundant trees at Bulindi (Table 3.7). Table 3.8 shows the density of cut stumps in the small diameter class and the density ratio of living stems to stumps for each species. Harvest levels of *Phoenix* palms are particularly high. For this species, the estimated ratio of stumps to live palms in the small diameter class was 1:2.6.

Timber Trees

A total of 98 trees along transects (15.9% of stumps) had been felled and sawn for timber (Table 3.9). A further 14 trees had likely also been cut for timber, but this could not be confirmed unequivocally. The 98 trees comprised at least 16 species.[5] The species with the most individuals logged was *Antiaris toxicaria* (36% of trees cut for timber), but *Albizia coriaria* (13%) and *Trilepisium madagascariensis* (12%) were also regularly targeted. Though most logged specimens (84.7%) were in the large diameter class (i.e. >50 cm), some individuals were harvested at considerably smaller sizes (e.g. 35–45 cm). The smallest individual unequivocally cut for timber was a specimen of *Lovoa trichilioides*, estimated to be just 30 cm DBH.

Table 3.8. Densities (ha $^{-1}$) of cut stumps and living stems in the small diameter class (10–20 cm DBH) for four commonly harvested tree species at Bulindi. Also shown for each species is the density ratio of small stumps to stems. The sampling area was 7.39 ha for stumps and 3.70 ha for stems.

Species	**No. Stumps**	**Stumps ha $^{-1}$**	**Stems ha $^{-1}$**	**Ratio (Stump : Stem)**
Antiaris toxicaria	34	4.6	20.3	1:4.4
Funtumia africana	27	3.7	14.1	1:3.8
Phoenix reclinata	250	33.8	86.2	1:2.6
Trilepisium madagascariensis	49	6.6	35.9	1:5.4

The density ratio of stumps to living stems of timber trees in the large diameter class is shown in Table 3.9. For six species, the estimated density of large stumps exceeds that of living specimens. These species include the most commonly logged tree, *Antiaris toxicaria*, the large specimens of which were being systematically removed from Bulindi forests during this research. Notably, no large standing specimens of the most valuable timber trees – the mahoganies *Khaya anthotheca* and *Entandrophragma* spp., and *Lovoa trichilioides* (Meliaceae) – were recorded in plots, having been removed before this study. For four other species fewer than two large living stems remained to each large stump. For all timber species, the ratio of large stumps to living trees is 1:1.5.

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[5] In addition to the 16 species recorded along transects ≥1 individuals of *Cordia millenii, Milicia excelsa* and the figs *Ficus mucuso, F. ovata* and *F. variifolia* were cut for timber during the study.

Table 3.9. Tree species harvested for timber at Bulindi. For each species the number of individuals recorded along transects that were logged for timber (pit-sawn or chain-sawn) and the estimated range of diameter (DBH) sizes are shown. Also shown for each species is the density (ha $^{-1}$) of cut stumps and living stems in the large diameter class (>50 cm DBH), and the ratio of large stumps to stems. Ratios are approximate because DBH of logged specimens could not be precisely measured; however, the associated error is assumed to be constant across species. Sampling area = 7.39 ha for cut stumps and 3.70 ha for live stems.

Species	**No. trees cut for timber** [a]	**Estimated DBH (cm)** [b]	**No Large Stumps**	**Large Stumps ha $^{-1}$**	**Large Stems ha $^{-1}$**	**Ratio (Stump : Stem)** [c]
Albizia coriaria	13 (1)	(40–) 45–100	11	1.5	2.4	1:1.6
Albizia spp. [d]	4	50–120	3	0.4	1.6	1:4.0
Antiaris toxicaria	35	45–120	31	4.2	2.7	**1:0.6**
Entandrophragma sp.	2	70–80	2	0.3	0	**1:0.0**
Funtumia africana	1 (3)	(40–) 70	1	0.1	0	**1:0.0**
Glenniea africana	8 (3)	(40–) 50–100	7	0.9	1.4	1:1.6
Khaya anthotheca	1	70	1	0.1	0	**1:0.0**
Lovoa trichilioides	7	30–90	4	0.5	0	**1:0.0**
Maesopsis eminii	1	70	1	0.1	0	**1:0.0**
Parkia filicoidea	1	60	1	0.1	0.8	1:8.0
Pseudospondias microcarpa	2 (1)	(60–) 100–120	4	0.5	4.1	1:8.2
Pycnanthus angolensis	1	40	0	0.0	0.0	–
Sterculia dawei	5 (2)	(45–) 70–100	5	0.7	0.8	1:1.1
Trichilia dregeana	2	70	2	0.3	0.3	1:1.0
Trilepisium madagascariensis	12 (4)	40–90	7	0.9	3.5	1:3.9
Zanha golungensis	1	130	1	0.1	0.3	1:3.0
Unknown spp.	2	60–70	2	–	–	–
Total:	98 (14)	30–130	83	11.2	17.3	1:1.5

[a] Numbers in parenthesis indicate additional individuals of each species that were probably cut for timber, but for which evidence was inconclusive (e.g. because the stump was very old, not in association with a pitsaw camp, or relatively small-sized);

[b] Values in parenthesis represent the diameter size of individuals probably cut for timber, where DBH is below that of individuals known to be logged;

[C] Ratios in bold indicate species for which the density of large stumps was greater than for living trees.

[d] The following *Albizia* spp. were not distinguished from stumps: *A. zygia*, *A. glaberrima* and *A. grandibracteata*.

3.4. Discussion

Tree Species Diversity

Forests in mainland tropical Africa are generally less species diverse per unit area than forests of the Neotropics and the Asia–Pacific tropics. For example, fewer than 100 species ha $^{-1}$ are typically recorded in African forests for trees ≥10 cm DBH, compared to maximums of 150–300 in some Asian and tropical American rainforests (Whitmore 1995; Richards 1996; Turner 2001; Parmentier et al. 2007). The relative poverty of African forests has been ascribed to the comparatively dry, more seasonal climate of the main Guineo–Congolian region, compared with rainforest zones in Asia and South America, as well as to contrasting climatic histories, constraints relating to the size of species pools, and patterns of anthropogenic disturbance (Richards 1996; White 2001; Parmentier et al. 2007). Within tropical Africa, Uganda's forests fall at the dry extreme of the Guineo–Congolian phytochorion; indeed, many forests along the Western Rift are classified as 'moist semi-deciduous' rather than 'true' rainforests, including Budongo and Bugoma (Langdale-Brown et al. 1964). Nevertheless, the number of tree species in 1-ha plots in Ugandan forests (30–67 species; Eilu et al. 2004) is within the range reported for other sites in tropical Africa (UNESCO 1978; Richards 1996; Boubli et al. 2004).

The estimated density of tree species at Bulindi (53 ha $^{-1}$) conforms to the African pattern of relatively low diversity, though is similar to species densities in other, much larger Ugandan forests (though total species richness is much lower). This probably reflects the fact that despite their small size, several physiognomic forest types are distinguishable in forest patches at Bulindi. Principal component analysis showed that riverine forest plots tended to separate themselves into swamp forest, mixed forest, and artificial 'cocoa forest' based on relative abundances of common species. These forest types comprise the chimpanzees' core habitat. A fourth forest type – ecotone forest – occurs away from waterbodies on drier ground. Species accumulation curves showed that this habitat, which includes both forest and grassland trees, is in fact most diverse. Recent and ongoing human disturbance in the forests at Bulindi might be expected to result in low tree species diversity. For example, in parts of Kiseeta and Kyamusoga understorey trees were removed and replaced with cocoa; in such areas species richness was low. Furthermore, the Bulindi forests were heavily logged prior to and during surveys. In Kibale and Kalinzu forests, logging led to a reduction in species richness and density (Struhsaker 1997; Muhanguzi et al. 2007). Conversely, 'intermediate' disturbance (e.g. Connell 1978) in the form of regular burning of bush and grassland around forest edges and hillside thickets may increase compositional complexity through maintenance of ecotone habitat. The data suggest that estimates of total species richness for forest patches within the chimpanzee range at Bulindi will increase with further sampling of such ecotone habitat (e.g. in hillside patches within Kandanda–Ngobya FR). This would enable a fuller understanding of the diversity and distribution of resources available to the chimpanzees.

Forest Structure

In many aspects, the structure of the small forest patches at Bulindi conforms to a typical tropical forest. The stem density of 467 trees per hectare is within the range of 300–700 stems given by Richards (1996), and is equivalent to average density in four major Ugandan forests, including Budongo (Eilu et al. 2004), but greater than densities recorded in heavily disturbed forest patches in central Uganda (Turyahabwe et al. 2008). Nevertheless, basal area per hectare at Bulindi (26.5 m^2) is at the lower end of the range of values for a selection of tropical forests given in Swaine et al. (1987), most of which fall between 30 and 50 m^2 per hectare.[6] In Ugandan forests, BA ranges between 14–45 m^2 ha^{-1} (Eilu et al. 2004; Turyahabwe et al. 2008). At Bulindi, BA has probably recently decreased due to the removal of many large stems for timber; even relatively light logging is associated with marked reductions in BA (Struhsaker 1997). The relatively low BA may also reflect the fact that sections of the forest are young, having developed on areas previously cleared for agriculture. Overall, Bulindi forests show many features characteristic of disturbed secondary forest (Richards 1996): a dense understorey of shrubs, small trees and climbers, and an irregular and broken canopy, with frequent large gaps created by logging. At the start of the study, some primary elements remained in mixed forest in Kyamalera, though this area was subsequently logged.

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[6] However, values greater than 100 m^2 ha^{-1} are reported for some primary forests (e.g. in Indonesia; Kessler et al. 2005).

Composition of Bulindi Forests

The core habitat for chimpanzees at Bulindi is comprised of swampy riverine forest patches – small forest islands amidst a mosaic of human-dominated farmland. Common tree species, whether occurring at higher densities in swamp or mixed forest, are characteristic of damp waterlogged conditions (Polhill 1952 et seq.). The most abundant species – the *Phoenix* palm – occurs at a very high overall density of >100 stems per hectare, and at much greater densities around swamps (e.g. 271 stems ha $^{-1}$ in Nyakakonge). Almost always associated with waterlogged conditions, aggregations of these palms are a common structural feature in groundwater and swamp forest in Uganda and elsewhere in East Africa (Bogdan 1958; Langdale-Brown et al. 1964; Kinnaird 1992a). Other common trees indicative of the swampy conditions at Bulindi are *Pseudospondias microcarpa* and *Macaranga schweinfurthii*.

The overall ecological dominance of the Moraceae family – the figs and mulberries – is notable as it appears to be an uncommon occurrence in African tropical forests (White 1983; Turner 2001; but see Fashing 2001). However, many African representatives of the Moraceae favour wetter forest types such as riverine forest (Polhill 1952 et seq.). Thus the overall high density of figs and other species of Moraceae at Bulindi reflects the wet habitat, but may also be influenced by light conditions associated with disturbance and edge effects (Gautier-Hion and Michaloud 1989; Fashing 2001). To what extent the dominance of Moraceae is influenced by human activities is difficult to assess. For example, while large specimens of other families (e.g. Meliaceae) are logged for timber at Bulindi, so too are members of the Moraceae (e.g. *Antiaris toxicaria*), though figs are usually ignored.

While tree species at Bulindi are characteristic of the region generally (Langdale-Brown et al. 1964; Howard 1991), compositionally the riverine forests show clear departures from Budongo, the nearest main forest block. Only five of the 20 commonest species recorded in forest plots at Budongo by Plumptre (unpubl. data) were recorded at Bulindi (Table 3.10). In particular, the top nine species at Budongo are entirely absent from Bulindi forests. Conversely, only two species common at Bulindi (*Trilepisium madagascariensis* and *Margaritaria discoidea*) were among the 20 most abundant species recorded in Plumptre's survey. Notably, the superabundant palm *Phoenix reclinata* is overall rare at Budongo, being confined to swamp margins (Eggeling 1947;

Nangendo et al. 2006). Several of the most important food trees for chimpanzees at Budongo (Reynolds 2005) do not occur at Bulindi (e.g. *Cynometra* and most *Celtis* spp.), which might imply the small riverine forests offer a poor habitat for chimpanzees. On the other hand, members of the Moraceae – the dominant tree family at Bulindi – often produce fleshy drupaceous fruits attractive to frugivores. In particular, fruits of the genus *Ficus* (figs) are an important resource for many tropical vertebrates including chimpanzees (e.g. Wrangham et al. 1993; Kinnaird et al. 1999). The question of habitat quality is considered more closely in the following chapters on forest food availability and chimpanzee diet (Chapters 4 and 5).

Table 3.10. The 20 most common tree species ≥10 cm DBH and their densities (stems ha $^{-1}$) in the Budongo Forest Reserve (A.J. Plumptre, unpubl. data). Data are from 820 x 154 m^2 circular plots (= 12.63 ha). Species are listed in descending order of abundance. For species recorded at Bulindi, densities are shown for comparison. A dash indicates the species was not recorded at Bulindi.

Species	**Family**	**Budongo Density**	**Bulindi Density**
1. *Celtis mildbraedii* Engl.	Ulmaceae	47.3	–
2. *Funtumia elastica* (Preuss) Stapf.	Apocynaceae	41.0	–
3. *Lasiodiscus mildbraedii* Engl.	Rhamnaceae	28.5	–
4. *Celtis zenkeri* Engl.	Ulmaceae	26.5	–
5. *Rinorea ardisiiflora* (Welw. ex Oliv.) Kuntze	Violaceae	24.5	–
6. *Celtis wightii* Planch.	Ulmaceae	22.3	–
7. *Cynometra alexandri* C.H. Wright	Fabaceae	18.9	–
8. *Celtis durandii* Engl.	Ulmaceae	17.3	–
9. *Uvariopsis congensis* Robyns & Ghesq.	Annonaceae	14.7	–
10. *Khaya anthotheca* (Welw.) C.DC.	Meliaceae	11.5	0.8
11. *Tapura fischeri* Engl.	Dichapetalaceae	11.4	–
12. *Trichilia rubescens* Oliv.	Meliaceae	10.9	0.8
13. *Croton macrostachyus* Del.	Euphorbiaceae	7.0	2.2
14. *Holoptelea grandis* (Hutch.) Mildbr.	Ulmaceae	6.7	–
15. *Trilepisium madagascariensis* DC.	Moraceae	6.4	60.5
16. *Alchornea laxiflora* (Benth.) Pax & K. Hoffm.	Euphorbiaceae	5.6	–
17. *Margaritaria discoidea* (Baill.) Webster	Euphorbiaceae	5.2	4.6
18. *Chrysophyllum albidum* G. Don	Sapotaceae	5.0	– *
19. *Alstonia boonei* De Wild.	Apocynaceae	4.4	–
20. *Apodytes dimidiata* E. May. Ex Arn.	Icacinaceae	4.3	–

* *Chrysophyllum albidum* was not recorded in plots at Bulindi, but ≥1 individual occurs (Appendix 2)

That the floral composition of Bulindi forests should differ in important respects from nearby main forest blocks is unsurprising. Whereas the core habitat of the Bulindi chimpanzees is a network of swampy bottomland forest patches, supporting a groundwater-dependant vegetation community, similar forest occurs only in narrow waterlogged valleys in Budongo and was considered a relatively unimportant habitat type by Eggeling (1947). Though forest patches at Bulindi share a common riverine flora, marked spatial variability in species composition and abundance was evident, both between and within fragments. Such variation is expected to result in seasonal differences in food availability across forest types and individual fragments, and could thereby exert an important influence on patterns of ranging and seasonal habitat use by the chimpanzees (Chapter 7).

It is important to note that this vegetation survey focused exclusively on trees – the dominant ecological feature in a forest, and arguably the most relevant category of forest plant for a frugivorous ape. However, chimpanzees and other animals also exploit non-tree forest plants for food (Chapter 5). In the present study, there was insufficient time and resources to extend sampling to include other life forms such as the herbaceous and shrub understorey, and the vine and liana community, but any future research at Bulindi should endeavour to do so.

Human Disturbance

The tree survey was conducted during a dynamic period in which forests at Bulindi were undergoing rapid changes in structure and floristic composition arising from human activities including extensive logging, clearance for agriculture, tree felling for charcoal production and cutting for building poles and fencing. Consequently, a survey conducted five years before or five years after the present study would yield different results. For example, the valuable timber trees *Khaya anthotheca*, *Entandrophragma* spp. (the African mahoganies), *Lovoa trichilioides* and *Milicia excelsa* occur at Bulindi, but virtually all medium to large specimens of these species have now been removed. Since some canopy trees, including the mahoganies, are not reproductively mature until they have attained a large size (Plumptre 1995), regeneration of these species is unlikely. Furthermore, logging creates gaps that favour colonisation by pioneer and light demanding species. Changes to structure and composition of Bulindi forests imply that the resources available for animals such as chimpanzees are also in a state of flux.

Data collected on species harvested and the density of stumps indicate that even the most common species are at risk from over-harvesting. For example, trunks of the *Phoenix* palm are widely used for construction and fencing, and during 2007 many farmers cut palms to build barns for drying tobacco. The data suggest that current harvesting levels of this species may be unsustainable. Similarly, despite being among the most common large forest trees, *Antiaris toxicaria* was logged to such an extent that by the study's end most large specimens with straight trunks had been felled. This species is one of several forest trees being promoted in Uganda as substitutes for the more valuable hardwoods, which have become scarce due to over-exploitation (Zziwa et al. 2006). Along with several other species (including *Sterculia dawei* and *Trilepisium madagascariensis*), *A. toxicaria* was being targeted for timber at Bulindi because trees of greater economic importance were no longer available (Plate 5). The extensive timber extraction meant that large sections of forest were in the process of becoming cutovers. Such areas are likely to be cleared completely for farming once the big trees are removed. This process of logging followed by clearance was already underway during the study and is discussed in further detail in Chapter 9.

Summary

1. A quantitative vegetation survey was conducted in forest patches utilised by chimpanzees at Bulindi to determine tree species richness, composition and community structure. The main habitat of the chimpanzees is swamp forest dominated by the palm *Phoenix reclinata* and mixed forest dominated by members of the Moraceae. The exotic cocoa tree is locally abundant in abandoned forest plantations. While tree species density and stem density was similar to other Ugandan forests, little overlap in common tree species exists between Bulindi and Budongo, the nearest large forest block.
2. The proportion of plots in different forest types varied among forest patches. Consequently, densities of individual species differed markedly among forests. Thus food sources for chimpanzees are expected to have a heterogeneous distribution in forests within this fragmented habitat.
3. Analysis of forest disturbance (indexed as the density of cut stumps) demonstrates that chimpanzee habitat at Bulindi is severely threatened by human activities, particularly unregulated commercial logging, which precedes total clearance for farming. Current harvesting levels of certain species are plainly unsustainable.

CHAPTER 4 – FOREST PHENOLOGY & FOOD AVAILABILITY

4.1. Introduction

The popular perception of a tropical forest is of a highly productive environment that provides a rich, abundant and regular food supply to support its diversity of inhabitants. In fact, food production in tropical forests is never constant. Phenology studies across the tropics consistently show marked temporal variation in availability of fruits and leaves, governed by climatic variables such as rainfall, temperature, irradiance and day length (reviews in van Schaik et al. 1993; van Schaik and Pfannes 2005). Thus primary consumers face periods of both food abundance and food scarcity. Sometimes these ‘boom and bust’ periods follow a seasonal, annual or supra-annual cycle, but plant phenologies are also subject to the influence of unpredictable climatic events (e.g. Tutin and Fernandez 1993c; Wright et al. 1999). Periods of food scarcity in tropical forests will exert greater selective pressures on animal consumers than periods when food is plentiful. In primates, lean periods are associated with major dietary switches and related behavioural adaptations such as changes in habitat use, ranging and grouping patterns (Hemingway and Bynum 2005).

Assessment of temporal fluctuations in forest food availability is necessary for understanding dietary trends and characterising the ecological niche of a population. In this study, identification of seasonal troughs in natural food supply was predicted to be important for interpreting chimpanzee behavioural ecology in the dynamic farm–forest landscape at Bulindi. Elsewhere, lows in forest fruit availability are associated with increased consumption of certain cultivars, but not others (Naughton-Treves et al. 1998; Hockings et al. 2009). At some sites chimpanzees consume greater quantities of low-quality foods such as foliage during periods of fruit scarcity (Tutin et al. 1991; Wrangham et al. 1991; Yamagiwa and Basabose 2006a). Another possibility is that the riverine forests at Bulindi offer a less seasonally variable food supply relative to *terra firma* forests (cf. Gautier-Hion and Brugière 2005). If so, the phenology of particular species could be the major determinant of seasonal foraging strategies and range use by chimpanzees.

In addition to depicting seasonal patterns of resource availability, phenological studies are useful for identifying plant species that provide a reliable source of food for animals when preferred foods such as ripe fruits are scarce. Such resources are referred to as 'fallback' foods (Marshall and Wrangham 2007; Marshall et al. 2009).[1] In some habitats, figs (*Ficus* spp.) fulfil this role because of their aseasonal fruiting (Terborgh 1986). Identification of fallback foods is especially important for the management of wildlife populations occupying degraded or human-dominated environments, since preservation or restoration of such plant species should be a focus of habitat conservation initiatives (Marshall et al. 2009).

The aims of this chapter are as follows:

1. Describe the fruiting and leafing phenology of forest trees that provide food for chimpanzees;
2. Consider the contribution of particular species (including figs) to seasonal levels of food availability;
3. Identify potential fallback foods for chimpanzees.

4.2. Methods

4.2.1. Estimating Food Availability

Because fruit makes up the bulk of chimpanzee diet at all sites where feeding ecology has been investigated (Chapter 5), phenological monitoring was conducted primarily to relate patterns of diet and ranging by chimpanzees at Bulindi to the availability of forest fruits. Three common methods for estimating habitat-wide fruiting phenology are fruit traps, transect sampling and fruit trails (Ganzhorn 2003), and several studies have compared the results of different methods (Malenky et al. 1993; Chapman et al. 1994; Hemingway and Overdorff 1999; Fawcett 2000; Parrado-Rosselli et al. 2006). Fruit traps consist of framed structures with bags suspended below to collect fallen fruits,

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[1] Though fallback and 'keystone' foods are sometimes treated synonymously, the keystone term is more properly applied to resources presumed to sustain whole communities of consumers during ecological 'crunches'. The removal of a keystone resource (such as figs) is expected to have a major impact on the carrying capacity of the vertebrate community (Terborgh 1986).

placed randomly or at intervals along transects. Phenology transects involve visual monitoring of fruit (or leaf and flower) production in all trees, typically above 10 cm DBH, within a specified width along vegetation transects, but plots can also be used. Fruit trails entail monitoring individuals of selected species of interest, such as known food trees of primates. Thus, unlike fruit traps and transects a fruit trail is a non-systematic method. Although some studies have used fruit traps to estimate food abundance of chimpanzee food trees (Furuichi et al. 2001a; Takenoshita et al. 2008), Chapman et al. (1994) found that estimates derived from traps did not correlate with estimates derived from either transect sampling or fruit trails (see also Parrado-Rosselli et al. 2006). However, estimates based on fruit trails were closely correlated with systematic transect monitoring (cf. Fawcett 2000). These authors recommend that if a non-systematic fruit trail is used, estimates should be calibrated to account for differences in species abundance by determining the actual densities of the selected species. Furthermore, the degree of correspondence between transect- and trail-based estimates is sensitive to the number or composition of species included (Chapman et al. 1994; Hemingway and Overdorff 1999). Thus, the ideal is to include as large a number of species in a fruit trail as is feasible. Similarly, very small sample sizes of individuals per species should be avoided (Hemingway and Overdorff 1999).

For this study the fruit trail method was selected for the following reasons. First, densities of all but the rarest tree species at Bulindi were known from tree surveys (Chapter 3), thus enabling calibration of estimates derived from a fruit trail. Second, since community-wide measures of food availability, as estimated from phenology transects or plots, will include both food and non-food tree species, results may not necessarily reveal patterns of resource availability relevant to study animals. Third, at Bulindi tree species that occur at relatively low densities, but which were predicted to be important food sources for chimpanzees, such as figs, would be underrepresented by surveying plot trees. Fourth, the relatively low average DBH of trees at Bulindi (Chapter 3) suggests that a substantial proportion of plot trees are immature. Phenology studies require a large time commitment. By choosing a fruit trail comprising mature individuals of selected trees species eaten by chimpanzees, I aimed to avoid collecting data on trees that either do not provide food for the apes or had yet to attain reproductive size (but see below).

Selection of tree species for a phenology trail

In studies that use phenology trails to estimate food availability for primates, tree species selected for monitoring are usually those confirmed in the diet of the study animal population (e.g. Fawcett 2000). However, phenology surveys at Bulindi began in December 2006 when few data on the feeding habits of the chimpanzees were available. (Intensive faecal analysis did not commence until January 2007, and encounters with chimpanzees had, at that point, yielded few direct observations of feeding). A comprehensive literature search was undertaken to identify tree species recorded at Bulindi, the fruits of which are eaten by chimpanzees at other sites. Particular attention was paid to studies from Budongo, Kibale and Kalinzu forests, in western Uganda, since these forests share many tree species with Bulindi (Wrangham et al. 1994; Newton-Fisher 1999; Furuichi et al. 2001a; Mitani et al. 2002; Reynolds 2005). A drawback to this approach is that plant species consumed avidly by chimpanzees at one site may be eaten rarely or ignored altogether at another, reflecting differences in abundance or, in some instances, potential food preferences of particular populations (Nishida et al. 1983; Boesch et al. 2006). Nevertheless, many species that were chosen are eaten by chimpanzees at multiple sites and several are major or 'preferred' foods; others are recorded as eaten at a single site only, but in most cases this is Budongo, the closest site to Bulindi.

Thirty tree species were selected for phenological monitoring (Table 4.1). These comprise nine fig species and 21 non-fig species (the three species of *Entandrophragma* are lumped in Table 4.1) and include two species of cultivar, cocoa and guava. Given that seven of these species are among the ten most common trees in Bulindi forests, including four of the five most common, and that together the selected species account for 70% of measured stems and 64% of total BA ha^{-1} for trees ≥10 cm DBH, overall forest phenology is probably sufficiently represented by these 30 species. The majority produce succulent fruit (drupes or berries), but species with arillate fruit (e.g. *Pycnanthus angolensis*), fleshy indehiscent pods (*Parkia filicoidea*, *Theobroma cacao*), dehiscent pods (*Sterculia dawei*) and wind-dispersed seeds (*Entandrophragma* spp.) are also represented.

Table 4.1. Tree species included in phenology surveys. Species were selected on the basis that the fruits are eaten by chimpanzees at other sites, particularly in western Uganda.

Species	**Family**	**Height category** [a]	**# Individuals** [b]	**Min. DBH (cm)** [c]	**Adult density (stems ha^{-1})** [d]	**Mean Adult DBH (cm)** [e]
1. Annona senegalensis Pers.	Annonaceae	U	10 (*7–10*)	**10**	1.4	11.7
2. Antiaris toxicaria Leschen.	Moraceae	C	20 (*18–21*)	30	8.9	46.2
3. Croton macrostachyus Del.	Euphorbiaceae	M	11 (*10–11*)	20	1.6	24.0
4. Entandrophragma spp. [f]	Meliaceae	M–C	15 (*13–17*)	–	–	–
5. Ficus exasperata Vahl	Moraceae	M	12 (*11–13*)	20	1.4	33.7
6. Ficus glumosa Del.	Moraceae	U	6	15	(0.15)	(35.6)
7. Ficus mucuso Ficalho	Moraceae	C	12 (*11–12*)	35	0.3	82.7
8. Ficus natalensis Hochst. [g]	Moraceae	C	32	40	1.9	74.1
9. Ficus ovata Vahl	Moraceae	C	22 (*19–22*)	35	0.8	56.5
10. Ficus sansibarica Warb.	Moraceae	C	1	–	(0.15)	(134.2)
11. Ficus sur Forssk.	Moraceae	M	40 (*39–41*)	20	3.5	36.3
12. Ficus vallis-choudae Del.	Moraceae	M	17 (*16–17*)	10	1.6	15.9
13. Ficus variifolia Warb.	Moraceae	C	4	35	(0.15)	(155.6)
14. Harungana madagascariensis Poir.	Guttiferae	U	10 (*9–11*)	10	1.4	16.6
15. Macaranga schweinfurthii Pax	Euphorbiaceae	U–M	18	15	10.8	27.4
16. Maesopsis eminii Engl.	Rhamnaceae	M	10	20	1.4	36.3
17. Morus mesozygia Stapf	Moraceae	M–C	11 (*9–11*)	30	1.6	49.8
18. Parkia filicoidea (Welw. ex) Oliv.	Fabaceae	C	12 (*7–12*)	30	1.9	46.5
19. Phoenix reclinata Jacq.	Arecaceae (Palmae)	U	25 (*24–25*)	10	106.5	18.0
20. Pseudospondias microcarpa (A. Rich.) Engl.	Anacardiaceae	C	24 (*22–24*)	35	7.6	57.9
21. Psidium guajava L. [guava tree]	Myrtaceae	U	9 (*5–9*)	**10**	(0.15)	(10.9)
22. Pycnanthus angolensis (Welw.) Warb.	Myristicaceae	M	19 (*17–19*)	20	1.1	32.9
23. Sterculia dawei Sprague	Sterculiaceae	M–C	12 (*11–12*)	20	1.9	48.5
24. Teclea nobilis Del.	Rutaceae	U	20 (*19–20*)	10	17.3	19.4
25. Theobroma cacao L. [cocoa tree]	Sterculiaceae	U	18 (*13–18*)	**10**	31.1	12.8
26. Trema orientalis (L.) Bl.	Ulmaceae	U	6 (*5–6*)	**10**	1.9	17.5
27. Trilepisium madagascariensis DC.	Moraceae	M–C	14 (*11–15*)	20	26.5	32.7
28. Zanha golungensis Hiern	Sapindaceae	M–C	10 (*9–10*)	30	0.8	45.2
All species			414 (*386–422*)			

Notes overleaf

Table 4.1. *notes*

[a] Species height category: U = understorey, M = mid-storey, C = canopy; assessment was based on observations of adult individuals of each species at Bulindi.
[b] Values represent the median (+ range where applicable) number of adult individuals of each species monitored per biweekly phenology sample.
[c] Values show the minimum size (≥10 cm DBH) at which monitored individuals were considered adult (see text). A minimum diameter is not given for *Entandrophragma* trees, which did not fruit during the study, or for *Ficus sansibarica* because only one very large individual was monitored. Values in bold indicate species that fruit <10 cm DBH.
[d] Species densities are adjusted to include adult individuals only. Numbers in parenthesis indicate species not recorded in plots; these species were assigned a density half that of the rarest plot tree species.
[e] Average DBH (cm) for adult trees recorded in plots. For non-plot trees, values in parenthesis are the mean DBH of the phenology specimens.
[f] Not all *Entandrophragma* specimens were identified to species level but the sample included individuals of *E. angolense* (Welw.) C.DC., *E. cylindricum* (Sprague) Sprague and *E. utile* (Dawe & Sprague) Sprague.
[g] A small proportion of *F. natalensis* individuals may belong to closely related species (e.g. *F. thonningii*, *F. pseudomangifera*) which are difficult to distinguish in the field in the absence of reproductive characters (Hamilton 1991); of three vouchers examined at Makerere University Herbarium, one was identified as *F. thonningii* Bl.

Fruit trail establishment and monitoring

The phenology trail covered all main forest fragments within the study area (five riverine and one hillside ecotone forest), though it did not penetrate the Nyakakonge sector of Mparangasi–Nyakakonge due to the network of swampy streams that made this forest difficult to access, particularly after heavy rain. But by monitoring individuals of each species across multiple forest patches that encompass most of the habitually used portion of the chimpanzees' range, I aimed to gain a more accurate measure of habitat-wide forest food availability than if sampling were limited to a single patch. Phenology sampling was restricted to forest mainly because it is the core habitat of the chimpanzees, but also because time constraints meant it was not possible to extend vegetation surveys and phenological monitoring to include the large areas of wooded grassland (e.g. Kandanda–Ngobya FR) towards the periphery of the apes' range.

Phenology trees were located along transects or along forest edges. Food trees growing outside of forest on agricultural land or around homesteads were not monitored, whether cultivated or otherwise. Thus all cocoa trees were in abandoned forest *shambas* and only naturalised guava trees were monitored. Hemingway and Overdorff (1999) found that phenophases of canopy and understorey species were asynchronous, and differed in magnitude and duration. Phenology species chosen for this study range in height from understorey trees to mid-storey and canopy trees (Table 4.1). The trail encompassed areas of swamp, mixed, cocoa and ecotone forest; thus all major forest types were represented.

Phenological monitoring was conducted twice per month between December 2006 and January 2008 (14 months), in the second and fourth week of each month, except during January 2008 when the fruit trail was walked once only (i.e. the trail was completed 27 times in total). Although most long-term studies record phenology monthly, a two-week inter-sample period was selected for this study. Chapman et al. (1994: 164) reported within-month variation in numbers of trees fruiting when monthly versus biweekly sampling regimes were compared and considered that such variability "may represent a significant change to some frugivores". Furthermore, fruits of certain species selected for monitoring, such as figs, typically do not remain on the tree long after ripening since they attract a variety of animals (pers. obs.), and consequently ripe fruit crops will frequently be missed in monthly surveys. The trail took 3–4 days to complete (or 6–8 days per month).

With the exception of the final survey all phenological monitoring was conducted by myself and a field assistant, thereby minimising inter-observer variability effects. Data for January 2008 were collected by an experienced field assistant who had helped record phenology during the previous ten consecutive surveys.

No. of trees monitored

For common species 15−25 reproductively mature individuals were monitored along the phenology trail (Table 4.1). Higher numbers for the most common figs *Ficus sur* and *F. natalensis* result from the expectation that knowledge of the fruiting patterns of large fig trees would assist in locating chimpanzees. For species that occur at relatively low densities I attempted to locate a minimum of ten adult individuals, though for several species fewer specimens were found (the single known specimen of *Ficus sansibarica* was included because of its prominent location in the heart of the chimpanzees' range). Each phenology tree was georeferenced and marked with a numbered aluminium tag, and its DBH measured.

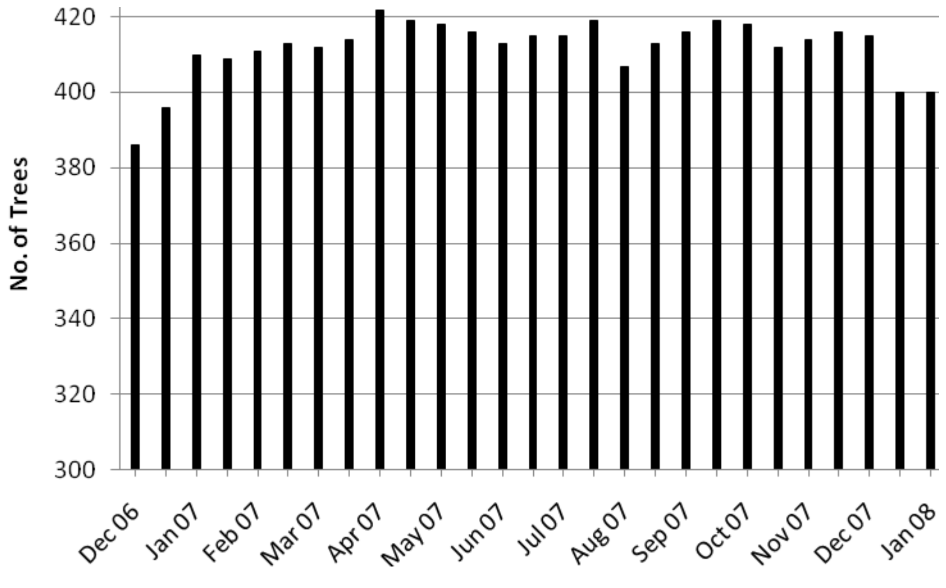

Figure 4.1. The number of phenology trees monitored per biweekly survey (Dec 2006–Jan 2008).

The number of mature trees monitored per sampling period was not constant during the study (median = 414, range: 386–422;[2] Figure 4.1). This was for several reasons. First, during December 2006 new individuals were still being added to the sample and new species were added in January 2007 (*Ficus glumosa*) and April 2007 (*Psidium guajava*). Second, while an effort was made to avoid close encounters with chimpanzees during phenology surveys, several times chimpanzee parties were inadvertently met in areas where target trees were located and reacted with alarm or intimidation, resulting in small numbers of trees being passed over. Third, the presence of pitsawing teams sometimes made data collection difficult or awkward (as when pitsawyers hid from researchers). Thus the slight decline in trees sampled during May–June and August 2007 is largely explained by the presence of pitsawyers in the northern part of Kyamalera. Fourth, individual trees were inadvertently missed on occasion. The most frequent cause of fluctuations across surveys in number of trees monitored was loss of phenology trees. In total 54 trees were lost (13% of the sample median): 17 were cut for timber (pit-sawn or chain-sawn), 16 were cut when forest was cleared for gardens, tobacco nurseries or a pine plantation (in some cases felled trees were first sawn for timber), eight were cut for building poles, five cocoa trees were part of an entire *shamba* cut in August 2007 apparently to discourage use by chimpanzees, four trees fell over during strong winds, two were crushed by felled timber trees, one was burnt dry by fire, and one died naturally (Appendix 3). In most cases a replacement tree was located during the same or the following survey, but no replacements were made after August 2007. Tree losses were particularly disruptive to data collection when several individuals of a species were cut concurrently, as occurred with the aforementioned cocoa (28% of the total sample of cocoa trees). Similarly, four of 12 (33%) *Sterculia dawei* specimens were logged with chainsaws in January–February 2007. In December 2007 four of 12 (33%) *Parkia filicoidea* trees were among ten phenology trees lost when forest was clear-felled in Kiseeta in preparation for planting pine. That event accounts for the drop in trees monitored in December 2007 (Figure 4.1). The phenology tree species most liable to require replacement was *Antiaris toxicaria* (Appendix 3). Of the original sample of 20 individuals, eight (40%) were logged for timber during the study (one replacement tree was also subsequently logged and another cut during forest clearance). Most monitored *Antiaris* that remained by the study's end either had

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[2] Specimens subsequently identified as immature and removed from the data set are excluded from these figures.

crooked trunks or were small or medium-sized. The median number of adult individuals monitored of each phenology species per sampling period (+ range) is shown in Table 4.1.

Estimating food abundance

A variety of methods have been used to estimate fruit abundance of tropical trees (Chapman et al. 1992). These include measurements of tree size (DBH or crown volume), assumed to reflect a tree's ability to produce fruit, and visual assessments of crop size. In some studies counts are made of the number of fruits in a section of the tree and extrapolated across the whole of the fruit-production area. A less time-consuming method involves ranking crop size, typically on a scale of 0–4 (e.g. Sun et al. 1996; Fawcett 2000). Alternatively, presence or absence of fruit can simply be recorded. Chapman et al. (1992) compared three methods: DBH, crown volume, and visual counts of total crop size. They found that DBH was the most consistently precise method, exhibiting low-levels of inter-observer variability, and was time-efficient relative to other methods. Fawcett (2000) compared estimates of habitat-wide food availability (discussed below) based on visual ranking of crop size with those derived from simple presence/absence scores, and found they were significantly correlated for all phenological states (e.g. flowers, fruits, leaves), indicating presence/absence scores are sufficient for detecting seasonal variation in food production. Nevertheless, the magnitude of the peaks and troughs in food availability – which may be important for consumers – may be lost with presence/absence data (Fawcett 2000). Furthermore, assessment of variation over time in amount of fruit produced by particular individuals or species requires estimates of abundance (Chapman et al. 2005).

For this study, I used DBH as a measure of patch size (Chapman et al. 1992), and a ranked score of fruit crop size to weight the DBH value. For each tree, the amount of ripe fruit was scored on a 0−4 scale (including 0.5 intervals), where a score of 1 indicates a cover of 25% and 4 implies a full cover (Fawcett 2000). Although chimpanzees are predominantly frugivorous, and the spatial–temporal distribution of fruits is particularly important for them, they also consume appreciable amounts of young leaves (e.g. Morgan and Sanz 2006), which are detectable in dung (Tutin and

Fernandez 1993a). For this reason leaf flushing was also monitored.[3] As noted above, phenology species were selected because their fruits are eaten by chimpanzees at other sites, but in most cases the palatability of the young leaves for apes is unknown. However, leaf flushing in the selected species is assumed to reflect community-wide patterns in availability of new leaves. The amount of young leaves on trees was scored using the same ranking system as described for fruit. Phenology trees were examined through binoculars. Trace quantities of both fruit and leaves were treated as zero (absent) amounts.

Fruit ripeness

Many phenological studies lump unripe and ripe fruits together because fruits of some species exhibit little change in colour during ripening, thereby making assessment of maturity difficult. For animal consumers that frequently eat fruits unripe a distinction between ripe and unripe may be unimportant in estimates of food availability. Chimpanzees are ripe fruit specialists, and whilst unripe fruits of certain species are occasionally eaten, overall consumption of unripe relative to ripe fruits is low (Wrangham et al. 1998; Boesch et al. 2006). Furthermore, the fruits of some species monitored for this study took several months to ripen (e.g. *Phoenix reclinata* and *Pseudospondias microcarpa*), during which time no evidence suggested chimpanzees ate them (i.e. seeds did not appear in dung until fully ripe fruit was observed on the trees). Thus lumping unripe and ripe fruits would overestimate food availability considerably. Conversely, by restricting the index to include ripe fruits only, food availability will be underestimated if unripe fruits of certain species are occasionally eaten; however, this bias is probably small by comparison. Therefore, a distinction was made between ripe and unripe fruit. In most phenology species ripe fruits were clearly distinguishable from unripe fruits in size and colour. For species with fruits that remain green when ripe (e.g. *Ficus ovata*), freshly fallen fruit was examined to infer ripeness. An exception was made for cocoa. Ripe cocoa pods were observed on trees in abandoned forest *shambas* only very rarely. The pods are eaten by a number of animals (e.g. monkeys, squirrels) as well as chimpanzees and probably seldom persist on trees long enough to ripen. The distinctive remains of chimpanzee feeding on cocoa were

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[3] Data were also collected on flower phenology but results are not presented here. Unlike fruit and leaves, flowers leave little or no recognisable trace in faeces. Consequently, flower phenology could not be examined in relation to the chimpanzee diet in this study, since the latter was investigated principally through dung analysis (Chapter 5).

found regularly throughout the study and, aside from when chimpanzees raided cultivated *shambas* outside of the forest and fed on ripe pods, cocoa consumed in the forest was almost exclusively unripe. Therefore unripe cocoa pods were treated as 'ripe' in the analysis.

4.2.2. Data Analysis

Food availability indices

As with abundance estimates for individual trees, different studies often use different methods to index habitat-wide food availability, confounding inter-site comparisons. For phenology transects, where all trees are monitored, a simple food availability index (FAI) for a given month can be calculated as the proportion of trees bearing fruit or by summing the DBH of fruiting trees (Chapman et al. 1994). Where only key species are monitored, as in this study, FAIs must take into account species density if results are to be extrapolated across the area studied. Measures of crop size (e.g. DBH or BA, and/or visual estimate) are used to weight the density estimate of fruiting trees (Chapman et al. 1994; Sun et. al. 1996).

Tree size at reproduction. A problem with many estimates of habitat-wide food availability, which are calibrated to account for variation in tree species densities, is the assumption that different taxa reach maturity at similar diameter sizes. In fact, reproductive size thresholds in tropical trees vary enormously, even among closely related species (Thomas 1996). For example, while many understorey trees are reproductive at 10 cm DBH or less, canopy species of comparable size are typically juvenile and will only flower or fruit once they have attained a much larger size. Plumptre (1995) examined the distribution of fruiting at different diameter classes in selected tree species at Budongo and showed that individuals of some canopy species must be about 40 cm diameter to produce fruit; most notably, only a small proportion of *Entandrophragma* spp. (Meliaceae) fruited below 80 cm DBH. Clearly, estimates of food availability based on species densities for trees ≥10 cm DBH will overestimate food production if the actual density of mature individuals is much lower.

Some studies have addressed this problem by defining adult trees as those above a specified DBH (e.g. 20 cm) and adjusting densities accordingly (Sun et al. 1996; Anderson et al. 2002; Gross-Camp et al. 2009). Ideally, however, an assessment of interspecies variation in size at reproductive onset is needed for greater accuracy, which requires a sufficient sample of trees in the lower diameter classes. Due to time constraints such a study was not feasible here, and the majority of phenology trees were selected on the basis of size (i.e. presumed maturity) as well as visibility. Even so, sample trees encompassed a range of diameters, and for most mid-storey and canopy species the original sample also included several small-sized individuals (between 10–35 cm DBH). This enabled a crude assessment of diameter size at maturity. Thus, where possible, the lower size threshold at which individuals of a species were considered adult fell midway between the DBH of the smallest stem that fruited (whether unripe or ripe fruits were seen) and the largest stem that did not, rounded to the nearest 5 cm. For example, all but one of 12 *Ficus mucuso* individuals of ≥40 cm DBH fruited, whereas all three specimens below 30 cm DBH did not; thus *F. mucuso* trees of ≥35 cm DBH were considered potentially mature. Ideally, a longer study is needed to classify trees as mature or immature in this way since smaller stems may exhibit irregular fruiting; however, the conservative measure of fruit production used here is preferable to an inflated estimate that arises if all trees >10 cm DBH are considered adult.

Overall, understorey species fruited at 10 cm DBH (and several in fact fruit at lesser diameters), mid-storey species tended to fruit at a minimum of 20 cm DBH, and larger canopy species did not fruit unless they were above 30 cm diameter (Table 4.1). A minimum fruiting size threshold based on height category was assigned for two species that lacked representatives in the smallest diameter classes. Immature sample trees were removed from the data set. The minimum fruiting diameter for each species was used to adjust density values to include adult individuals only for calculating habitat-wide food availability. Densities of four rare species were unknown because the species was either not encountered in vegetation plots (*Ficus sansibarica*, *F. glumosa* and guava) or was represented by a juvenile specimen only (*F. variifolia*). These species were arbitrarily assigned an adult density half that of the lowest recorded density for a plot tree (0.15 individuals ha^{-1}).

A monthly forest fruit availability index (F_{m1}) was calculated as follows:

$$F_{m1} = \sum_{k=1}^{n} F_{km} \text{ x } D_k \text{ x } S_k$$

where F_{km} denotes the mean ripe fruit score of all sampled individuals in species k during month m, D_k denotes the density (stems ha $^{-1}$) of adult trees of species k, and S_k is the mean size in centimetres DBH of adult trees of species k (e.g. Fawcett 2000).[4] Thus monthly food availability values were calculated for each of the 14 months of the study. Seasonal peaks and troughs in food availability were identified by standardising the monthly scores as Z-values (obtained by subtracting the mean from each monthly value and dividing by the standard deviation). Positive values are months of above-average food availability and negative values are months of below-average food availability.

Plumptre (2006) noted that phenology measures are greatly influenced by the point in time at which individual trees are monitored. As mentioned above, it was observed during this study that ripe figs in particular do not remain on the tree for long due to consumer activity. On many occasions fig trees observed with large ripe fruit crops outside of phenological sampling were recorded with very small amounts of fruit just 1–3 days later. Possibly, a simple presence/absence score for ripe fruit would better reflect food availability in the days in and around the sampling period. For this reason, I calculated a second FAI based on presence/absence of ripe fruit and assessed its concordance with the FAI derived from mean ranked scores.

The second monthly forest fruit availability index (F_{m2}) is calculated as:

$$F_{m2} = \sum_{k=1}^{n} P_{km} \text{ x } D_k \text{ x } S_k$$

where P_{km} denotes the proportion of individuals with ripe fruit in species k during month m, D_k denotes the density (stems ha $^{-1}$) of adult trees of species k, and S_k is the mean size in centimetres DBH of adult trees of species k (e.g. Fawcett 2000; Mitani et al. 2002).

A different way of depicting phenological patterns is to plot the number or proportion of phenology species producing ripe fruit each month (White 1994; Tutin et al. 1997).

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[4] Mean DBH of non-plot species is the average DBH of the phenology specimens.

Although this simple index is not an estimate of availability, since it does not take into account species density, patch size or fruit crop size, it is useful for detecting community-wide fruiting patterns. Thus fruit availability was also assessed as the proportion of monitored species that had at least one individual with ripe fruit each month. Fruiting patterns of individual species were also examined. A *fruiting event* in a species is defined as a period of ripe fruiting with an interval of more than one month (i.e. a minimum of three sampling periods) separating it from other such events. An *extended fruiting* event lasted for six or more months (Newstrom et al. 1994).

For young leaves, an FAI derived from ranked abundance scores was calculated as for ripe fruit. An index based on presence/absence scores was deemed inadequate for revealing peaks and troughs in flushing because, unlike ripe fruit, small amounts of new leaves were observed on trees year-round. The FAI for young leaves is based on species densities and mean DBH for all trees ≥10 cm DBH, since it was not necessary to correct for reproductive size of trees. For all indices the monthly FAI is the average of the two biweekly records for each month.

Statistics

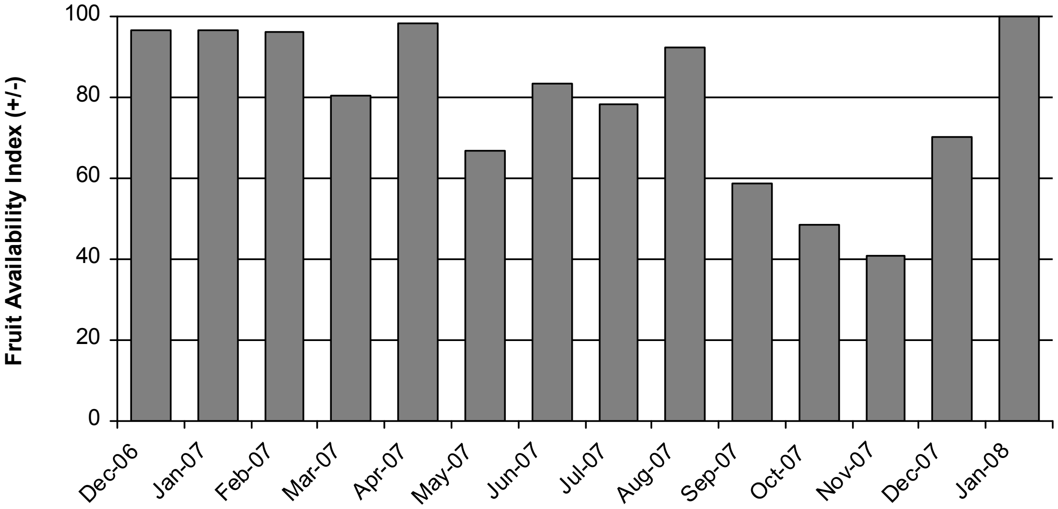
Pearson correlation coefficients were employed to test for correspondence between food availability indices. Variables were tested for normality and in one case log-10 transformation was done to meet the assumptions of the correlation. Linear regression was used to examine the relationship between a dependent and an independent (predictor) variable. Residuals of the dependent variable were inspected for normality, and log-10 transformations were applied where appropriate (Chen et al. 2003). All tests are two-tailed and $p < 0.05$ was considered to indicate significance. The analysis was performed using SPSS version 17.

4.3. Results

4.3.1. Comparison of Fruit Availability Indices

The monthly index of ripe fruit availability derived from visual estimates (ranks) of total crop size was highly correlated with the index based on presence/absence of ripe fruit ($r = 0.852$, $n = 14$, $p < 0.001$). This indicates that the simple method of recording whether a tree has ripe fruit or not is sufficient for detecting temporal variation in phenology. Nevertheless, despite the close overall agreement between the two methods it can be seen in Figure 4.2 that peaks and troughs in monthly fruit availability are more pronounced when data from ranked scores are used. This finding parallels that of a previous study by Fawcett (2000) at Budongo. Most notably, fruit availability during April and August 07 appears high based on presence/absence scores, but is moderate when the ranked data are used. In part, this reflects the fact that monthly abundance estimates are highly sensitive to differences in average fruit crop scores of the most common species. For instance, *Trilepisium madagascariensis* is the second most abundant species in Bulindi forests with the highest BA ha $^{-1}$; consequently, even a small proportion of sample trees with fruit will influence the monthly food availability estimate. In April two of fifteen *Trilepisium* individuals were recorded with ripe fruit. However, fruit crop size was in fact marginal (scored as 0.5 in both *Trilepisium* individuals). Therefore when ranked crop size data are used the contribution of this relatively minor fruiting event to the monthly estimate is considerably less than if fruit presence is the measure of abundance. In August the discrepancy is largely attributable to different estimates produced by the two methods for the superabundant *Phoenix* palm. August marked the end of the *Phoenix* fruiting season, and while the proportion of palms with fruit was still relatively high average remaining fruit crops were small. As noted by previous researchers (Chapman et al. 1994), I have no 'true' measure of forest-wide fruit availability at Bulindi with which to assess the accuracy of the two methods. However, since temporal variation in average fruit crop size of the most common species has an important bearing on overall monthly estimates, the FAI derived from ranked data is used in all subsequent analyses unless otherwise specified.

(A)



(B)

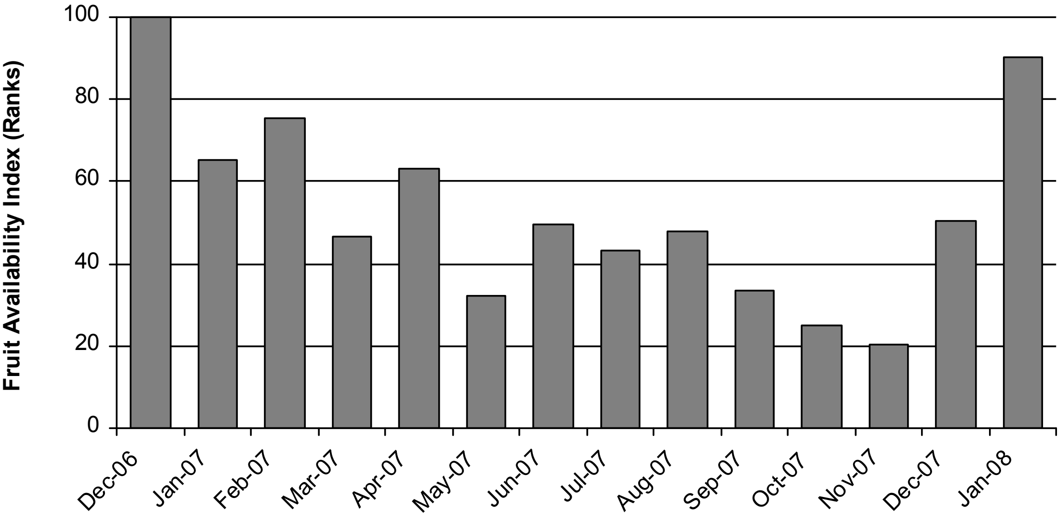


Figure 4.2. Monthly availability of ripe forest fruit derived from two methods: (A) presence/absence scores and (B) visually estimated ranks of crop size. Results are expressed as an index of 100 where the month with the highest value = 100 (following Fawcett 2000).

4.3.2. Monthly Changes in Fruit Availability

Figure 4.3 shows monthly FAI scores as standardised Z-values. The mean score is represented by 0; thus positive values indicate months with above-average fruit availability while negative numbers represent below-average months. Fruit was especially abundant in December 06 and January 08 (>1 SD above the mean), while October and November 07 emerge as particularly fruit-poor months (>1 SD below). Overall, the main period of fruit abundance was at the beginning of the study in December–February (and had begun again in January 08, the final month) whereas September–November was the major period of fruit scarcity in Bulindi forests and can be regarded as the 'low fruiting season'. Fruit availability during most other months was at intermediate to low levels.

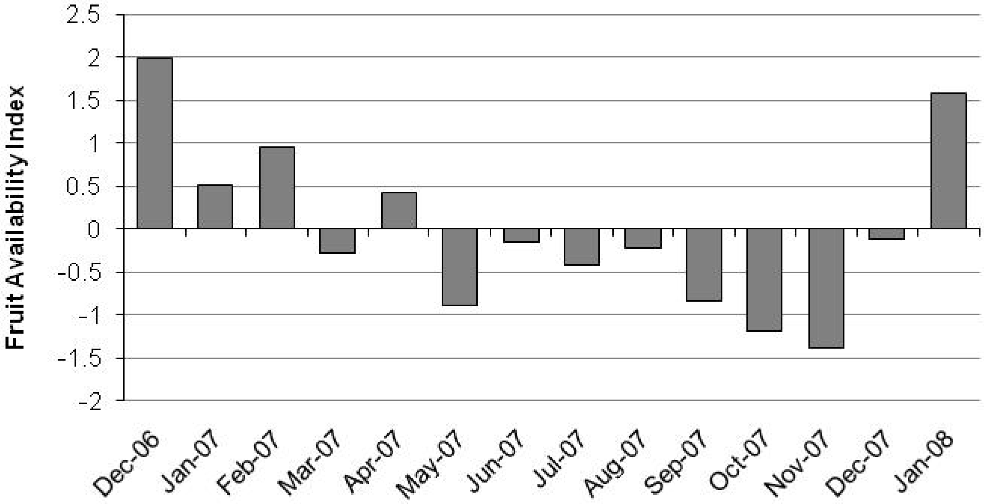


Figure 4.3. Monthly availability of ripe forest fruit shown as standardised Z-values. The mean monthly value is 0 and the SD is 1. Positive values indicate months of above-average food availability and negative values are months of below-average food availability.

The percentage of phenology species producing ripe fruit each month is shown in Figure 4.4. The correlation between the monthly proportion of species with at least one individual recorded with ripe fruit and the FAI was positive but non-significant (r = 0.471, p = 0.09). January and April 07 stand out as months when the greatest proportion of species were observed with ripe fruit (48% and 57%, respectively), though higher abundance estimates were obtained in December 06, February 07 and January 08 (Figure 4.3). Also, troughs in the proportion of species fruiting are not as apparent as troughs in abundance as indicated by the monthly FAI, and only November 07 emerges as a month when relatively few species had ripe fruit; for all other months the proportion of species seen with fruit was >30%. The discordance is because the FAI largely reflects the fruiting patterns of the most common species (see below), and many non-figs that fruited during the low fruiting season were relatively low-density species (e.g. *Croton macrostachyus*, *Pycnanthus angolensis*, *Sterculia dawei*). The proportion of fruiting species that were figs remained relatively constant throughout the study (Figure 4.4), and was greater than their representation in the sample (30%) in 12 of 14 months ($\chi^2 = 7.143$, $df = 1$, $p = 0.008$).

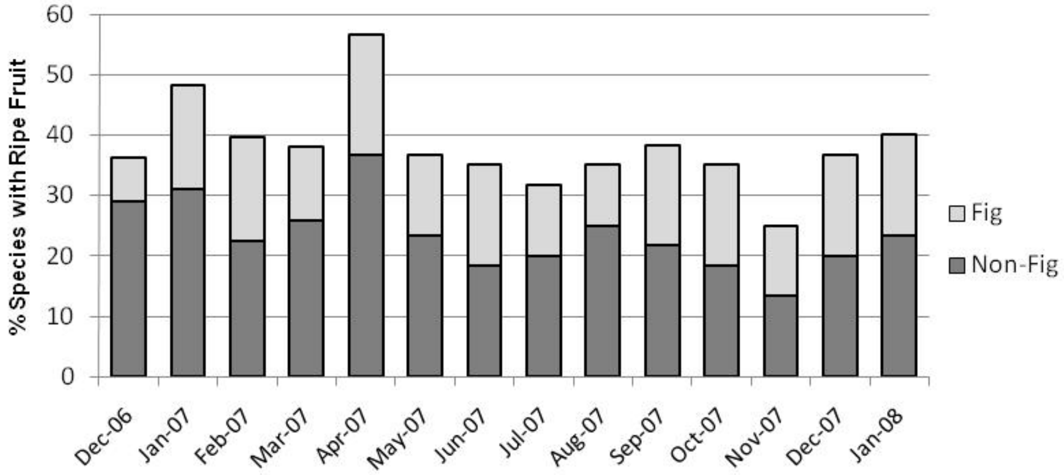


Figure 4.4. The proportion of phenology species with ripe fruit each month. Fig species (light grey bars), which fruit asynchronously and throughout the year, are distinguished from non-fig species (dark grey bars).

For many species the proportion of sample trees fruiting during a given survey was low (typically <30%), even during peak fruiting events. For example, *Antiaris toxicaria* fruited between February–May 07 but the proportion of sample trees with ripe fruit was only 5–15% during that time.

4.3.3. Species Fruiting Patterns

Phenology species differed considerably in the duration and frequency of ripe fruiting events (Table 4.2). With the exception of the three *Entandrophragma* spp., all phenology species produced ripe fruit between December 06 and January 08. Since only two of the monitored individuals of *Entandrophragma* were above 50 cm DBH, which may be a minimum reproductive size for these trees (Plumptre 1995), it seems likely that most or all individuals in the sample were immature. Aside from figs, within-species fruiting synchrony was the prevalent pattern for most monitored species. During the 14-month monitoring period several species exhibited a single, distinct fruiting season lasting 1–4 months (*Antiaris toxicaria*, *Macaranga schweinfurthii*, *Maesopsis eminii*, *Morus mesozygia*, *Parkia filicoidea*, *Zanha golungensis*). Aside from *Macaranga*, which fruited during the relatively low fruiting months of August–September, the fruiting of these species was concentrated between February–April when forest fruit availability was at medium to high levels. These species were again seen with flower or unripe fruit during the final phenology survey in January 08, suggesting a single annual fruiting cycle may be typical for these taxa (Table 4.2).

Table 4.2. Fruiting characteristics of phenology tree species, Dec 2006–Jan 2008.

Phenology Tree Species	**# Months with Ripe Fruit [1]**	**# Ripe Fruit Events Recorded [2]**	**Fruiting cycle [3]**	**Max. Length of Ripe Fruit Event [4]**
1. Annona senegalensis Pers.	4 / 14	2	Sub-annual	3 mo
2. Antiaris toxicaria Leschen.	4 / 14	1	Annual	4 mo
3. Croton macrostachyus Del.	5 / 14	2	Sub-annual	≥3 mo
4. Entandrophragma spp. [3 species]	0 / 14	0	unknown	unknown
5. Ficus exasperata Vahl	2 / 14	–	Asynchronous	–
6. Ficus glumosa Del.	9 / 13	–	Asynchronous	–
7. Ficus mucuso Ficalho	7 / 14	–	Asynchronous	–
8. Ficus natalensis Hochst.	14 / 14	–	Asynchronous	–
9. Ficus ovata Vahl	8 / 14	–	Asynchronous	–
10. Ficus sansibarica Warb.	3 / 14	–	Asynchronous	–
11. Ficus sur Forssk.	14 / 14	–	Asynchronous	–
12. Ficus vallis-choudae Del.	14 / 14	–	Asynchronous	–
13. Ficus variifolia Warb.	1 / 14	–	Asynchronous	–
14. Harungana madagascariensis Poir.	6 / 14	2	Sub-annual	≥2 mo
15. Macaranga schweinfurthii Pax	2 / 14	1	Annual	2 mo
16. Maesopsis eminii Engl.	2 / 14	1	Annual	2 mo
17. Morus mesozygia Stapf	1 / 14	1	Annual	1 mo
18. Parkia filicoidea (Welw. ex) Oliv.	3 / 14	1	Annual	3 mo
19. Phoenix reclinata Jacq.	11 / 14	1	Continual	≥9 mo *
20. Pseudospondias microcarpa (A. Rich.) Engl.	8 / 14	2	Sub-annual	5 mo
21. Psidium guajava L. [guava tree]	8 / 10	1	Continual	≥8 mo *
22. Pycnanthus angolensis (Welw.) Warb.	13 / 14	2	Continual	≥8 mo *
23. Sterculia dawei Sprague	12 / 14	2	Continual	≥10 mo *
24. Teclea nobilis Del.	6 / 14	2	Sub-annual	5 mo
25. Theobroma cacao L. [cocoa tree]	14 / 14	1	Continual	≥14 mo *
26. Trema orientalis (L.) Bl.	12 / 14	2	Continual	≥6 mo *
27. Trilepisium madagascariensis DC.	3 / 14	2	Sub-annual	2 mo
28. Zanha golungensis Hiern	1 / 14	1	Annual	1 mo

[1] Cells show the number of months (N = 14) in which at least one monitored tree was recorded with ripe fruit. Individuals of *F. glumosa* and *Psidium guajava* were monitored for 13 and 10 months only, respectively.

[2] Successive ripe fruiting events were separated by >1 mo (i.e. at least three sampling periods).

[3] Refers to fruit production. Proposed fruiting cycles, as indicated by this study, are based on the classification scheme of Newstrom et al. (1994): Continual – unripe or ripe fruit produced with only sporadic breaks lasting <1 mo; Annual – only one major fruiting cycle within 12 months; Sub-annual – fruiting in more than one cycle within 12 months. Individual *Ficus* spp. trees fruit asynchronously and irregularly.

[4] Values are the largest number of consecutive months spanned by a ripe fruiting event. Minimum estimates are given for species that had ripe fruit during the first or final phenology survey. *Asterisks indicate species that exhibited extended ripe fruiting events (≥6 months); extended fruiting events could include one or more peak phases of production. Unripe and ripe cocoa pods were not distinguished (see text).

A number of species fruited twice within 12 months, with intervals of 2–6 months between fruiting events (e.g. *Annona senegalensis, Pseudospondias microcarpa*). Twice-yearly fruiting could be characteristic of such species or, alternatively, fruiting events may follow an irregular cycle. For example, *Pseudospondias* was at the end of a fruiting event at the start of phenology surveys in December 06; chimpanzees were seen feeding on the fruits from mid-October. This fruiting event was concentrated at the end of the main wet season but continued into the dry months of December–January. In January 07 several *Pseudospondias* started to flower while ripe fruit was still present on other trees. By February and March many trees bore large clusters of unripe fruit. The fruits began to ripen in late April, after an interval of three months. May and June, when the ripe fruits were abundant, were wet months. This second fruiting event was over by early July, and flowering was not observed for three months until October, followed by emerging fruits in November. In mid-January 08 the first ripe fruits were seen, after an interval of six months, at the height of the dry season.

Six species showed continuous fruit production: ripe or unripe fruit was recorded in all months. These same species also displayed extended phases of ripe fruiting, i.e. lasting ≥6 successive months (Table 4.2). For such species the fruiting event was not confined to a particular season and could include peaks and troughs in production. Species with extended fruiting phases included pioneer species (e.g. *Pycnanthus angolensis*) as well as non-pioneers (e.g. the *Phoenix* palm) and the two cultivated exotics, guava and cocoa.

Several species exhibited indistinct or poor fruiting events. For example, ripe *Sterculia dawei* pods were recorded in small quantities on a minority of specimens in 12 of 14 months, but a peak fruiting season was not discernable. Poor fruiting events were observed in the common trees *Trilepisium madagascariensis* and *Teclea nobilis*. In both species, moderate quantities of unripe fruit were present on trees in two seasons, yet ripe fruits were seen subsequently in trivial amounts on only a small proportion of individuals. It is uncertain if the fruits were aborted or consumed by animals before ripening.

Figs

Individual fig trees fruited asynchronously and irregularly. In the most common species (*Ficus sur* and *F. natalensis*), ripe figs were recorded in all months. Accordingly, the proportion of months in which fig species were recorded with ripe fruit was positively correlated to the number of individuals monitored of each species ($r = 0.755$, $p = 0.02$). When data for all species were lumped, availability of figs was relatively consistent during most months; however, notable spikes occurred in January and April 07 and January 08 (Figure 4.5), which were months of high overall fruit availability. Even so, monthly fig availability did not correlate with availability of non-fig species ($r = 0.163$, $p = 0.58$), and ripe figs were readily available during fruit-poor months of May and September–November. Individual fig trees showed great variability in the number of fruiting cycles observed during the study. For example, several *F. sur* were recorded with ripe fruit crops 5–6 times during the study, whilst some conspecifics of reproductive size did not fruit at all.

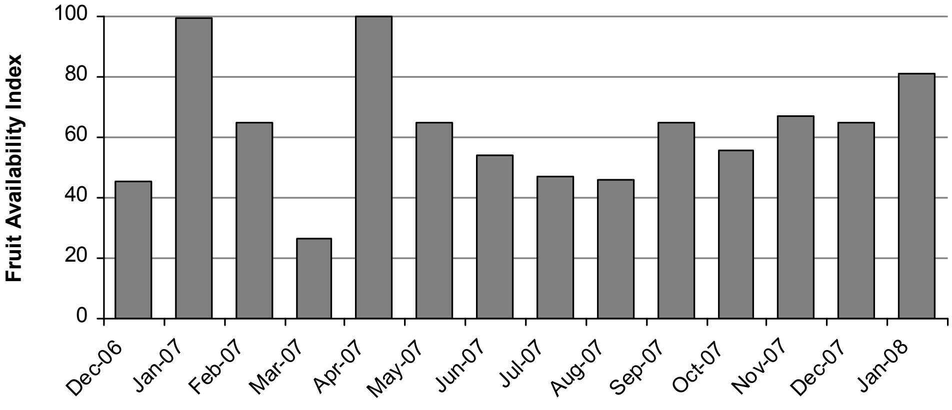


Figure 4.5. Monthly availability of ripe figs (*Ficus* spp.) in forest patches. Results are expressed as an index of 100 where the month with the highest value = 100.

Influence of common species on the FAI

The FAI was heavily influenced by the fruiting patterns of two common species: *Phoenix reclinata* and cocoa (*Theobroma cacao*). As shown in the previous chapter, these two species are the first and fourth most abundant tree species in Bulindi forests, respectively. Moreover, both showed extended fruiting: ripe *Phoenix* fruits were available in 11 of 14 months, whereas cocoa pods were available in all months.

Together, they accounted for >60% of the estimated total food availability in all months of the study, and >80% in nine of the 14 months (Figure 4.6).

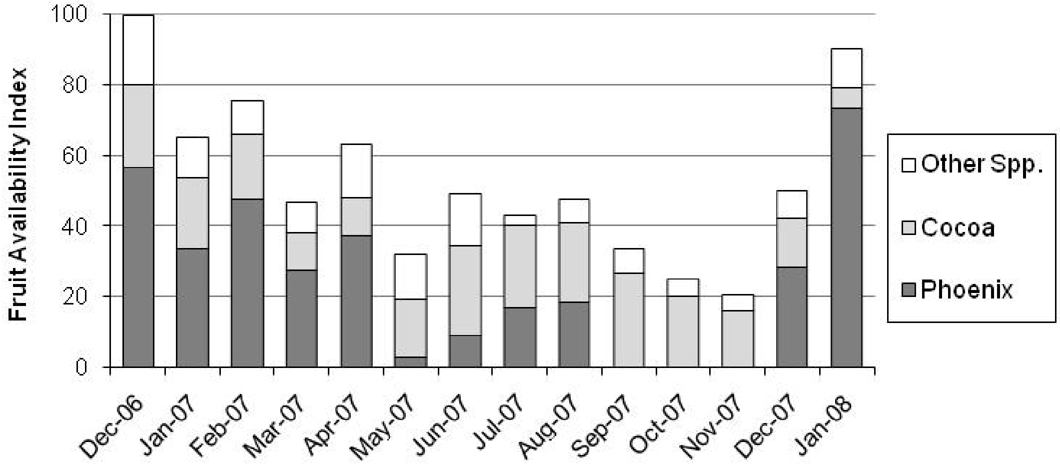


Figure 4.6. Contribution of two common phenology species, *Phoenix reclinata* and cocoa (*Theobroma cacao*), to monthly estimates of forest fruit availability. Results are expressed as an index of 100 where the month with the highest value = 100.

Phoenix reclinata

The extended fruiting event of *Phoenix* palms comprised two consecutive phases. In December 06, at the start of phenological monitoring, *Phoenix* was in a peak fruiting phase, the fruits on many palms having ripened the previous month. The palms continued to fruit heavily until the end of April 07. Thus, this first fruiting phase lasted approximately six months and may be considered the palm's 'major' fruiting season. In May 07 few palms remained with ripe fruit but clusters of unripe fruit that followed a flowering event in February–March were approaching maturity. A second, shorter phase of fruiting was evident from late June, after an interval of just one month, lasting two months through to August (Figure 4.6).[5] During this lesser fruiting season, a smaller proportion of the palms fruited compared to the major season, and fruit crops were smaller. The palms were flowering again in July and August and many bore large clusters of unripe fruit from late-August and September, though ripe fruit was not seen until mid-December – an interval of about 3½ months. By January 08 many palms had full crops of ripe fruit. Thus the final two months of the study seemed to mark the

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[5] These major and minor fruiting seasons are not considered separate fruiting events because of the brief interval in ripe fruit production, and the continuous production of unripe fruit across seasons.

beginning of the major fruiting season once more. While fruiting peaks were evident in some months (e.g. December 06 and January 08), individual palms tended to fruit asynchronously within seasons and many bore fruit clusters at different stages of maturity. Thus fruiting was staggered both between and within individual trees, resulting in continuous fruit production in this species over many months (Plate 6).

The three months between September–November 07 marked the only time during 14 months when ripe palm fruits were unavailable. In fact, the availability of ripe *Phoenix* fruits was a highly significant predictor of the FAI for all monitored species, accounting for 90% of the total variation in monthly estimates of ripe forest fruit availability (R^2 = 0.897, $F_{1,12}$ = 104.79, p <0.001; Figure 4.7). Therefore the fruiting pattern of this single superabundant species exerted a critical influence on temporal levels of forest food availability. No correlation existed between the FAI of *Phoenix* and the FAI for all other species combined (r = -0.088, p = 0.76).

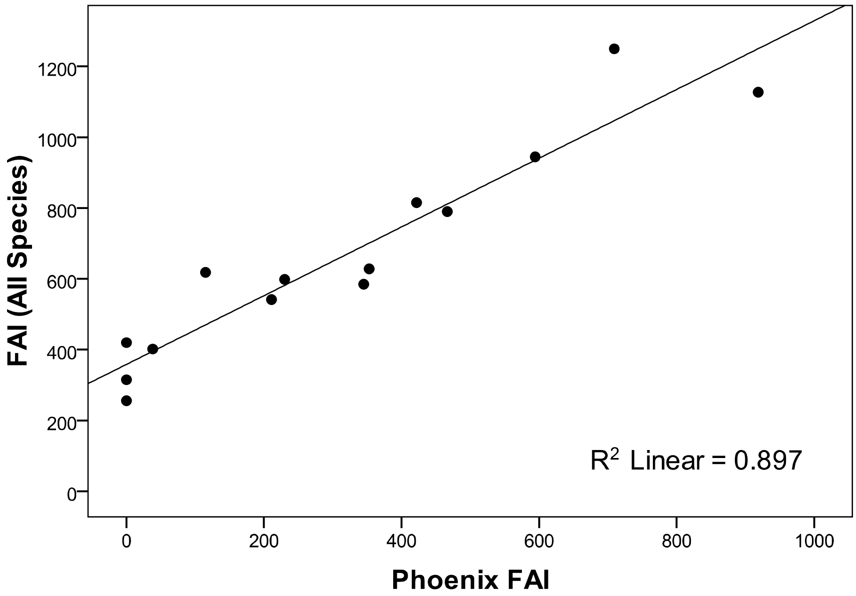

Figure 4.7. Relationship between the monthly availability of ripe *Phoenix reclinata* fruits and the fruit availability index (FAI) for all monitored species.

Theobroma cacao

While the abandoned forest cocoa *shambas* produced pods year-round, a moderate peak in availability was evident between June and October 07. During the September–November low fruiting season cocoa accounted for >75% of estimated forest fruit availability each month (Figure 4.6). Although the cocoa FAI was uncorrelated with the FAI for all other species (r = -0.440, p = 0.12), a significant negative correlation does exist if presence/absence scores are used instead of ranked crop size data (r = -0.719, p = 0.004). That is, the proportion of sample cocoa trees bearing pods increased during months when availability of other forest fruits was low, but average crop size apparently did not. This may be because chimpanzees, and possibly other animals, fed heavily on cocoa during that time (i.e. pods were being removed from the trees daily).

With the exception of the common swamp tree *Pseudospondias microcarpa*, which accounted for 19% and 25% of the total FAI in May and June 07, respectively, few other phenology species had more than a marginal influence on monthly fruit availability levels when considered individually. The impact of low density species, such as most figs, on the monthly FAI was negligible. However, when fig species were lumped their contribution to the overall FAI ranged from 1.6% in December 06 – the month with highest fruit availability – to 11.8% in November 07, when fruit was least available. This is expected because the continuous availability of figs means their contribution to overall levels of forest food availability increases as availability of non-fig fruit decreases (r = -0.724, p = 0.003).

4.3.4. Leaf Flushing

Although small quantities of young leaves were observed on trees of many species year-round, leaf flushing peaked during January–February 07 and again in January 08. By contrast, May through September was a period of low availability (Figure 4.8). Unlike ripe fruit, the overall FAI for young leaves was not influenced by the phenology of the superabundant *Phoenix* palm ($R^2 = 0.00$, $F_{1,12} = 0.00$, $p = 0.96$): emerging fronds were recorded on palms in all months and scores remained constant throughout the study. The availability of young leaves was positively and significantly correlated with fruit availability (r = 0.632, p = 0.015). Thus new leaves were most abundant when ripe fruit was also relatively plentiful.

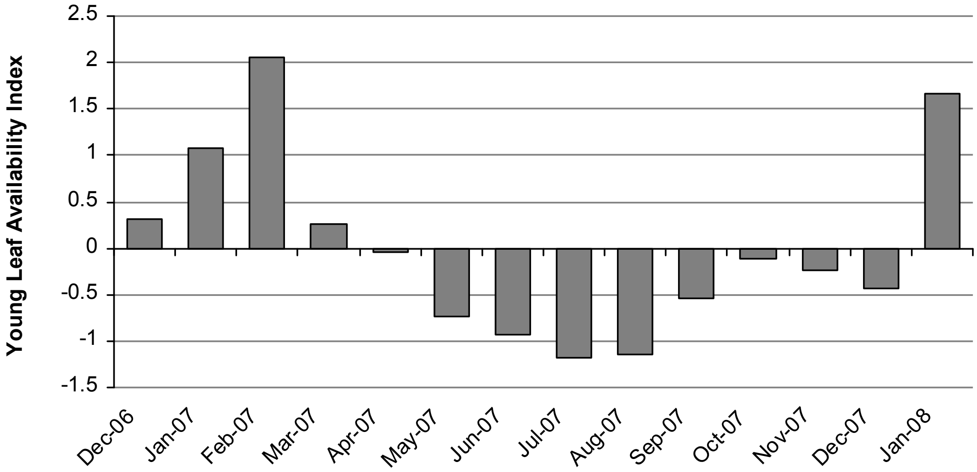

Figure 4.8. Monthly availability of young leaves shown as standardised Z-values. The mean monthly value is 0. Positive values indicate months of above-average availability and negative values are months of below-average availability.

4.3.5. Food Availability and Rainfall

Leaf flushing followed the start of the main dry season in December–February, when individual trees of many species shed their leaves, peaking in February prior to the onset of rains in March (Figure 4.9). Although rainfall during the study period did not significantly predict availability of young leaves, the correlation between the two variables is negative ($R^2 = 0.255$, $F_{1,11} = 3.77$, $p = 0.08$). In the case of ripe fruit, the negative correlation with rainfall is significant ($R^2 = 0.361$, $F_{1,11} = 6.21$, $p = 0.03$). In both cases the correlation would have been strengthened were rainfall data available for January 08, a very dry month when availability of fruit and new leaves was high (Figure 4.9). Dry months were therefore a time of relative plenty in Bulindi forests.

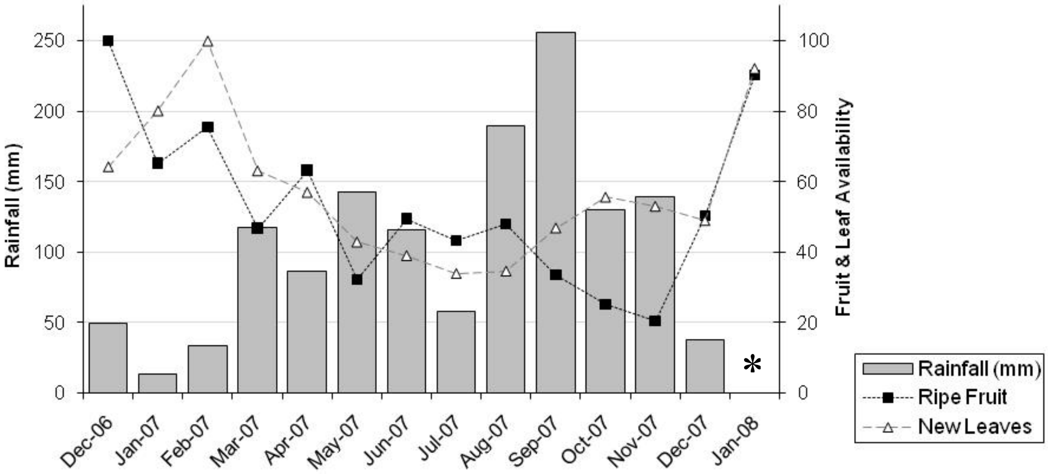

Figure 4.9. Availability of ripe fruit and young leaves (lines) in relation to monthly rainfall (bars; Dec 06–Dec 07). * Rainfall data were unavailable for Jan 08 but January is a dry month (<50 mm rainfall, 2001–7). For both fruit and leaves, the FAI is expressed as an index of 100 where the month with the highest value = 100.

4.4. Discussion

The availability of ripe fruit and young leaves of forest trees was estimated over 14 months via phenological sampling. The results demonstrate that food production in forest patches at Bulindi was seasonally variable and included periods of relative food abundance and food scarcity. Overall, food availability was estimated to be highest between December and February, during the peak fruiting phase of *Phoenix reclinata*, and at intermediate to low levels in other months. In particular, fruit tree production was especially low during three consecutive months in September–November, which constitute the 'low fruiting season' in this study. The seasonal fruiting of species that exhibited an annual fruit cycle was concentrated in February–April.

Food Availability and Seasonality

Seasonality in plant resource availability is expected in environments subject to temporal climatic variability (van Schaik et al. 1993; Richards 1996; van Schaik and Pfannes 2005). As shown in Chapter 2 the climate at Bulindi is bimodal with two wet seasons and a 3-month dry season in December–February, where rainfall averages <50 mm each month. A second, transient dry season occurs in June, separating the wet seasons. In this study peaks in availability of both ripe tree fruit and young leaves occurred during the main dry season. The peak in leaf flushing in February, at the end of the dry season, may be characteristic of seasonal forests that experience several consecutive dry months (van Schaik et al. 1993; Richards 1996; Anderson et al. 2005), and probably indicates seasonal water stress (Reich and Borchert 1984). Peaks in fleshy or animal-dispersed fruit production are reported to occur during wet months in many tropical forests (e.g. Rathcke and Lacey 1985; Terborgh 1986; White 1994; Sun et al. 1996). However, in a recent meta-analysis of tropical phenological studies, van Schaik and Pfannes (2005) found that, except in very seasonal environments, links between rainy seasons and fruiting peaks are weak, although they noted that production of fruits with high water content is expected to be concentrated in wet months when moisture availability is greatest. Even so, most monitored species at Bulindi produce succulent fruits, yet fruit availability was highest throughout the main dry season and lowest towards the end of the August–November rainy season.

While dry seasons are regarded as a time of fruit scarcity in many chimpanzee habitats (Hladik 1977; Goodall 1986; Kuroda et al. 1996a; Doran 1997; Tutin et al. 1997; Leciak et al. 2005; Reynolds 2005; Hernandez-Aguilar 2006; Moscovice et al. 2007; Takenoshita et al. 2008), a review of seasonal fruit phenology at chimpanzee study sites across their geographic range suggests dry season peaks in availability are in fact not uncommon. For example, in West Africa, a pattern similar to that at Bulindi of peak fruit production during the main dry season and fruit scarcity in the latter part of the wet season was observed at Taï forest, Côte d'Ivoire (Anderson et al. 2005). At Bossou, in Guinea, fruit availability was also highest during the dry season and early rainy season (Yamakoshi 1998; Hockings 2007), while at Fongoli, Senegal, the proportion of plants in fruit peaked during the late dry season (Pruetz 2006). Bossou, and in particular Fongoli, are characterised by a strong seasonality, with distinct dry seasons lasting four and eight months, respectively. In East Africa, in the montane forest at Kahuzi, eastern DRC, monthly fluctuations in fruit abundance correlated negatively with rainfall in some, but not all, years, and there was some variability according to forest type (Yamagiwa et al. 2008).

In western Ugandan forests, which exhibit a moderate seasonality with bimodal wet and dry seasons, studies indicate a mixed relationship between fruit production and season. At Kalinzu high rainfall was associated with peaks in the number of species and number of individual trees fruiting (Muhanguzi et al. 2003). In the southeast at Bwindi fruit availability was lowest in dry months at two sites, yet monthly rainfall did not correlate with monthly abundance scores at either site (Nkurunungi et al. 2004). At the Kanyawara site in Kibale fruiting peaks tended to span the end of the wet season and start of the dry season, but showed less temporal regularity 10 kilometres away at Ngogo (Chapman et al. 1999). Notably, studies at Budongo – 25 km north of Bulindi – show that periods of fruit scarcity generally occur during dry months (Fawcett 2000; Tweheyo and Babweteera 2007), suggesting that seasonal fruit production in riverine forests at Bulindi is asynchronous with the main Budongo forest block. However, peaks in leaf flushing occur at roughly the same time of year at both sites. Within tropical Africa, the environmental conditions favouring increased fruit abundance during rainy months and reduced production in dry months appear to be characteristic of lowland rainforests of Central Africa (Kuroda et al. 1996a; Tutin et al. 1997; Takenoshita et al. 2008). East and west of this region environmental seasonality is often more pronounced and phenological patterns are more varied.

Factors Influencing Phenological Patterns

In general, the phenology of tropical forests follow seasonal, annual, and in some instances supra-annual, cycles (van Schaik et al. 1993; van Schaik and Pfannes 2005). Further to temporal variation in rainfall, and in particular the length and severity of the dry season, the timing of phenophases in plants are influenced by proximate abiotic factors such as temperature, irradiance and day length (e.g. Tutin and Fernandez 1993c; van Schaik et al. 1993; Wright and van Schaik, 1994; Anderson et al. 2005; Chapman et al. 2005; van Schaik and Pfannes 2005), as well as activity and abundance of animal pollinators, seed dispersers and seed predators (Janzen 1979; Baker et al. 1983; Rathcke and Lacey 1985).

Long-term phenological studies in tropical forests are revealing marked inter-annual variation in community- and species-level phenological activity, affecting the quantity of food available for animal consumers across years (Newstrom et al. 1994; Tutin et al. 1997; Struhsaker 1997; Chapman et al. 1999, 2005; Yamagiwa et al. 2008). Inter-annual variation in production may reflect short-term fluctuations in environmental conditions that cause deviations from 'typical' phenology cycles, or may be indicative of longer-term climatic changes (Chapman et al. 2005). In the absence of long-term phenology data, the generality of the patterns observed at Bulindi during this 14-month study cannot be assessed. There is some indication, however, that precipitation patterns during the observation period were unusual, perhaps as a result of La Niña (*New Vision* 2007) (see Figure 2.4). Though inter-annual variability in rainfall is not uncommon in East Africa (Conway et al. 2005), meteorological extremes associated with El Niño and La Niña events can cause major fluctuations in forest fruit production in particular years (cf. Wright et al. 1999). For example, at Kibale the 1983 El Niño was associated with widespread reproductive failure among sampled tree species (Struhsaker 1997). Conversely, heavy rainfall due to El Niño in 1997 apparently triggered fruiting in many trees at Kalinzu (Muhanguzi et al. 2003). Any influence of the 2007 La Niña event on fruiting patterns at Bulindi is currently unknown. Certainly, in some species a very low proportion of individuals fruited and fruit crops on those that did fruit were small (e.g. *Trilepisium madagascariensis*, *Teclea nobilis*), though this could be for a number of reasons. For example, it may be usual for individuals of such species to produce large fruit crops only once every few years. Chapman et al. (2005) examined long-term phenology data from Kibale and found that in certain species the proportion of individuals taking part in fruiting events remained very low over multiple consecutive years. However, reductions in proportion of individuals fruiting or declines in fruit crop size over time were also apparent in some species. These authors suggest that local climate change may be causing changes in fruit production. It is also conceivable that at Bulindi fruit production in some species (e.g. *Antiaris toxicaria*, *Sterculia dawei*) was adversely affected by logging activities, for example through a reduction in the density of reproductively mature conspecifics. Adult tree density of some forest species was reduced during the study, though this could not be factored into monthly abundance estimates.

Extended Fruiting

Several phenology species had fruiting events lasting six months or longer. Extended fruiting promotes seedling recruitment in gaps such as logged clearings, and may be a strategy of light-demanding pioneer species in disturbed forest (Muhanguzi et al. 2003). Indeed, two of the examples from this study are pioneers (*Pycnanthus angolensis*, *Trema orientalis*). Yet non-pioneers such as *Phoenix reclinata* also produced ripe fruit over a prolonged period. It is unclear if this pattern is typical of these species.

Regardless, all species with extended fruiting displayed considerable inter-individual asynchrony in fruit production with individual trees bearing fruits at different stages of maturity. White (1994) suggested that species that fruit during and just after main dry seasons at Lopé, Gabon, tend to produce fruit over long periods because environmental conditions limit the amount of fruit that can ripen simultaneously. Extended and staggered fruiting may also be a strategy to avoid intra-specific competition for animal dispersers (Yamagiwa et al. 2008). Species with extended fruiting phases will be especially important for consumers if they constitute an important part of the annual diet, or if their fruits are available during lean periods when few other species in the community are fruiting.

The Influence of Phoenix *Palms on Overall Levels of Fruit Availability*

Fluctuations in estimated levels of forest fruit abundance were dictated to a large extent by the fruiting cycle of the *Phoenix* palm which, as shown in the previous chapter, is dominant in swamp forest and thus abundant at Bulindi. In fact, monthly estimates of fruit availability for all species were so closely correlated with availability of *Phoenix* fruits that if the palm is removed from the data set the identified seasonal peaks and troughs disappear and a different pattern emerges, largely affected by the fruiting events of *Pseudospondias microcarpa* and monthly variation in cocoa availability. In this study the 'low fruiting season' corresponded to the period when ripe palm fruits were unavailable.

The palms produced ripe fruit in 11 of 14 months. Kinnaird (1992a,b) noted that *Phoenix* fruited out of synchrony with many other species in riverine forest along Kenya's Tana River, and suggested the palm may be a determinant of mangabey (*Cerocebus galeritus*) persistence in that habitat. Although data were not presented on ripe fruiting phenology, seeds and fruits of the palm were important items in the mangabey's diet throughout the year, suggesting a prolonged fruiting cycle. Conversely, in gallery forest at Kanfarandé, Guinea, Leciak et al. (2005) recorded fruits on *Phoenix* palms in only three months of the year. Thus the duration of fruiting events is likely to depend on local environmental conditions.

Methodological Considerations

Previous studies suggest that estimates of food availability derived from a fruit trail are sensitive to the number and composition of the species sampled (Malenky et al. 1993; Hemingway and Overdorff 1999; Fawcett 2000). In this study the monthly FAI was highly sensitive to the fruiting patterns of the most abundant species. By contrast, the contribution of low density species to measures of food availability was negligible. Yet fruits of certain rare species may be important for animals at certain times of the year. An example from this study is the small understorey tree *Caloncoba crepiniana*, which was not encountered during tree surveys but was a major food for chimpanzees in August–September when fruit was relatively scarce (Chapter 5). Had this tree been included in phenology surveys its fruiting would have made virtually no impression on estimated food availability due to its small size and very low density. As noted by other researchers (Mammides et al. 2008; Marshall and Leighton 2006), ideally estimates of food abundance should be weighted to take into account the relative importance of particular species, for example as a fallback food or in terms of frequency in the diet or nutritional quality. However, relative importance is difficult to quantify. For example, the value of a particular food item in a given month will be influenced by the concurrent availability (and value) of other foods, which may vary from one year to the next and across short spatial scales (Boesch et al. 2006; Mammides et al. 2008).

Are the Riverine Forests at Bulindi a Good Habitat for Chimpanzees?

Estimates of food availability are rarely comparable across study sites and habitats due to differences in methodologies used. Theoretically, the amount of food available for chimpanzees at one site could be compared with another if total biomass of foods per unit area could be calculated on a temporal basis. Even if this were possible, however, inter-site comparisons of food abundance and habitat quality would need to account for variables such as nutritional content of foods and biomass of competitors, which will differ between sites. Accordingly, it is difficult to assess the quality of the riverine forests at Bulindi for chimpanzees in relation to other habitats *per se*. Nevertheless, the following observations can be made.

Despite the uncertain influence of climatic conditions on fruit production during this study, phenological data support the tentative hypothesis that these riverine forests are highly productive. In particular, the extended fruiting of the superabundant *Phoenix* palm suggests that ripe fruit may be plentiful during most of the year. However, the value of the riverine forests to frugivores may depend more critically on the occurrence of species that provide fruit during months when the palms do not. Keystone foods should be available at all times or else consistently available during periods of fruit scarcity (Terborgh 1986; Tutin et al. 1997; Peres 2000). Due to their aseasonal and asynchronous fruiting, figs are considered keystones in many tropical forests (Terborgh 1986; O'Brien et al. 1998; Kinnaird et al. 1999), except where they occur at very low densities (Gautier-Hion and Michaloud 1989). In the riverine habitat at Bulindi fig trees occur at a relatively high density compared to many *terra firma* forests (Chapter 3). Ripe figs were available throughout the year, albeit at relatively low levels, and might therefore compensate for seasonal troughs in *Phoenix* fruit production. Even so, the introduced cocoa trees – which also produced fruit year-round – occurred at a far greater density. In managed *shambas* there are two peak harvesting seasons, together totalling about six months, which constitute most of the annual production (Kayobyo et al. 2001). Similar peak seasons were not identifiable in abandoned forest *shambas* at Bulindi because pods were always consumed before fully ripe. In fact, the potential importance of figs during fruit-scarce periods might be obscured because (unripe) cocoa pods accounted for >75% of estimated forest fruit abundance during the low fruiting season in September–November. Thus, the introduction of cocoa trees into riverine forests in the 1960s and 1970s could have provided an artificially abundant and year-round food source that may have had an important effect on densities and foraging strategies of frugivorous mammals, including chimpanzees.

Data on the composition and phenology of forests at Bulindi provide a possible explanation for the unexpected widespread occurrence of chimpanzees in small riverine forests across northern Hoima (McLennan 2008). *Phoenix reclinata* palm swamps are a common feature of waterlogged valleys in this region (pers. obs.). Furthermore, cocoa gardens were widely established in forests across Hoima from the late 1950s (*Atlas of Uganda* 1967). These observations imply that prior to recent forest clearance and extensive timber harvesting Hoima's riverine forests may have represented a fruit-rich habitat for chimpanzees and other frugivores. Gautier-Hion and Brugière (2005) considered Central African riverine forests to be a good habitat for primates because food availability is less seasonally variable relative to *terra firma* forest, which in part reflects a higher density of figs (see also Gautier-Hion and Michaloud 1989). If a similar ecological scenario characterises Hoima's riverine palm forests, the probable keystone value of figs could have been artificially supplanted in some areas by cocoa.

Finally, whilst young leaves sometimes constitute a fallback food for frugivorous primates, including chimpanzees (e.g. Kuroda et al. 1996a; Tutin et al. 1997), at Bulindi the peak in leaf flushing occurred in the late dry season when ripe fruit was also abundant. A similar pattern is reported at Bossou, Guinea (Takemoto 2003). This suggests that the value of young leaves as a fallback food during the low fruit season may be limited at Bulindi. The chimpanzees' diet in relation to patterns of food availability is the subject of the following chapter.

Summary

1. The phenology of 30 tree species recorded in chimpanzee diets at a range of sites was monitored in forest patches at Bulindi over 14 months. Food availability was seasonally variable, including periods of relative abundance and scarcity. Availability of both ripe fruit and young leaves was at highest levels during the main dry season (December–February). A three-month 'low fruiting season' was evident during September–November.
2. Phenology tree species exhibited a variety of fruiting patterns. Fruiting was synchronised among species that fruited only once during the study (in February–April). Several species fruited twice within 12 months. Continual or extended fruiting (lasting six or more months) occurred in six species, including two exotic cultivars (cocoa and guava). Fig fruits were available year-round at relatively constant levels.
3. Fruiting patterns of the abundant *Phoenix reclinata* palm accounted for most of the monthly variation in overall levels of fruit availability. The three month interval when ripe palm fruits were unavailable corresponded to the low fruiting season. At that time cocoa in abandoned forest gardens constituted most available fruit, suggesting a role as an artificial fallback food. The extended fruiting of the palms coupled with year-round availability of figs and cocoa suggests riverine forests at Bulindi are a rich habitat for frugivores such as chimpanzees.

CHAPTER 5 – DIET & FEEDING ECOLOGY.

I. PLANT FOODS

5.1. Introduction

Description and characterisation of the diets of wild animals is fundamental to understanding ecological divergence and adaptation in species. In primates, dietary studies of taxa that occupy a diversity of environments enable comparison of the ecological niche and flexibility of populations in different habitats (Fashing 2001; Chapman et al. 2002; Robbins et al. 2006; Russon et al. 2009). For populations subsisting in dynamic human-dominated landscapes, knowledge of the diet provides a means of assessing a species' response to habitat alteration and disturbance (Chapman et al. 2007; Riley 2007a; de Freitas et al. 2008; Strum 2010). Detailed site-specific information on diet and feeding ecology are essential for informing effective, locally appropriate conservation and management strategies.

Chimpanzees are omnivorous; they supplement a predominantly plant-based diet comprising fruits, leaves, piths, flowers and other plant parts with insects and vertebrates (Hladik 1977; Wrangham 1977; Nishida and Uehara 1983; Goodall 1986; Sugiyama and Koman 1987; McGrew et al. 1988; Wrangham et al. 1991; Tutin and Fernandez 1993b). Nevertheless, in all habitats where they have been studied, whether in dense lowland rainforest, dry savanna woodland or montane forest, the chimpanzee diet is dominated by ripe fruits (Newton-Fisher 1999; Tashiro et al. 1999; Basabose 2002; Stanford and Nkurunungi 2003; Boesch et al. 2006; Morgan and Sanz 2006; Pruetz 2006; Moscovice et al. 2007; Deblauwe 2009; Gross-Camp et al. 2009). Thus chimpanzees are considered ripe-fruit specialists (Ghiglieri 1984; Wrangham et al. 1998). Across studies, the proportion of observed feeding time devoted to frugivory is typically between 60–80% (e.g. Goodall 1986; Wrangham et al. 1998; Newton-Fisher 1999; Hockings et al. 2009) but populations vary somewhat in the amount of time spent feeding on other plant parts. For example, at Budongo leaves comprise 15–20% and flowers ~10% of feeding time, whilst stems and piths of terrestrial herbaceous vegetation (THV) account for a relatively negligible portion of the feeding effort (Newton-Fisher 1999; Fawcett 2000; Tweheyo et al. 2004). In contrast, Kanyawara chimpanzees at Kibale devoted <10% of feeding time to leaves but up to 20% on piths of THV; time spent eating flowers was minimal (Wrangham et al. 1998; Emery-Thompson and Wrangham 2008). Such inter-community differences may reflect variation among sites in the availability and abundance of particular plant resources in the habitat.

Chimpanzee diets show seasonal variation. As discussed in Chapter 4 food production in tropical forests is never constant and consumers face seasonal periods of relative abundance and scarcity. Researchers have found that during ripe fruit shortages chimpanzees continue to pursue a largely fruit-based diet; however, they increase consumption of abundant but less digestible foods of lower nutritional density such as leaves, bark and the fibrous piths of THV (Nishida 1976; Hladik 1977; Tutin et al. 1991; Wrangham et al. 1991; Kuroda et al. 1996a; Doran 1997; Wrangham et al. 1998; Fawcett 2000; Basabose 2002). These foliage items are regarded as ‘fallback’ foods for chimpanzees in many habitats since they are consistently available but eaten in greater quantities when preferred fruit foods are scarce (Marshall and Wrangham 2007; Marshall et al. 2009). However, higher-quality fruits can function as fallback foods too. For example, the asynchronous fruiting of figs (*Ficus* spp.) causes year-round fruit production and at some sites chimpanzees increasingly rely on figs as overall fruit availability declines (e.g. Wrangham et al. 1993, 1996). Elsewhere, however, figs are not a dependable resource for frugivores due to their very low densities (Gautier-Hion and Michaloud 1989; Tutin et al. 1997). Occasionally, chimpanzees have access to high-quality fallback foods that are both continuously available and abundant in the habitat. As a result, consumption of leaves and THV may lack the strong seasonality observed in some populations (e.g. oil-palm [*Elaeis guineensis*] nuts and *Musanga cecropioides* fruit at Bossou: Yamakoshi 1998; *Musanga leo-errerae* fruit at Kalinzu: Furuichi et al. 2001a).

Studies indicate that where chimpanzee home ranges encompass or border the fields and plantations of people the apes readily incorporate cultivated crops into their diet (Dunnett et al. 1970; Sabater-Pi 1979; Takasaki 1983a; Naughton-Treves et al. 1998; Reynolds et al. 2003; Tweheyo et al. 2005; McLennan 2008; Hockings et al. 2009). Human crops offer important advantages over many wild foods: spatially clumped, they afford greater foraging efficiency, are often energy-rich but low in secondary compounds, and are easy to digest (Altmann and Muruthi 1988; Forthman-Quick and Demment 1988). Thus, although consumption of agricultural crops by chimpanzees may be an adaptation to the loss of natural foods where forest has been heavily encroached upon, chimpanzees might also exploit human foods because they are tasty and of high nutritional quality, regardless of the availability of wild foods. Alternatively, crops may be high-quality fallback foods eaten when wild foods are scarce. Relevant quantitative data on this subject are available for two sites. In Uganda, chimpanzees at Kibale NP fed on banana fruit and pith at the park's edge year-round but pith consumption peaked when ripe fruits of major forest food species were unavailable. However, maize-raiding was unaffected by forest fruit availability (Naughton-Treves et al. 1998). In the most detailed study of chimpanzee crop-raiding to date, Hockings et al. (2009) found that chimpanzees at Bossou in Guinea raided crops, particularly sugar fruits (e.g. papaya, banana, orange and pineapple), at significantly higher frequencies when wild fruits were scarce, suggesting these fruits are fallbacks. On the other hand, rice pith and maize fruit consumption were tightly linked to availability. Other less rigorous studies also report increased use of some human foods by chimpanzees during periods of wild fruit shortage (Sabater-Pi 1979; Reynolds et al. 2003). Farmers around Budongo Forest reported a rise in sugarcane raiding by chimpanzees and other primates during the main period of forest fruit scarcity (Tweheyo et al. 2005). Taken together these studies suggest that chimpanzees may consume agricultural foods throughout the year, but whereas some crops appear to be fallbacks others are sought out independently of wild food abundance.

Where eaten, the importance of human crops in the chimpanzee diet varies from site to site according to habitat features. For example, chimpanzees that range at the periphery of large protected areas (e.g. Kibale; Naughton-Treves et al. 1998) appear to depend less on cultivated foods relative to populations that live wholly within agricultural landscapes. At Bossou, where the chimpanzees' range encompasses cultivated and abandoned fields as well as primary and secondary forest, the apes consume a wider range of crops than other studied populations (Sugiyama and Koman 1992; Hockings et al. 2009) and raided crops accounted for up to 16.6% of monthly feeding time (Hockings et al. 2009). Though quantitative data are lacking, chimpanzees north of Bulindi at Kasokwa FR – a forest strip surrounded by farmland – reportedly depend more on human foods than natural foods during dry season months (Reynolds et al.

2003). At Bulindi, chimpanzees arguably inhabit the most disturbed and dynamic forest–farm landscape in which this species has been studied. As such, cultivated foods are predicted to constitute an important part of their diet and their dependence on human foods could surpass that of the Bossou and Kasokwa apes.

This chapter presents data on the feeding ecology of chimpanzees in the fragmented forest–farm mosaic at Bulindi. The study's aims were as follows:

1. Describe the plant food diet of the chimpanzees in terms of parts eaten, number of food items, and number of species; and compare dietary breadth and composition at Bulindi with other studied populations;
2. Examine monthly variation in the relative proportion of fruit and foliage in dung, and the diversity of the fruit diet; and determine whether seasonal changes in forest food availability influence diet composition;
3. Identify the most important fruit foods eaten during the study;
4. Assess the contribution of agricultural foods to the chimpanzees' diet and determine whether patterns of consumption relate to fluctuations in forest fruit availability;
5. Identify fallback foods (wild or cultivated) for this community.

5.2. Methods

Chimpanzees at Bulindi were unhabituated and quantitative data on diet are from dung analysis. Although this method underestimates the contribution of some foods that leave few or no recognisable remains in dung (discussed below), it is frequently employed in ecological studies of unhabituated great apes when behavioural observations of feeding are expected to be limited (Tutin and Fernandez 1993a; Doran et al. 2002; McGrew et al. 2009). Dung data were supplemented by information from feeding traces as well as direct observations of feeding behaviour.

5.2.1. Data Collection

Faecal Specimens

Beginning November 2006 fresh faecal specimens (≤1 day old) were collected from beneath night nests, on habitually used trails, and from areas recently vacated by apes (McGrew et al. 1988). Chimpanzee dung was readily distinguishable from that of black and white colobus and tantalus monkey by size, colour, form, and/or consistency. Baboon dung was seldom seen since they tended to avoid areas frequently used by chimpanzees, but when encountered it could usually be distinguished by colour and form, and particularly by its pungent odour. If the identity of the depositor was in doubt (as when baboons were known to have recently passed), the dung was not collected. Only one dung specimen was collected per night nest. If successive dung piles (e.g. along trails) were judged to be from single individuals, only one specimen was collected. However, since defecation was rarely observed the possibility that individuals sometimes contributed >1 dung to the total dungs collected per day cannot be excluded. Comparison of the dried contents of dungs collected sequentially indicated 19 cases of probable replication and these were removed from the data set; all other dungs were treated as independent.

At the collection site the following information was recorded: location (GPS reading); deposition site (e.g. below nest or on trail); associated traces (nest, knuckle marks, feeding traces); and whereabouts of chimpanzees (e.g. nearby, recently passed, unknown). Dungs were assigned a reference number, stored in plastic bags and rinsed through a 1 mm mesh sieve within three days of collection (Tutin and Fernandez 1993a). The undigested contents were analysed once fully dried. Some researchers analyse dungs immediately after washing (Tutin and Fernandez 1993a; McGrew et al. 2009), while others dry the residues before examining them (Tashiro et al. 1999; Basabose 2002). McGrew et al. (2009) call for standardisation of methods used in primate faecal analysis and propose a technique for analysing wet dungs. But no reasons were offered that support analysis of wet over dry specimens. In my experience undigested faecal matter is more easily manipulated and separated once dry. For example, during the six months of this study when chimpanzees fed on mangos, dungs often contained dense clumps of mango fibre and it was difficult to detect some other food items embedded within the soggy fibres (e.g. small seeds, ant heads). Once dry, the fibrous mass could be properly separated and the contents thoroughly inspected.

Feeding Traces

From October 2006 fresh feeding traces that could be attributed with certainty to chimpanzees were recorded, based on the presence of associated fresh signs (dung, knuckle marks, nests) or the recent departure of apes from the same locality (cf. McGrew et al. 1988). Some feeding traces were species-specific – for example, the compact ‘wadges’ of fruit skin and seeds, discarded once the chimpanzee has extracted the juices (Plate 7). Only one record was made per food item per forest patch on a given day. For example, when a large party of chimpanzees visited Kiseeta and fed on cocoa, the discarded half-eaten pods were often numerous and distributed throughout the forest *shambas* but a single record was made only. However, if cocoa feeding remains were also found in Kyamusoga forest on the same day, a second record was made. Data from feeding traces provided an indication of the frequency that certain plants that are difficult to identify taxonomically from dung were consumed (e.g. piths).

Direct Observations

Observations of feeding behaviour were made opportunistically during encounters with chimpanzees. Feeding observations were few during the initial months of research but increased as the study progressed. This was due in part to improved tracking capabilities, but also reflects the chimpanzees’ greater tolerance of us during the latter months of research, when a degree of habituation had occurred (Chapter 8). During feeding observations, records were made on plant parts consumed and maturity of fruit and leaves.

5.2.2. Data Analysis

Unless otherwise indicated, analysis is restricted to January 2007–January 2008 (13 months) when an effort was made to collect chimpanzee faecal samples daily. During this period dungs were collected on an average of 17 days each month (range 10–22; Figure 5.1). Mean number of specimens collected per ‘dung collection day’ was 6.6 (± 4.5 SD), excluding days when no specimens were found. The number of independent dung samples analysed was 1436 (monthly mean = 110.5, *N* = 13, range 49–149; Figure 5.1). In general, monthly sample size increased during the latter half of the study due to increased familiarity with chimpanzee movements and trail networks.

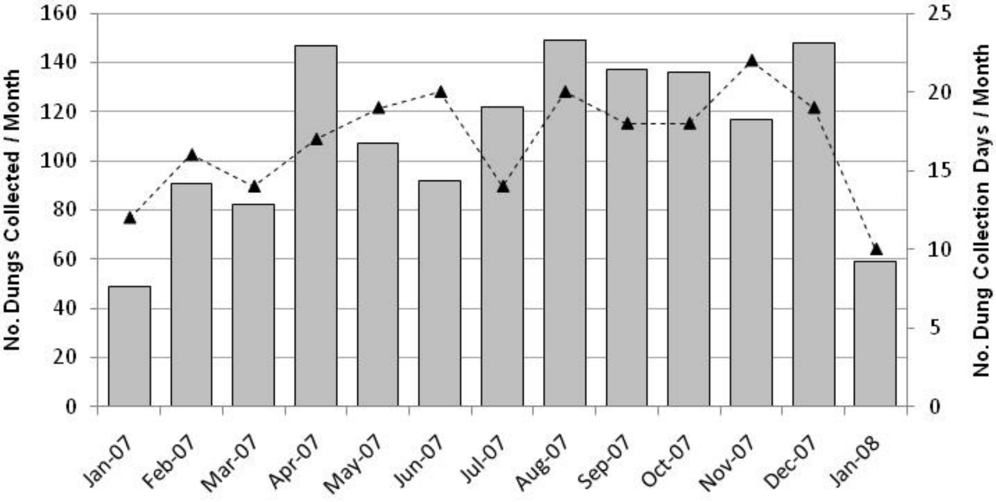

Figure 5.1. Variation in number of fresh dung specimens collected each month (bars) and number of dung collection days per month (line), Jan 2007–Jan 2008 (*N* = 1436).

Dried dung specimens were examined macroscopically and the contents listed as fruit seeds (small = <2 mm; medium = 2–5 mm; large = ≥5 mm), other fruit remains (skins, pulp, fibres), foliage (including fibrous piths and stems, green leaf fragments, whole undigested leaves, and bark), and other items (principally animal foods). For each dung, the volume percentage of major food categories (fruit, foliage, other) was estimated at 5% intervals with respect to the total mass of the specimen (Kuroda et al. 1996a). The combined % scores for fruit seeds and other fruit remains gave an overall *fruit score* per dung. The combined % scores for leaves, piths and bark gave a *foliage score*; this is equivalent to the 'fibre score' used in some studies (e.g. Doran et al. 2002). Medium and large seeds of individual fruit species were counted, whereas the volume percentage of small seeds (principally *Ficus* seeds) was estimated at 5% intervals.[1] Abundances of pith and green leaf fragments – the main constituents of the foliage component of dungs – were ranked on a 0–4 scale where 0 = absent, 1 = rare, 2 = few, 3 = common, and 4 = abundant (Tutin and Fernandez 1993a). In some studies this scale of abundance is used to estimate the representation of major food categories in dung, but I used the volume

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[1] When medium-sized seeds were especially numerous (e.g. *Lantana camara* or guava), the total quantity was estimated by counting seeds in a subsection of the dung and extrapolating to the whole.

percentage method so that fruit and fibre scores are proportional to one another; abundance ranks are not precise enough to allow assessment of the relative amounts of food categories in dung.

Although a standardised definition of an 'important' food item is lacking in great ape diet studies (Rogers et al. 2004), I defined *important fruits* as those present in at least 50% of dungs in ≥1 month since this criterion is often employed in the literature (Wrangham et al. 1991; Rogers et al. 2004; Hohmann et al. 2006; Pruetz 2006). I also considered fruit species to be important if they occurred in >10% of the total dung sample (e.g. Moscovice et al. 2007) (Table 5.1). This was because certain fruits that were eaten regularly, but not necessarily intensively, had a greater overall representation in faeces than some other species that occurred in the majority of dungs for brief periods only. A fruit species appearing in the largest proportion of dung specimens in a given month was the 'top-ranked' species for that month. *Seasonally important* foods were available for only a portion of the year.

Table 5.1. Definitions of food classifications used in this study.

Classification	**Definition**
Important fruit species	Residue observed in at least 50% of dungs in ≥1month or >10% of all dungs; important fruits that were seasonally available are 'seasonally important'
Preferred fruit species	Residue observed in dungs at significantly greater frequencies with increased availability
Staple food	Food item eaten throughout the year, not necessarily in accordance with availability
Fallback food	Food item available year-round or for extended periods (≥6 months), eaten in inverse proportion to the availability and/or intake of ripe fruit.

Ideally, quantitative assessment of dietary preference necessitates an estimate of the abundance of all foods in the study animal's habitat at a given time (Marshall and Leighton 2006; Marshall and Wrangham 2007). However, few food items were confirmed in the diet of chimpanzees at Bulindi prior to phenological surveys, thus some foods were not monitored. Therefore *preferred fruits* were defined simply as species that occurred in dungs at significantly increasing frequencies – or, in the case of figs, in greater quantities – with an increase in availability. Note that important fruits need not necessarily be preferred. A *staple food* denotes a regular item in the diet, utilised in most or all months of the year (Doran et al. 2002; Rogers et al. 2004).

Identification of *fallback foods* for a population (or keystone resources for a community) requires long-term study to account for inter-annual changes in food availability (Tutin et al. 1997; Yamagiwa and Basabose 2009). Nevertheless, items were regarded as potential fallback foods for chimpanzees if intake was inversely correlated with availability and/or consumption of ripe fruit (Marshall and Wrangham 2007; Marshall et al. 2009) (Table 5.1). Staple foods can be fallbacks if they are increasingly utilised when availability of preferred foods declines (Marshall and Wrangham 2007).

As shown in Figure 5.1, dung sample sizes varied across months. Following Doran et al. (2002) I evaluated the effect of sample size on three measures of fruit content derived from dung analysis: (1) monthly mean number of fruit species per dung; (2) total number of fruit species found in dungs per month; and (3) the monthly mean proportion of fruit per dung specimen (i.e. the % fruit score). Measures one and two assess fruit diversity in the diet whilst three evaluates fruit quantity. Whereas sample size had no effect on measures one and three (Spearman rank correlations; monthly mean no. fruit sp.: $r_s = 0.055$, $n = 13$, $p = 0.86$; % fruit score: $r_s = -0.214$, $p = 0.48$), a positive relationship exists between sample size and the total number of fruit species in dungs per month ($r_s = 0.720$, $p < 0.01$). This is because the likelihood of recording infrequently eaten fruits increases with larger monthly sample sizes. This measure of dietary fruit diversity was therefore not considered in the analysis.

Limitations of dung analysis for describing diet. Chimpanzees usually swallow fruit seeds whole, permitting identification of seeds passed in faeces (Lambert 1999). However, it is rarely possible to identify taxonomically other plant parts such as piths, leaf fragments and bark in dung, and certain foods such as flowers may leave no recognisable trace at all. Thus the diversity of the vegetative component of the diet is underestimated by faecal analysis (Tutin and Fernandez 1993a; Doran et al. 2002). Nevertheless, the method allows quantification of seasonal variation in the relative amount of fruit and foliage in the diet, which can be used as a rough index of dietary quality since chimpanzees are ripe fruit specialists. Dung analysis also gives information on frequency and seasonality of insectivory and meat-eating (reported in Chapter 6), as well as certain medical plant use (Wrangham 1995; Huffman et al. 1996).

Dietary Composition

Data collected using the above three methods were collated to produce a list of known food items recorded in the chimpanzee diet during the study period. Food lists enable rapid assessment of similarities and variance in diet among populations (e.g. Russon et al. 2009). Dietary composition of plant foods eaten is described in terms of diversity (number of species and taxonomic families), life form (divided into five categories: tree, shrub, herb, climber or grass), and parts consumed (seven categories: fruit, leaf, pith, flower, seed, bark, sap). Seed consumption was distinguished from fruit consumption if the mature seed component of a pod was actively fed upon (i.e. chewed) as opposed to merely swallowed whilst the chimpanzee fed on the associated fruit pulp or aril. Life forms of plant foods follow the *Flora of Tropical East Africa* (Polhill 1952 et seq.) and Synnott (1985). Plant species nomenclature follows the *Flora of Tropical East Africa*.

Identification of Samples

Vouchers of fruiting plants encountered within the study area, as well as plants associated with fresh feeding traces, were collected for taxonomic identification at Makerere University Herbarium, Kampala, and Kew Gardens, UK. A reference collection of the seeds was used to identify seeds found in chimpanzee dung. Seeds recovered from dung were identified to species level where possible.

Statistics

Correlation and regression analysis were used to assess the association between measures of dietary composition (e.g. fruit and foliage content, diversity of fruit foods), consumption of particular foods and forest fruit availability. Consumption (or ‘intake’) of individual species or broader food categories was indexed as (i) the % of monthly dungs containing the food item, or (ii) the monthly mean volume % or abundance rank of the item in dungs. Certain variables used in correlations were non-normally distributed, even following transformation, and therefore non-parametric Spearman rank coefficients were employed throughout. Kruskal–Wallis one-way ANOVAs were used to test for monthly variation in fruit and foliage scores, number of different fruit species and proportion of fruit species that were cultivated per dung. Food availability indices (FAI) for ripe fruit and young leaves (based on ranked scores of abundance) were calculated as described in Chapter 4. Statistical analyses are based on phenological and dietary data spanning 13 months (January 07–January 08); phenology data were available for December 06 but were not included in the analysis because of the small sample of dungs collected in that month ($n = 4$). Qualitative information from feeding traces and direct observations supplement dietary data from faecal specimens, but were not used in statistical analysis.

Linear regression was used to examine the relationship between consumption of a particular food item and its availability. To identify potential fallback foods I first used exploratory correlation analysis to identify independent variables (IV) associated with the particular item (p <0.10). The IVs included monthly measures of fruit availability (ripe fruit FAI) and intake (mean fruit score), plus measures of the diversity of the fruit diet (mean number of fruit species in dungs, and number of 'important' fruits dominating monthly dungs). If two or more IVs were negatively associated with the potential fallback food I performed a multiple regression analysis to determine the simultaneous and individual effect of IVs. The backward stepwise method was employed, wherein all predictor variables (i.e. IVs) are entered into the model. The variable that correlates least strongly with the dependent variable is removed and the regression is recalculated. Unless the model is significantly weakened by its removal, the weakest predictor is deleted. When more than two IVs are included, the process is repeated until only variables that contribute significantly to the strength of the model are retained (Field 2005). Residuals of dependent variables were inspected for normality. If non-normality was indicated, Kolmogorov–Smirnov and Shapiro–Wilk tests were run to test if standardised residuals differed significantly from a normal distribution (Chen et al. 2003; Field 2005). If non-normality was confirmed by either test, log-10 transformations were applied to IVs (Chen et al. 2003). Variables expressed as percentages were converted to proportions and transformed to arcsine square roots unless all values fell within the range of 0–30%, in which case standard square root transformations were applied (Ahrens et al. 1990). In all regressions statistics generated in SPSS indicated no problems associated with collinearity or multicollinearity, and the Durbin–Watson statistic showed that the assumption of independent errors was met. Tests were performed using SPSS version 17.0. All tests were two-tailed and values of p <0.05 were considered significant; p-values <0.10 are reported as non-significant trends.

5.3. Results

5.3.1. Dietary Composition

Number of Plant Parts and Plant Species Eaten

Table 5.2 lists plant species recorded in the chimpanzee diet at Bulindi each month between October 06 and January 08 (16 months). During this time the chimpanzees ate a minimum of 96 different plant food items from at least 82 species (74 identified, 8 unidentified), represented by at least 36 taxonomic families. In fact, the actual number of species for which there was evidence of consumption by chimpanzees almost certainly exceeds this figure. Some plant genera have seeds that are not easily distinguished at the species level in dung (e.g. *Aframomum*, *Cissus*, *Ficus*, *Landolphia*). For these taxa, identification of species eaten was dependent on observation of feeding or evidence from feeding traces. Similarly, chimpanzees probably fed on >1 species of cultivated banana (*Musa* spp.) but taxonomic identification of different varieties was not attempted. Food items that likely comprise >1 species are considered ‘species groups’ in Table 5.2. Several fruit seeds found in dung could not be identified and are referred to in the table by the reference number of the first dung specimen in which they occurred. Other unidentifiable plant food items in dung were piths and chewed leaf fragments, bark pieces and flower remains.

Figure 5.2 plots the cumulative number of plant food items recorded in the chimpanzee diet each month. The number of new food items was still steadily rising in the final month of the study, indicating that additional foods would continue to be recorded with further research. Nevertheless, most plant foods eaten frequently by chimpanzees during the study – either seasonally or throughout the year – are probably represented in the food list. Thirteen of 82 (16%) plant species were recorded as food items once only during the study (e.g. in a single dung specimen). The life forms of food species are shown in Table 5.3. Trees and shrubs were most commonly eaten but chimpanzees also ate a variety of climbing plants and herbs.

Table 5.2. List of plant food items recorded in the diet of Bulindi chimpanzees, Oct 06–Jan 08. For each species (or species group), the following information is listed: life form, part(s) eaten, criteria used to determine consumption, and the months in which each plant part was recorded in the diet.

Food Species	Family	Life Form [1]	Part Eaten [2]	Criteria [3]	Months in which food item was recorded eaten [4]															
					Ot 06	Nv	Dc	Ja 07	Fb	Mr	Ap	My	Jn	Jl	Ag	Sp	Ot	Nv	Dc	Jn 08
1. *Acalypha* sp. *	Euphorbiaceae	S	L †	F														x		
2. *Acanthus pubescens* (Thomson ex oliv.) Engl.	Acanthaceae	S	P	T												x		x	x	
[*Aframomum* spp. ○]	Zingiberaceae	H	Fr [R]	F, T				x	x	x	x	x	x	x	x	x	x	x	x	x
			P	T										x			x	x		
3. *Aframomum angustifolium* (Sonnerat) K. Schum.	Zingiberaceae	H	Fr [R]	O												x				
4. *Aframomum verrucosum* Lock	Zingiberaceae	H	Fr [R]	T													x	x		
			P	T										x						
5. *Allophylus africanus* P. Beauv.	Sapindaceae	T	Fr [R]	F														x	x	
6. *Allophylus ferrugineus* Taub.	Sapindaceae	T	Fr [R]	F															x	
7. *Ampelocissus abyssinica* (A. Rich.) Planch.	Vitaceae	C	Fr [R]	F, T													x	x		
8. *Ampelocissus africana* (Lour.) Merr.	Vitaceae	C	Fr [R]	F		x										x	x	x	x	
9. *Aneilema nyasense* C.B. Clarke	Commelinaceae	H	L †	F				x	x	x	x	x	x	x	x	x	x	x	x	x
10. *Annona senegalensis* Pers.	Annonaceae	T	Fr [R]	F, O										x	x	x				
11. *Antiaris toxicaria* Leschen.	Moraceae	T	Fr [R]	F, O					x	x	x	x	x							
			Fl	O				x												
			L [YL]	O											x				x	
12. *Artocarpus heterophyllus* Lam. # [jackfruit]	Moraceae	T	Fr [R]	T									x			x				
13. *Caloncoba crepiniana* (De Wild. & Th. Dur.) Gilg	Flacourtiaceae	T	Fr [R]	F, T										x	x	x	x			
14. *Canavalia virosa* (Roxb.) Wight & Arn.	Fabaceae (subfam. Faboideae)	S	Sd	F, T															x	
15. *Capparis erythrocarpos* Isert	Capparaceae	S	Fr	F					x	x		x	x	x	x					
16. *Carica papaya* L. # [papaya]	Caricaceae	T	Fr [R, UR]	F, O, T		x		x	x	x	x	x	x	x	x	x	x	x	x	x
17. *Celtis africana* Burm. f. *	Ulmaceae	T	L •	T													x			
18. *Cissus* spp. ○	Vitaceae	C	Fr	F													x		x	x
19. *Citrus sinensis* (L.) Osb. # [orange]	Rutaceae	S	Fr [R]	O, T											x	x	x	x		
20. *Coccinia barteri* (Hook. f.) Keay	Cucurbitaceae	C	Fr	F						x	x	x		x		x	x			

Cont. overleaf

Table 5.2 *cont.*

Food Species	**Family**	**Life Form** [1]	**Part Eaten** [2]	**Criteria** [3]	**Months in which food item was recorded eaten** [4]															
					Ot 06	**Nv**	**Dc**	**Ja 07**	**Fb**	**Mr**	**Ap**	**My**	**Jn**	**Jl**	**Ag**	**Sp**	**Ot**	**Nv**	**Dc**	**Jn 08**
21. *Coccinia* sp.	Cucurbitaceae	C	Fr	F						x	x		x	x	x	x			x	x
22. *Crotalaria rogersii* Bak. f.	Fabaceae (subfam. Faboideae)	H	L [YL]	T											x	x	x	x		
23. *Croton sylvaticus* Krauss	Euphorbiaceae	T	Fr [R]	F												x		x		
24. *Cyperus papyrus* L.	Cyperaceae	H	P •	T												x		x	x	
25. *Cyphomandra betaceae* (Cav.) Sendtn.	Solanaceae	S	Fr [R]	T						x						x				
26. *Desmodium velutinum* (Willd.) DC.	Fabaceae (subfam. Faboideae)	H	L †	F						x		x	x	x	x		x			
27. *Dioscorea alata* L. # [yam] *	Dioscoreaceae	H	P	T										x						
28. *Dovyalis macrocalyx* (Oliv.) Warb.	Flacourtiaceae	S	Fr [R]	F, T						x	x	x								
29. *Entada abyssinica* (Steud. ex) A. Rich. *	Fabaceae (subfam. Mimosoideae)	T	L [YL]	T												x				
[*Ficus* spp. ○]	Moraceae	T,S	Fr	F		x		x	x	x	x	x	x	x	x	x	x	x	x	x
30. *Ficus asperifolia* Miq.	Moraceae	S	Fr	O																x
31. *Ficus exasperata* Vahl	Moraceae	T	Fr [UR]	F, O, T					x			x						x		
32. *Ficus mucuso* Ficalho	Moraceae	T	Fr [R]	O, T								x					x			
33. *Ficus natalensis* Hochst.	Moraceae	T	Fr [R]	O	x				x	x		x	x		x		x	x		
34. *Ficus sur* Forssk.	Moraceae	T	Fr [R, UR]	O, T			x			x				x	x			x	x	
35. *Ficus thonningii* Bl.	Moraceae	T	Fr [R]	T							x									
36. *Ficus variifolia* Warb.	Moraceae	T	Fr [R]	F, O										x					x	
			L [YL]	O											x					
			Sp	O										x						
37. *Grewia mollis* Juss.	Tiliaceae	T	Fr	F															x	x
38. *Grewia pubescens* P. Beauv.	Tiliaceae	S	Fr	F				x	x	x	x								x	x
39. *Grewia* sp.	Tiliaceae	S	Fr	F															x	
[*Landolphia* spp. ○]	Apocynaceae	C	Fr [R]	F, T				x	x	x	x							x	x	
40. *Landolphia landolphioides* (Hallier f.) A. Chev.	Apocynaceae	C	Fr [UR]	T												x				
41. *Lantana camara* L.	Verbenaceae	S	Fr [R]	F				x	x		x	x	x		x	x	x	x	x	
			L †	F												x	x	x	x	
42. *Lantana trifolia* L.	Verbenaceae	S	Fr	F								x				x	x		x	x
43. *Leea guineensis* G. Don *	Vitaceae	S	Fr	F									x							
44. *Macaranga schweinfurthii* Pax	Euphorbiaceae	T	Fr	F										x		x				

Cont. overleaf

Table 5.2 *cont.*

Food Species	**Family**	**Life Form** [1]	**Part Eaten** [2]	**Criteria** [3]	**Months in which food item was recorded eaten** [4]															
					Ot 06	**Nv**	**Dc**	**Ja 07**	**Fb**	**Mr**	**Ap**	**My**	**Jn**	**Jl**	**Ag**	**Sp**	**Ot**	**Nv**	**Dc**	**Jn 08**
45. *Maesopsis eminii* Engl. *	Rhamnaceae	T	Fr	F							x									
46. *Mangifera indica* L. # [mango]	Anacardiaceae	T	Fr [R, UR]	F, O, T								x	x	x	x			x	x	x
47. *Marantochloa leucantha* (K. Schum.) Milne-Redh.	Marantaceae	H	Fr	F												x	x			
			P	T									x	x	x	x	x	x	x	x
48. *Margaritaria discoidea* (Baill.) Webster	Euphorbiaceae	T	Fr	F															x	
49. *Monanthotaxis ferruginea* (Oliv.) Verdc.	Annonaceae	S	Fr [R]	F, O, T		x				x					x		x	x	x	x
50. *Morus mesozygia* Stapf	Moraceae	T	Fr [R]	F, O, T						x	x	x						x	x	
			L [YL]	O						x										
51. *Musa* spp. ○ # [banana]	Musaceae	H	Fr [R]	F, O, T								x			x	x	x	x	x	x
			P	T			x						x	x	x	x	x	x	x	
52. *Oncoba spinosa* Forssk. *	Flacourtiaceae	T	Fr	F																x
53. *Palisota schweinfurthii* C.B. Clarke	Commelinaceae	H	P	T										x		x				
54. *Parkia filicoidea* (Welw. ex) Oliv.	Fabaceae (subfam. Mimosoideae)	T	Fr [R, UR]	F, O, T						x	x	x								
			Sd	F, O, T						x	x	x								
			L [ML]	F						x	x	x	x		x	x				
55. *Passiflora* spp. ○ # [passion fruit]	Passifloraceae	C	Fr [R]	F, T									x	x				x		
56. *Pennisetum purpureum* Schumach.	Poaceae (Gramineae)	G	P	O, T						x	x	x	x	x	x	x	x	x	x	x
57. *Phoenix reclinata* Jacq.	Arecaceae (Palmae)	T	Fr [R]	F, O, T		x	x	x	x	x	x	x	x	x	x	x			x	x
58. *Pseudospondias microcarpa* (A. Rich.) Engl.	Anacardiaceae	T	Fr [R, UR]	F, O, T	x	x	x	x	x		x	x	x	x	x					
			L • [YL]	O, T					x										x	x
59. *Psidium guajava* L. # [guava]	Myrtaceae	T	Fr [R, UR]	F, O, T		x		x	x	x	x	x	x	x	x	x	x	x	x	x
60. *Psychotria peduncularis* (Salisb.) Steyerm. *	Rubiaceae	S	Fr	F															x	
61. *Pycnanthus angolensis* (Welw.) Warb. *	Myristicaceae	T	Fr	F				x												
62. *Rothmannia whitfieldii* (Lindl.) Dandy	Rubiaceae	S	Fr	F, T				x												
63. *Rubus pinnatus* Willd.	Rosaceae	S	Fr	F, T					x				x	x	x	x	x	x	x	x
64. *Saccharum officinarum* L. # [sugarcane]	Poaceae (Gramineae)	G	P	O, T	x			x		x				x	x	x	x	x	x	x
65. *Sida rhombifolia* L. *	Malvaceae	S	L •	T														x		
66. *Sorghum arundinaceum* (Desv.) Stapf	Poaceae (Gramineae)	G	Sd?	F									x			x		x		
67. *Sterculia dawei* Sprague	Sterculiaceae	T	Fr	F, T										x	x	x	x	x		
68. *Theobroma cacao* L. # [cocoa]	Sterculiaceae	T	Fr [R, UR]	F, O, T		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
69. *Toddalia asiatica* (L.) Lam.	Rutaceae	S	Fr	F													x		x	x
70. *Trichilia dregeana* Sond.	Meliaceae	T	L [YL]	F, O, T											x	x	x	x	x	

Cont. overleaf

Table 5.2 *cont.*

Food Species	**Family**	**Life Form [1]**	**Part Eaten [2]**	**Criteria [3]**	**Months in which food item was recorded eaten [4]**															
					Ot 06	**Nv**	**Dc**	**Ja 07**	**Fb**	**Mr**	**Ap**	**My**	**Jn**	**Jl**	**Ag**	**Sp**	**Ot**	**Nv**	**Dc**	**Jn 08**
71. *Uvaria angolensis* Oliv.	Annonaceae	C	Fr	F							x					x	x			x
72. *Vangueria madagascariensis* Gmelin	Rubiaceae	T	Fr	F															x	
73. *Vitex doniana* Sweet	Lamiaceae	T	Fr [R]	F, O															x	x
74. *Zanha golungensis* Hiern	Sapindaceae	T	Fr [R]	F							x	x								
Unidentified / Uncertain species																				
75. *?Erythrococca trichogyne* *	? Euphorbiaceae	S	L †	F									x							
76. *?Zehneria scabra*	? Cucurbitaceae	C	Fr	F									x	x	x					
77. Unknown grass spp. ○	Poaceae (Gramineae)	G	L †	F							x		x					x		
78. Unknown climber sp. *	?	C	L	O																x
79. Unknown seed #1 (“D284”)	?	?	Fr	F							x									
80. Unknown seed #2 (“D343”)	?	?	Fr	F							x	x	x						x	
81. Unknown seed #3 (“D506”)	?	?	Fr	F									x							
82. Unknown seed #4 (“D1038”) *	?	?	Fr	F													x			
Unknown bark fragments ○	?	?	B	F				x	x	x	x	x		x	x	x	x	x	x	
Unknown flower fragments ○	?	?	Fl	F					x	x	x		x	x	x	x	x			

[1] Life Form: T = tree, S = shrub, H = herb, C = climber (liane or vine), G = Grass;

[2] Part Eaten: Fr = Fruit, L = Leaf, P = Pith, Fl = Flower, Sd = Seed, B = Bark; Sp = Sap. Observations on fruit ripeness and maturity of leaves eaten are given, where known: R = ripe, UR = unripe including ‘half-ripe’ fruits; YL = young leaf, ML = mature leaf;

[3] Criteria: F = Faecal Specimen, O = Direct Observation, T = Feeding Trace;

[4] Feeding data are mainly from Jan 07 when systematic dung collection and analysis began – records for Oct–Dec 06 are included for supplementary purposes only;

x = indicates the food item was eaten during the month; blanks do not mean that the food item was not eaten or was unavailable in that month, it simply indicates it was not recorded as eaten;

? = indicates that taxonomic identification could not be made or remains to be confirmed; for unknown seeds numbers in parenthesis indicate the dung specimen in which the seed first occurred, used as a subsequent identifier; ‘unknown bark’ and ‘unknown flower’ fragments are not listed as additional species or species groups since these plant parts might be from species included in the list;

○ = Denotes a ‘species group’ (food items known or suspected to compromise >1 species);

* = Food species recorded only once (i.e. in a single dung specimen or feeding observation);

† = Leaves swallowed whole for assumed self-medicative purposes;

• = Indicates that leaves/pith were ‘wadged’ and discarded (i.e. ingestion not confirmed);

\# = Cultivated food items [and common name].

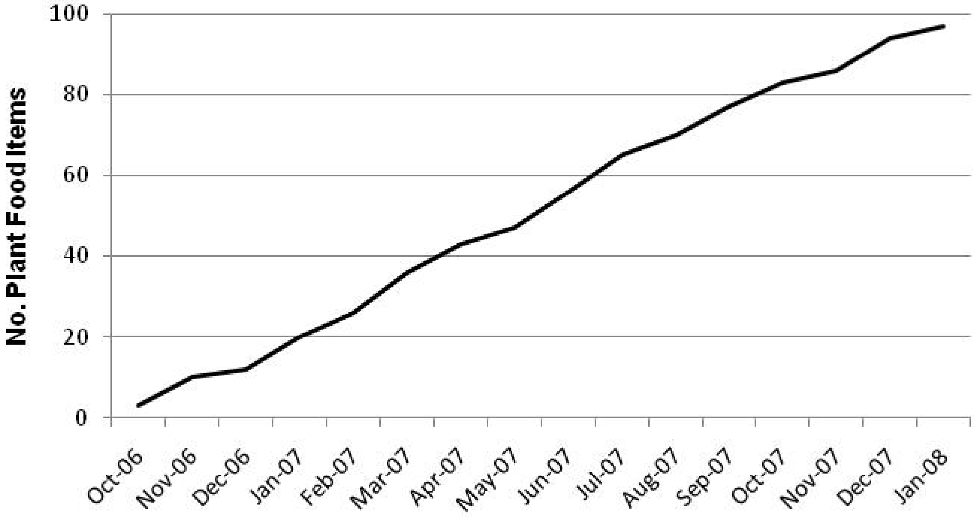

Figure 5.2. Cumulative number of plant food items recorded in the chimpanzee diet, Oct 2006–Jan 2008 (*n* = 96).

As expected, evidence for consumption of many food items was indirect. Of 96 plant parts eaten, 66 were recorded in dung (69%) and 43 from feeding traces (45%). Thirty-two were observed being eaten (33%). Only 13 items (14%) were verified by all three methods. Evidence for consumption of 40 items (42%) – of which 31 were fruits – came exclusively from dung. Of 30 items *not* recorded in dung, the majority (67%) were plant parts that were rarely identifiable taxonomically in faeces (e.g. piths and leaves), and figs that are difficult to discriminate to species-level from the seeds alone.

Table 5.3. Breakdown of plant foods by species life form and part eaten. The life form of four fruit seeds found in dung was undetermined. Chimpanzees ate ≥1 part of several species.

Species Life Form	***n***	**%**	**Plant Part Eaten**	***n*** [1]	**%**
Tree	34	41.5	Fruit	63	65.6
Shrub	20	24.4	Leaf	17	17.7
Climber [2]	10	12.2	Pith	9	9.4
Herb	10	12.2	Seed	3	3.1
Grass	4	4.9	Flower	2	2.1
Unknown	4	4.9	Bark	1	1.0
			Sap	1	1.0
Total:	82	100%	Total:	96	100%

[1] The total no. of plant parts eaten excludes generic *Aframomum*, *Ficus* and *Landolphia* food items (considered 'species groups' in Table 5.2); for these genera only plant parts of identified species were counted to avoid replication;

[2] Climbers include lianas and vines.

Parts Eaten

Numerically, the chimpanzee diet was dominated by fruits. Fruits of at least 63 plant species were consumed (66% of plant food items) (Table 5.3), comprising 31 species of tree, 15 species of shrub, nine climbers, four herbs and four species of undetermined life form (i.e. unidentified seeds). The taxonomic family that contributed the most fruit species to the diet was the Moraceae (ten species, including seven figs), which was the dominant tree family in Bulindi forests (Chapter 3). Non-fruit plant foods included leaves, piths, flowers, bark and sap (Table 5.3); seeds accounted for only three recorded plant foods (3.1%), and were lumped with the fruit component of dungs in the analysis to distinguish them from foliage food items.

The leaves of at least 17 species were eaten (17.7% of plant foods), including six that were swallowed whole for assumed self-medicative purposes and passed undigested in dung (see below). The chimpanzees fed on at least nine species of pith or stem (9.4% of plant foods), including six taxa of THV and three cultivars. Evidence for consumption of other non-fruit plant foods was sparse. Only one species of flower was confirmed eaten – chimpanzees were seen feeding on flowers of *Antiaris toxicaria* in January 07 – but unidentified flower remains were occasionally visible in dung between February–October (1% of all dungs) when *Antiaris* was not flowering, suggesting ≥1 other species was consumed (Table 5.2). Unidentified bark pieces occurred in dung at low frequencies throughout the study (1.7% of all dungs). A single observation of sap ingestion was made in July 07 when an adult male repeatedly licked exudate from the bough of a fruiting *Ficus variifolia*, apparently having first stripped the outer bark with his teeth.

Direct observations and indirect evidence suggested the chimpanzees overwhelmingly ate ripe fruits (Table 5.2). The residues of many species began to appear in dung only once the fruits were known to be fully ripe. Occasionally, fruits were also eaten 'half-ripe' (e.g. *Ficus sur*, mango, *Parkia filicoidea*). Fully unripe fruit was apparently rarely eaten. In September 07 chimpanzees fed on small unripe *Landolphia landolphioides* fruits, but all other evidence indicated *Landolphia* fruit was consumed ripe. In November 07 unripe figs of *Ficus exasperata* were eaten. Ripe forest fruit was relatively scarce in September–November, but it is uncertain if chimpanzees ate more unripe fruit at this time compared to when ripe fruit was more abundant. A notable exception is cocoa. Although chimpanzees selected ripe pods when they raided cultivated *shambas* outside of the forest, they consistently ate pods that had yet to ripen from abandoned forest *shambas*, perhaps due to feeding competition from other animals. Observations of leaf-eating indicated chimpanzees selectively fed on emerging or young leaves (Table 5.2). However, leaves found whole in dung, and thus not ingested for nutritional benefit, appeared to be mature in most cases.

Whole Leaf-Swallowing

Whole undigested leaves were recovered in 149 dungs (10.4% of the total sample) and leaf-swallowing occurred in all months between January 07 and January 08 (3.7–23.7% of monthly dungs). Five species of shrub or herb and at least 1 species of grass were swallowed (Table 5.2). The most commonly swallowed leaves were *Aneilema nyasense* (Commelinaceae), occurring in 82% of cases ($n = 122$).

Cultivars

At least ten species of cultivated plant were eaten (16% of identified food species), including the fruits of eight species (banana, cocoa, guava, jack-fruit, mango, orange, papaya and passion-fruit) and the piths of three (banana, sugarcane, and yam) (Table 5.2). Local residents variously claimed chimpanzees ate pumpkin, tomato, pineapple and avocado fruits, and maize pith, but the reliability of such reports varied and evidence for consumption of these additional cultivars was lacking or inconclusive.[2]

5.3.2. Frugivory

Faecal specimens were overwhelmingly dominated by the seeds, skins and pulp of fruit. The average monthly fruit score (the mean % fruit per dung) was 82.6% (± 7.9 SD), and there were no months when the foliage intake exceeded that of fruit. Figure 5.3 depicts monthly variation in mean fruit and foliage scores (lower chart) in relation to availability of ripe forest fruit (upper chart). The proportion of fruit in the diet varied significantly across months (Kruskal–Wallis one-way ANOVA, $H = 332.16$, $df = 12$, p

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[2] For example, pumpkin feeding traces were once found on a trail earlier traversed by chimpanzees; however, the remains could potentially have been left by baboons. In the case of tomato, a single dung contained a quantity of bright red fruit pulp, unlike the pulp of any other known fruit food. Possibly this was tomato (but pips were not seen).

<0.001). Nevertheless, fruit accounted for >80% of dung contents in all months *except* August–November (four months) when mean fruit score dropped to just above 70%. This includes the main 'low fruiting season' as indicated by phenological sampling (September–November). Indeed, the monthly FAI for ripe fruits was a significant predictor of mean fruit score in dung ($R^2 = 0.406$, $F_{1,11} = 7.53$, $p = 0.02$; Figure 5.4). Although this suggests that chimpanzees increased their fruit intake as it became more plentiful in the forest, it can be seen from Figure 5.3 that levels of fruit consumption were relatively constant outside of August–November despite apparent fluctuations in availability. For example, the chimpanzees maintained a high level of frugivory in May when fruit availability was estimated to be low.

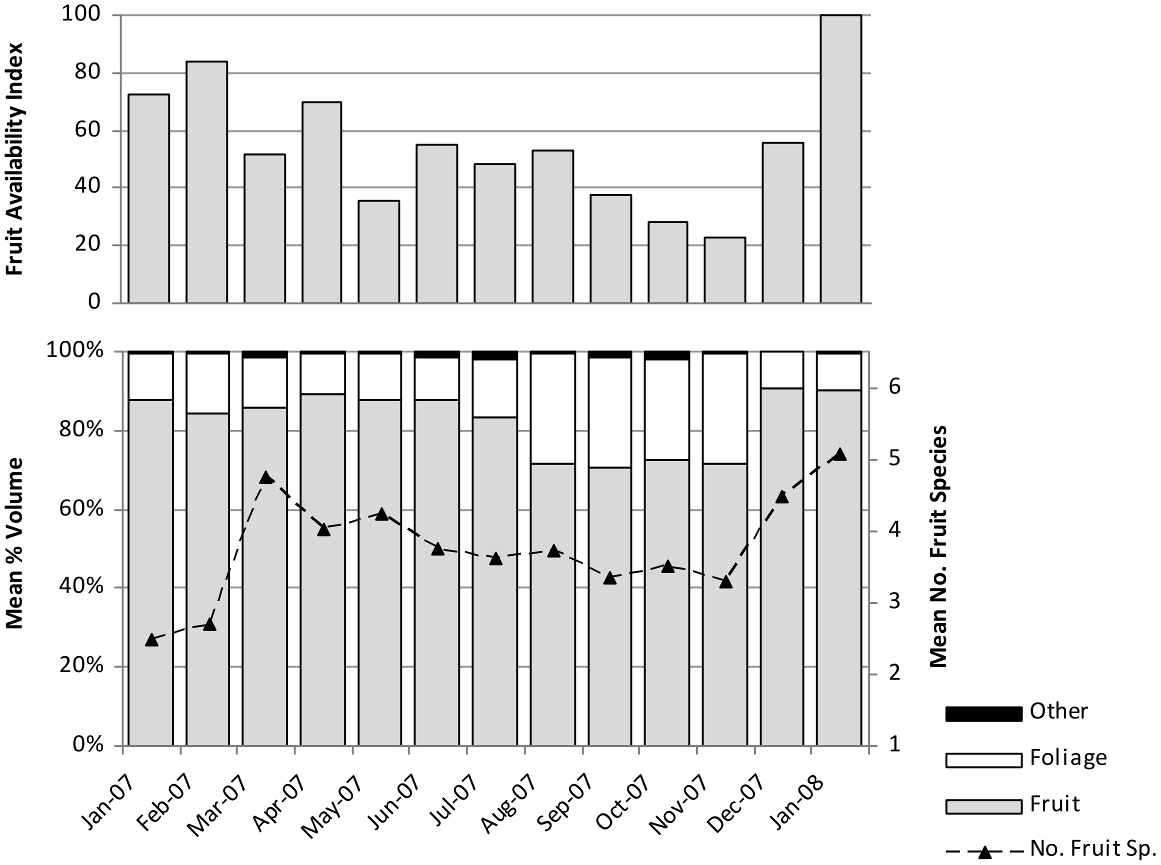

Figure 5.3. *Lower chart*: monthly variation in the mean % volume of fruit, foliage and other items (bars), and no. of different fruit species (dashed line), in chimpanzee dung (Jan 07–Jan 08). *Upper chart*: bars indicate ripe fruit availability in forest fragments for the same period; fruit availability is expressed as an index of 100 where the month with the highest value = 100. 'Other' items are principally animal foods.

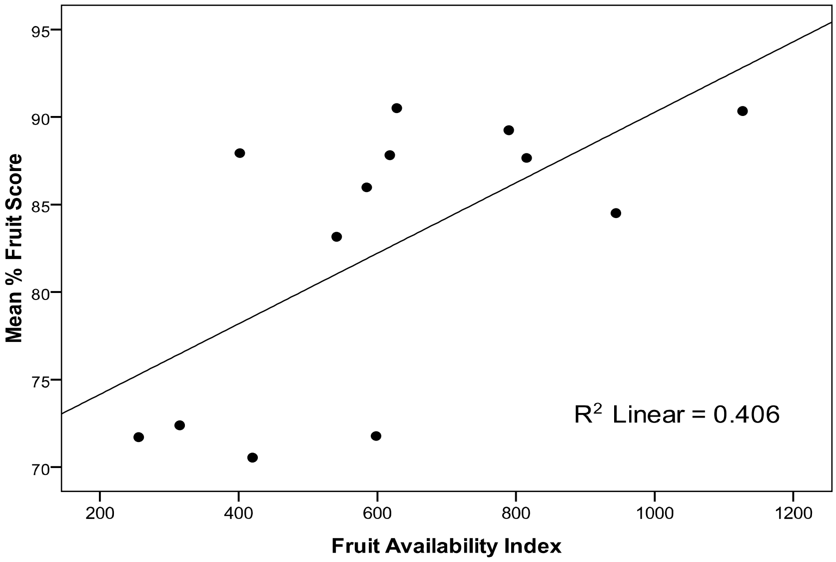

Figure 5.4. Relationship between the monthly availability of ripe forest fruit and mean fruit score (% volume) in dung.

Diversity of Fruit Diet

Fruit remains were present in all but one of the 1436 dungs analysed (99.9%). The mean number of individually distinguishable fruit species (including 'species groups') per dung specimen was 3.8 ± 1.56 SD (range 0–10; median = 4). In some instances the actual number of different fruit species in dung probably exceeded the total recorded: consumption of a species was mainly indicated by seed presence, but non-seed fruit parts were sometimes taxonomically identifiable in the absence of seeds (e.g. syrupy pulp of *Sterculia dawei*, mango fibres, papaya skin, cocoa and banana pulp). When non-seed residues were present in trace quantities it was difficult to confirm the fruit species with confidence.

The number of different fruit species per dung varied significantly across months (Kruskal–Wallis one-way ANOVA, $H = 230.29$, $df = 12$, $p < 0.001$). Thus the diversity of the fruit component of the diet was not constant. The average number of species per dung was lowest in January 07 (2.5) and highest one year later in January 08 (5.1). The diversity of fruits in dung peaked in March–May 07 and December 07–January 08, and was least varied during January–February 07 at the start of the study (Figure 5.3). It is conceivable that small quantities of cultivar pulp (e.g. cocoa and banana) were overlooked in January–February 07 through lack of familiarity with non-seed fruit residues. However, cocoa pulp was recorded in dungs at low frequencies in both months, and descriptive records made when dungs were washed did not indicate unusual or unidentifiable fruit residues were observed. Monthly variation in average number of fruit species per dung did not correlate with estimates of either the abundance or diversity of forest fruit (ripe fruit FAI: $r_s = 0.165$, $p = 0.59$; proportion of phenology species with ripe fruit: $r_s = 0.102$, $p = 0.74$).

Important Fruit Species

A variety of different fruit species were recorded in dung each month (range: 12–29). Even so, in a given month the chimpanzees' diet tended to be dominated by a small number of fruit species, the residues of which occurred in the majority of dungs. Seventeen species (including three species groups) were identified as 'important' fruit foods for Bulindi chimpanzees (Table 5.4). These include 11 trees (64.7%), three shrubs (17.6%), two vines (11.8%) and one herb (5.9%) (Plate 8). Four species of cultivar are represented (cocoa, guava, mango and papaya). The number of fruit species represented in ≥50% of monthly dungs varied. In all months there were at least two such species, and in three months (March and May 07, and January 08) five species occurred in the majority of dungs (Table 5.4). Although the number of species appearing in at least half of the monthly dung sample was positively but weakly correlated with fruit intake, as assayed by the mean fruit score ($r_s = 0.558$, $p = 0.048$), it was not related to the monthly FAI for ripe fruit ($r_s = -0.043$, $p = 0.89$) or the proportion of phenology species fruiting ($r_s = 0.236$, $p = 0.44$).

Figure 5.5 plots the total number of fruit species occurring in ≥50% of monthly dungs against a subset that includes *forest tree species only*; thus non-trees and cultivars found predominantly (guava and mango) or exclusively (papaya) outside of forest were excluded from this second measure. (Cocoa was retained because it occurs mainly within forest). The two measures are uncorrelated ($r_s = 0.351$, $p = 0.24$). The chimpanzees' diet was dominated by fruits of 3–4 forest tree species between March and May 07 when the greatest diversity of 'seasonally important' forest trees fruited concurrently (*Antiaris toxicaria*, *Morus mesozygia*, *Parkia filicoidea*, *Phoenix reclinata*). In contrast, a single forest tree-fruit source – figs, which were always available – dominated the diet between October and December. No seasonally important forest trees were fruiting at that time (although *Phoenix* had begun to ripen in December, hence fruit availability was estimated to have increased after November;

Figure 5.3). Other fruit foods dominating the diet during October–December were non-tree forest plants and cultivars (Table 5.4).[3]

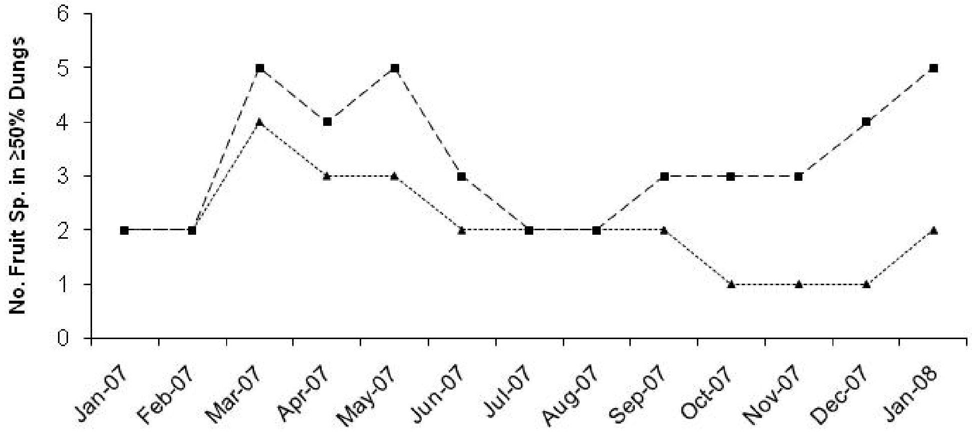

Figure 5.5. Monthly variation in (i) the total number of different fruits (upper dashed line) and (ii) the number of different forest tree-fruits only (lower dotted line) occurring in ≥50% of dungs.

5.3.3. Examination of Fallback Foods

Fruit availability was monitored in seven important fruit species, plus nine representatives of the genus *Ficus*. For seven of the nine unmonitored species (of which eight were cultivars or life forms other than trees), phenology patterns could be approximated based on qualitative observations. Fruits of eight important species were seasonally available: *Antiaris toxicaria*, *Morus mesozygia*, *Pseudospondias microcarpa* and *Parkia filicoidea* (monitored); *Caloncoba crepiniana*, *Dovyalis macrocalyx*, mango, and *Monanthotaxis ferruginea* (unmonitored). Fruiting events in these species lasted 1–4 months. In each case chimpanzees fed heavily on the fruits once ripe and continued to do so for the duration of the fruiting event. Outside of fruiting events these species did not appear in dung. With the exception of *Caloncoba*, all these species occurred in ≥50% of dungs in months when other seasonally important fruits were also consumed at high frequencies, suggesting they constitute ‘preferred’ fruits.

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[3] While a number of phenology species had ripe fruit during the September–November ‘low fruiting season’ (Chapter 4), most of the non-figs do not produce fleshy fruits (e.g. *Macaranga schweinfurthii*, *Pycnanthus angolensis*), and were not favoured by chimpanzees.

Table 5.4. Important fruit species in the diet of Bulindi chimpanzees. Species listed are those that appeared in ≥50% of dungs in at least one month (Jan 07–Jan 08) or >10 % of all dungs (*N* = 1436).

Species	**Life Form**	**% Total Dungs**	**% monthly dungs containing each important species** [1]													**Mean monthly % in dung**	**# Months in dung (*n* = 13)**	**# Months in ≥50% dungs**	**# Months as top ranked sp.**
			Jn 07	**Fb**	**Mr**	**Ap**	**My**	**Jn**	**Jl**	**Ag**	**Sp**	**Ot**	**Nv**	**Dc**	**Jn 08**				
1. *Ficus* spp. ○ *	Tree [#]	86.6	**94**	**92**	**90**	**80**	**87**	**77**	**86**	**100**	**83**	**91**	**94**	**78**	**71**	86.4	13	13	6
2. *Psidium guajava* [guava] *	Tree	50.5	12	46	**54**	44	**56**	37	37	46	**84**	**88**	**59**	28	29	47.6	13	5	1
3. *Phoenix reclinata* *	Tree	43.9	**96**	**95**	**70**	**98**	**50**	9	**75**	40	2	–	–	22	**81**	50.0	11	7	4
4. *Aframomum* spp. ○	Herb	27.0	10	11	29	9	8	9	44	38	37	**55**	32	16	37	25.8	13	1	0
5. *Monanthotaxis ferruginea*	Vine	19.8	–	–	4	–	–	–	–	1	–	26	**56**	**93**	**71**	19.3	6	3	1
6. *Mangifera indica* [mango]	Tree	17.8	–	–	–	–	5	**78**	40	2	–	–	●	**55**	**76**	19.8	6	3	0
7. *Carica papaya* [papaya]	Tree	14.1	4	11	1	1	7	3	10	17	23	11	21	34	29	13.3	13	0	0
8. *Pseudospondias microcarpa* *	Tree	13.0	8	1	–	1	**50**	**92**	34	1	–	–	–	–	–	14.4	7	2	1
9. *Theobroma cacao* [cocoa] *	Tree	12.3	4	2	6	1	3	●	9	28	8	29	32	7	20	11.5	12	0	0
10. *Caloncoba crepiniana*	Tree	11.7	–	–	–	–	–	–	3	**53**	**59**	3	–	–	–	9.1	4	2	0
11. *Rubus pinnatus*	Shrub	10.7	–	2	–	–	–	1	11	9	3	15	14	**55**	3	8.7	9	1	0
12. *Parkia filicoidea* *	Tree	9.8	–	–	13	**69**	26	–	–	–	–	–	–	–	–	8.4	3	1	0
13. *Coccinia* spp. ○	Vine	8.6	–	–	26	10	1	1	3	1	14	1	–	17	**59**	10.2	10	1	0
14. *Dovyalis macrocalyx*	Shrub	8.4	–	–	44	**56**	2	–	–	–	–	–	–	–	–	7.9	3	1	0
15. *Lantana camara*	Shrub	6.4	2	2	–	1	**64**	2	–	3	1	4	4	1	–	6.5	10	1	0
16. *Antiaris toxicaria* *	Tree	5.9	–	1	**59**	5	26	1	–	–	–	–	–	–	–	7.1	5	1	0
17. *Morus mesozygia* *	Tree	4.4	–	–	**62**	5	1	–	–	–	–	–	2	1	–	5.5	5	1	0
No. fruit species in ≥50% of monthly dungs:			2	2	5	4	5	3	2	2	3	3	3	4	5				

[1] Cells show the monthly % dungs containing each of the listed species. Values of ≥50% are emboldened and indicate a species was 'important' in the monthly diet; highest monthly values are underlined and indicate the top-ranked fruit species for each month;

● = indicates the species was recorded eaten during the month from feeding trail evidence and/or observation but was not seen in dung; a dash indicates that the species was not recorded eaten in the month by any method;

* = species included in phenology surveys;

○ = Denotes a 'species group' (comprising >1 species);

[#] Of seven fig species confirmed in the diet, six are trees but one is a shrub.

Seven important food taxa produced fruit year-round or for extended periods (≥6 consecutive months). These were cocoa, *Ficus* spp., guava, and *Phoenix reclinata* (monitored), and *Aframomum* spp., *Lantana camara* and papaya (unmonitored). Since these species were potential fallback foods for the chimpanzees, patterns of availability and consumption were examined in further detail.

(i) Wild Fruits

Figs (*Ficus* spp.)

Figs were the most commonly eaten fruit, present in 87% of all dungs collected (Table 5.4). Observations indicated that chimpanzees fed most often on ripe fruits of the two commonest figs at Bulindi: *F. natalensis* and *F. sur*.[4] Fig residue was present in >70% of dungs in all months (mean: 86.4 ± 8.3 SD) and figs were the top-ranked fruit food in six months. The mean volume of monthly dungs composed of fig varied from 9.7–34.5% (mean across months: 21.3% ± 7.3 SD). Thus, while figs were the most consistently common fruit in dungs, fig residue seldom accounted for the greatest proportion of dung volume. More often large seeds of seasonally important species (e.g. *Parkia*, *Monanthotaxis*) dominated dungs (Plate 9).

Variation in fig consumption across months (as indicated by mean volume % fig in dung) was not predicted by the monthly FAI for ripe figs ($R^2 = 0.031$, $F_{1,11} = 0.35$, $p = 0.56$). Thus chimpanzees' intake of figs was independent of their availability in the habitat. Nor was fig consumption significantly influenced by variation in the monthly FAI for non-fig fruits, although the relationship was negative ($R^2 = 0.117$, $F_{1,11} = 1.45$, $p = 0.25$). Exploratory correlation analysis indicated three variables were associated with monthly fig intake: mean fruit score, mean number of fruit species in dung, and number of 'important' fruit species in monthly dungs. These were included as independent variables (IVs) in a multiple regression. Only 'mean fruit score' and 'mean number of fruit species' were retained in the final model ($R^2 = 0.567$, $F_{2,10} = 6.54$, $p = 0.015$), together accounting for 57% of the variance in monthly levels of fig consumption. The effect of neither IV remained significant when the effect of the other was held constant,

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[4] Seven fig species were confirmed eaten (Table 5.2) but circumstantial evidence (discarded fig 'wadges' and/or fresh nests in the vicinity of fruiting trees) suggested chimpanzees ate fruits of additional fig species including *F. vallis-choudae*, *F. ovata* and *F. sansibarica*.

suggesting fig intake was influenced by an interaction of these variables (Table 5.5). In both cases the relationship with fig consumption was negative. Thus chimpanzees ate more figs when overall levels of fruit intake decreased, and ate fewer figs when the diversity of the fruit diet increased. Although clearly a staple, the results suggest figs were not a preferred food.

Table 5.5. Regression model parameters. Consumption of potential fallback foods (figs, guava, cocoa, papaya, foliage, pith, green leaf fragments [GLF], and non-seasonal fruit cultivars combined) was regressed against measures of frugivory. Consumption of food items was indexed as (i) monthly % dungs containing the item [guava, cocoa, papaya, *Phoenix*]; (ii) monthly mean % volume in dungs [fruit and foliage scores, fig]; (iii) monthly mean abundance score in dungs [pith, GLFs]; and (iv) monthly mean % fruits in dungs that were non-seasonal cultivars [fruit cultivar consumption]. 'Important' species were those found in ≥50% of monthly dungs. In each regression independent variables (IVs) were selected if exploratory correlation analysis indicated a relationship. For multiple regressions (all cases except papaya) only the final model retaining IVs that significantly strengthened the model are shown. Values are the standardised Beta coefficients (*ß*), which give a measure of the strength of the IV in the model, the values of *t*-tests and their significance. Significant values are emboldened.

Consumption of potential fallback food Independent variable	***ß***	***t***	***p***
Fig consumption (mean % volume fig in dung)			
Mean % fruit score	-0.477	-2.106	0.061
Mean no. fruit spp. in dung	-0.425	-1.876	0.090
Guava consumption (% dungs with guava)			
Mean % fruit score	-0.728	-3.517	**0.005**
Cocoa consumption (% dungs with cocoa)			
Mean % fruit score	-0.665	-2.952	**0.013**
Papaya consumption (% dungs with papaya)			
No. 'important' spp. in dungs (forest trees only)	-0.616	-2.590	**0.025**
Foliage consumption (mean % foliage score) *			
Ripe fruit availability	-0.591	-2.794	**0.019**
No. 'important' spp. in dungs	-0.410	-1.939	0.081
Pith consumption (mean abundance score) *			
Ripe fruit availability	-0.520	-2.448	**0.034**
Mean no. fruit spp. in dungs	-0.468	-2.203	0.052
GLF consumption (mean abundance score) *			
% dungs with *Phoenix*	-0.665	-2.953	**0.013**
Fruit cultivar consumption (mean % cultivar fruits)			
Mean % fruit score	-0.877	-6.043	**<0.001**

* Foliage, pith and GLFs were not regressed against 'mean % fruit' because foliage and fruit scores are necessarily inversely related to one another.

Phoenix reclinata

As shown in the previous chapter, 90% of the monthly variation in the fruit FAI of all 30 phenology species was explained by the availability of ripe *Phoenix* palm fruits, which were available in all but three months. *Phoenix* seeds appeared in 44% of dungs (only figs and guava were eaten more frequently). In seven months the seeds appeared in the majority of dungs, often in large numbers, and it was the top-ranked fruit species in four months (Table 5.4). The availability of ripe *Phoenix* fruits was a highly significant predictor of the frequency of the seeds in dung ($R^2 = 0.539$, $F_{1,11} = 12.84$, $p = 0.004$; Figure 5.6). In contrast, the monthly fruit FAI excluding the palm had no effect on frequency of *Phoenix* in dung ($R^2 = 0.028$, $F_{1,11} = 0.31$, $p = 0.59$). Similarly, *Phoenix* consumption did not correlate with either measure of the diversity of the fruit diet (mean number fruit sp. per dung: $r_s = 0.094$, $p = 0.76$; number of important fruit species in monthly dungs: $r_s = -0.034$, $p = 0.91$). Thus chimpanzees ate ripe *Phoenix* fruits when they were available, regardless of the availability of other fruiting plants, including other major fruit foods. In this respect chimpanzees ate *Phoenix* fruits like other seasonally important and 'preferred' fruits, despite the extended fruiting of the palm.

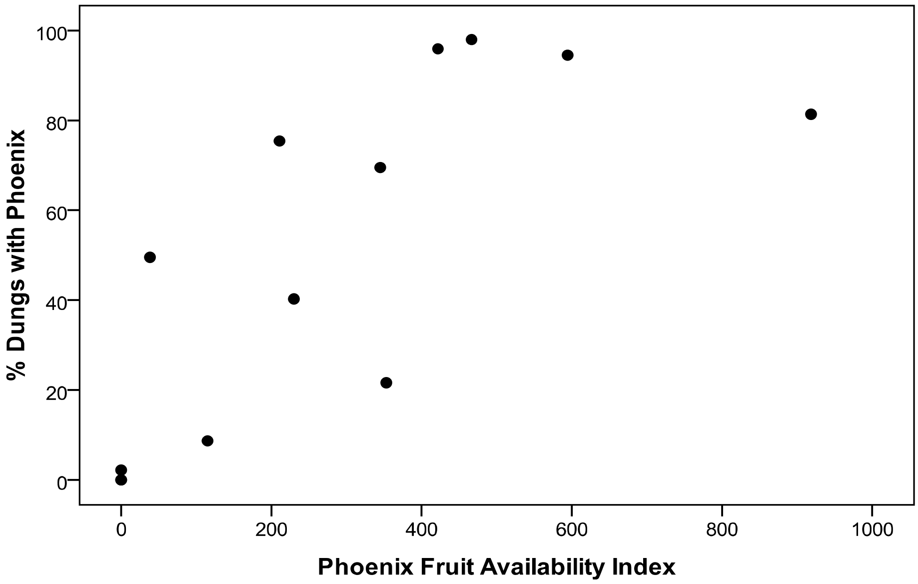

Figure 5.6. The monthly percentage of dungs containing *Phoenix reclinata* seeds in relation to its availability. The regression line is not shown because untransformed data are plotted for readability.

Aframomum spp.

Although detailed phenology studies of African wild ginger (*Aframomum* spp.) are lacking, the fruits are probably available over long periods (A. Poulsen, pers. comm., 2009). At Bulindi these herbs are common both in wet forest and edge habitat, and chimpanzees ate the fruits in all months (mean monthly frequency in dung: 25.8%), suggesting year-round availability. Only in one month (October 07) were the seeds present in the majority of dungs (Table 5.4). An increase in consumption was evident from July onwards, including the September–November low fruiting season, and the quantity of seeds in dungs was overall highest during this period. Even so, the monthly ripe fruit FAI was not a significant predictor of monthly variation in *Aframomum* consumption ($R^2 = 0.122$, $F_{1,11} = 1.52$, $p = 0.24$). The lack of correlation is due to the influence of an outlier month (January 08), when the frequency of *Aframomum* seeds in dung was high but ripe forest tree fruit (predominantly *Phoenix*) was abundant (Figure 5.7). If this month is excluded, the inverse relationship between forest fruit availability and *Aframomum* consumption is significant ($R^2 = 0.377$, $F_{1,10} = 6.05$, $p = 0.034$). Moreover, *Aframomum* seeds appeared in dung at significantly higher frequencies when the proportion of fruit in the diet decreased ($r_s = -0.734$, $p = 0.007$; January 08 excluded).[5]

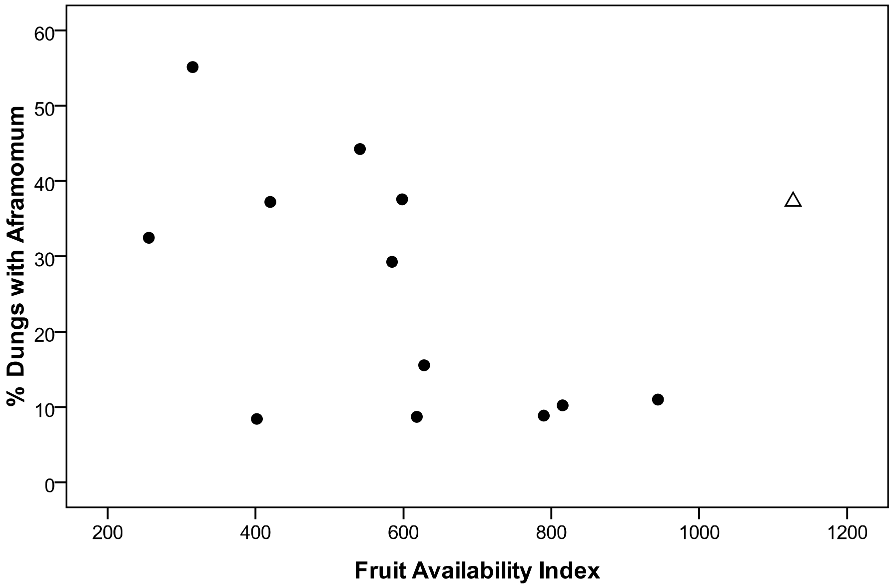

Figure 5.7. The percentage of dungs containing seeds of *Aframomum* spp. in relation to monthly availability of ripe forest fruit. The triangle on the right of the graph represents an outlier month (Jan 08).

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[5] Results of a multiple regression including the ripe fruit FAI and 'mean fruit score' as IVs are not reported because residuals remained significantly non-normally distributed following data transformation.

Lantana camara

Seeds of *L. camara* occurred in the majority of dungs in a single month (May 07), during a lull in forest fruit availability. For two weeks dungs were dark purple in colour and full of the fruit skins and seeds of this invasive shrub, which is established over large areas of logged forest at Bulindi. Outside of this brief period the seeds appeared in dung at low frequencies and in trivial quantities (Table 5.4). Qualitative observations suggest *L. camara* flowered and fruited throughout the year (cf. Sharma et al. 2005), yet the chimpanzees did not feed heavily on the fruits during the low fruiting season in September–November.

(ii) Cultivated Fruits

Guava (Psidium guajava)

Chimpanzees ate guavas from small naturalised trees and shrubs in edge or regenerating habitat, and raided larger trees in villages. The seeds occurred in 50% of dungs, making guava the most commonly eaten fruit after figs (Table 5.4). Guava fruits mature year-round, though there are 1–2 peak seasons of ripening (Thaipong and Boonprakob 2005). Guava was eaten in all months, although the frequency and quantity of seeds in dung fluctuated considerably. In five months guava seeds appeared in ≥50% of dungs. Consumption was highest in September–November during a fruiting peak of large (unmonitored) domestic guava trees, many of which bore full ripe fruit crops; during this period dung specimens regularly contained >1000 guava seeds. Observations suggested that chimpanzees obtained guavas at this time mainly through raiding these domestic trees. The monthly guava FAI did not predict variation in guava consumption (R^2 = 0.087, $F_{1,8}$ = 0.76, p = 0.41).[6] This may be because the monitored naturalised guavas bore only small fruit crops and exhibited little seasonality in production. Two IVs were negatively correlated with guava consumption and were included in a multiple regression: mean fruit score and the ripe fruit FAI of all species excluding guava. Only 'mean fruit score' was retained in the final model (R^2 = 0.529, $F_{1,11}$ = 12.37, p = 0.005) (Table 5.5). Thus chimpanzees ate more guavas when overall fruit intake was reduced. An inverse relationship between guava feeding and the diversity of the fruit diet was not

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[6] n = 10 months because guava phenology was not monitored before April 07.

apparent, however (mean number fruit sp. per dung: $r_s = -0.209$, $p = 0.49$; number of important fruit species in monthly dungs: $r_s = 0.111$, $p = 0.72$). For example, in March–May dungs were dominated by the seeds of several seasonally important fruits, but guava seeds appeared in increased quantities too. An earlier fruiting peak of the domestic trees is thought to have occurred at this time (though this was not confirmed by observations). Regardless, chimpanzees fed heavily on guava when a variety of seasonally important forest fruits were available.

Cocoa (Theobroma cacao)

Cocoa was eaten in all months and was detected in 12.3% of dungs inspected (Table 5.4). Neither the cocoa FAI nor the ripe fruit FAI (excluding cocoa) significantly predicted monthly variation in cocoa consumption, as indicated by frequency of residues (pulp and, occasionally, seeds) in dung (cocoa FAI: $R^2 = 0.008$, $F_{1,11} = 0.09$, $p = 0.77$; FAI excl. cocoa: $R^2 = 0.056$, $F_{1,11} = 0.65$, $p = 0.44$). This is contrary to evidence from feeding traces and behavioural observations indicating a sharp rise in cocoa feeding from mid-August through November when availability of other forest tree fruits was low (in particular, *Phoenix* palms were not fruiting). In these months chimpanzees were regularly located in Kiseeta forest where highest densities of cocoa occur (Chapter 7), and fresh cocoa feeding traces were seen at a frequency, and in quantities, not previously witnessed. The discrepancy is most likely due to difficulties in detecting undigested fruit pulp in dungs in the absence of mature seeds. In spite of this, the % dungs in which cocoa was detected clearly peaked during this period (Table 5.4).

Two IVs were included in a multiple regression analysis (mean fruit score, and the number of important forest tree fruits in monthly dungs). Only 'mean fruit score' was retained in the final model ($R^2 = 0.442$, $F_{1,11} = 8.72$, $p = 0.013$) (Table 5.5), suggesting chimpanzees ate more cocoa when overall fruit intake was reduced. Local reports and feeding trace evidence also indicated the chimpanzees increasingly sought ripe cocoa from cultivated *shambas* outside of the forest at this time. For example, only in October and November 07 were chimpanzees known to travel >300 m through gardens to feed on ripe pods in village *shambas* in Kiseeta and Kyabawaza.

Papaya (*Carica papaya*)

The large fruits of the papaya tree were eaten in all months and availability was assumed to be relatively constant (see Hockings et al. 2009). Since papaya trees are not naturalised, chimpanzees obtained the fruits exclusively from trees located outside the forest in village areas. Feeding remains showed that while chimpanzees usually ate ripe papaya fruits, unripe ones were also occasionally taken. The frequency of seeds in the dung was low during most months (monthly mean: 13.3%, range 1–34%), but increased from August at the start of the low fruiting season (Table 5.4). Consumption levels were lowest in March–April when several seasonally important forest species fruited concurrently, but peaked in December 07 and January 08 which were months of high food abundance due to the ripening of *Phoenix* fruits. Thus variation in consumption rates was not predicted by the monthly fruit FAI ($R^2 = 0.001$, $p = 0.90$). Monthly variation in the % dungs containing papaya was also not associated with overall fruit intake or the diversity of fruits in dung. Nevertheless, the number of important fruits in monthly dungs that were forest tree species was a significant negative predictor of papaya consumption ($R^2 = 0.379$, $F_{1,11} = 6.71$, $p = 0.013$; Table 5.5): chimpanzees ate more papaya when fewer forest tree fruits dominated the diet. As with cocoa, actual rates of papaya feeding are probably higher than faecal data imply; dungs occasionally contained papaya-like fruit pulp in the absence of identifying seeds.

(iii) Foliage Consumption

The mean proportion of dungs composed of foliage (foliage score) varied significantly across months (Kruskal–Wallis, $H = 315.69$, $df = 12$, $p < 0.001$). On average, foliage accounted for ≤15% of dung contents in all months apart from August–November when foliage scores increased to 25–28% (Figure 5.3). Monthly foliage scores were inversely correlated with fruit scores ($r_s = -0.978$, $p = <0.001$). Three IVs were negatively associated with monthly changes in foliage score: ripe fruit FAI, mean number of fruit species, and number of important fruit species in monthly dungs. (Mean fruit score was not included as an IV since higher fruit scores necessarily result in lower foliage scores and vice versa). Only the ripe fruit FAI and ‘number of important fruits’ were retained in the final multiple regression model ($R^2 = 0.555$, $F_{2,10} = 6.23$, $p = 0.017$), though ripe fruit availability had a stronger independent effect (Table 5.5). Chimpanzees therefore increased their intake of non-fruit vegetative foods when ripe fruits of important species were scarce (Figure 5.8).

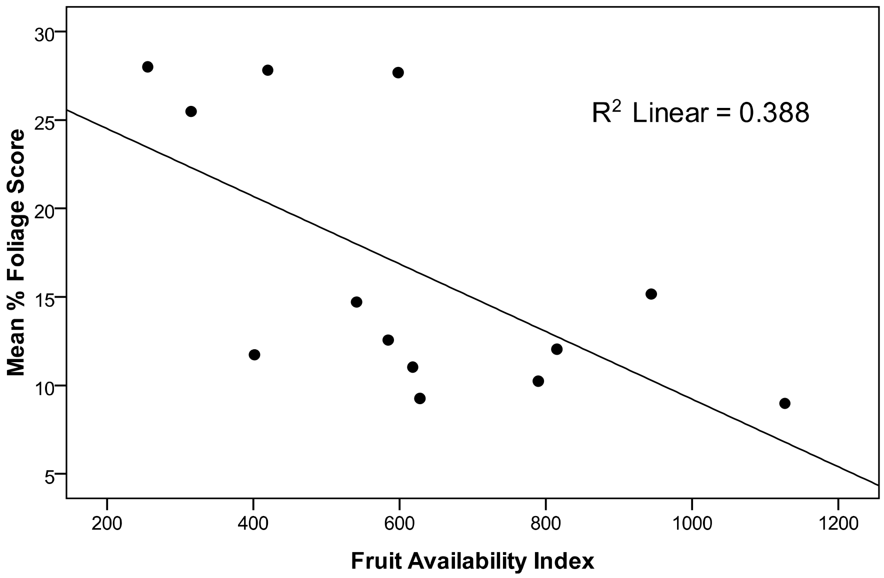

Figure 5.8. Regression of the mean foliage score (% volume in dung) on the monthly availability of ripe forest fruit.

The foliage component of dungs consisted predominantly of piths and leaves. However, monthly mean abundances of piths and green leaf fragments (GLFs) in dung were not correlated (r_s = 0.429, p = 0.14), implying differing patterns of utilisation.[7] Fibrous vegetative pith was present in dung at high frequencies throughout the study (88.2% of dungs; monthly mean: 87.2% ± 8.4 SD, range: 69.5–97.8%). Feeding trace evidence suggested that elephant grass (*Pennisetum purpureum*), the common forest herb *Marantochloa leucantha*, and sugarcane (*Saccharum officinarum*) – which the chimpanzees obtained through crop-raiding – were the most frequently eaten piths. Figure 5.9 shows monthly variation in the mean abundance of piths and GLFs in dungs. Although pith was a regular component of dungs in all months, abundance scores peaked during August–November. A multiple regression of the effects of ripe fruit availability and 'mean number of fruit species' on pith abundance scores in dung was overall significant (R^2 = 0.559, $F_{2,10}$ = 6.33, p = 0.017). Of the two IVs, the negative

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[7] The appearance in dung of whole undigested leaves, ingested for assumed medicinal rather than nutritional purposes (Wrangham 1995; Huffman et al. 1996), was distinguished from chewed green leaf fragments that result from ordinary feeding behaviour.

effect of ripe fruit availability was stronger (Table 5.5). Notably, pith-eating was strongly and positively correlated with the intake of figs ($r_s = 0.753$, $p = 0.003$; Figure 5.10).

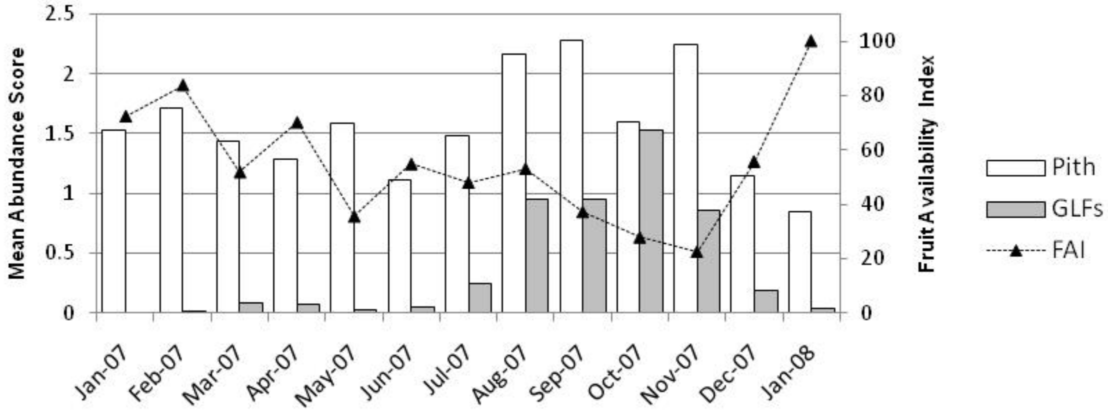

Figure 5.9. Monthly variation in mean pith and green leaf fragment (GLF) abundance scores (bars) in chimpanzee dung. The dashed line shows the ripe fruit availability index (FAI), expressed as an index of 100.

Relative to pith, GLFs were seen in fewer dungs overall (24.5%) and consumption exhibited a far stronger seasonality (monthly mean frequency in dungs: 20.7% ± 24.4 SD, range: 0.0–70.6%). For six months, between January and June 07, GLFs scarcely appeared in dungs at all. Thus, unlike piths, young leaves were not a staple item in the diet. From the end of July intake increased abruptly and GLFs became a major component of dungs throughout August–November, following the end of the *Phoenix* fruiting season. Consumption peaked in October (Figure 5.9). By January 08, when *Phoenix* fruits were again ripe, intake of GLFs had declined to negligible levels. Although GLF intake was inversely related to ripe fruit availability ($R^2 = 0.412$, $F_{1,11} = 7.72$, $p = 0.018$), multiple regression revealed that the frequency of *Phoenix* seeds in monthly dungs was the strongest negative predictor of GLF abundance ($R^2 = 0.442$, $F_{1,11} = 8.72$, $p = 0.013$) (Table 5.5). Conversely, GLF consumption was positively correlated with cocoa intake ($r_s = 0.696$, $p = 0.008$).

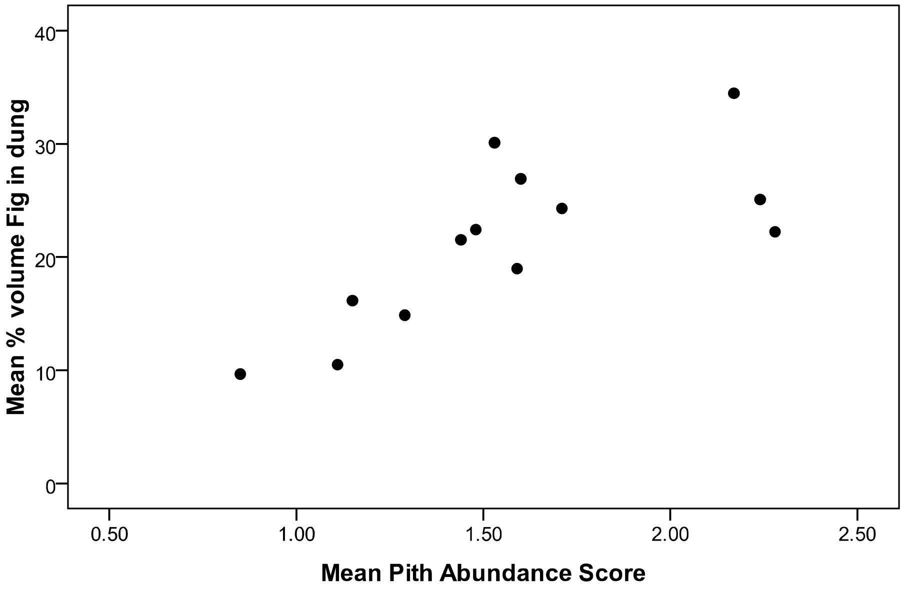

Figure 5.10. Relationship between the monthly mean abundance of piths and the mean % volume of fig in dungs.

Chimpanzees were recorded feeding on several leaf species during August–November but they appeared to eat leaves of *Trichilia dregeana* in particular. From September translucent young leaf parts, distinguishable from other GLFs by the yellowish colour, began to appear in dungs in increasing quantities. On six occasions chimpanzees were observed feeding on the newly-emerged, yellow-pink leaves of *T. dregeana*. Signs of leaf-feeding were frequently found beneath *T. dregeana* trees after chimpanzees had vacated an area. During feeding, chimpanzees stripped new *T. dregeana* leaves from terminal ends of branches with an upward motion of the wrist, packing fistfuls of leaves into the mouth for chewing. It seems likely that most or all of the distinctive yellow leaf fragments in dungs during this period were *T. dregeana*. Although this tree was not included in phenology surveys, leaf flushing in *T. dregeana* did not correspond with that of the majority of monitored species. As shown in the previous chapter leaf flushing peaked at the start of the year (in January–February), a time when GLFs seldom occurred in dung. Accordingly, the monthly FAI for young leaves was not a predictor of GLF consumption ($R^2 = 0.158$, $F_{1,11} = 2.06$, $p = 0.18$).

5.3.4. Patters of Cultivar Consumption

Unlike cocoa, guava and papaya, which were available year-round, the fourth cultivar defined as an 'important fruit'– mango – was seasonally available and evidently a highly preferred food: when available, chimpanzees ate mangos at high frequencies regardless of the concurrent availability of other important fruits (e.g. *Phoenix reclinata* and *Pseudospondias microcarpa*). Chimpanzees also ate ripe banana fruits, which were continuously available. However, the frequency of consumption was not satisfactorily determined. Undigested banana pulp was only rarely detected with confidence in dung (n = 13; 0.9%), most frequently in November 07, but observations and feeding trace evidence indicated bananas were probably a regular item in the diet. A large plantation (estimated size: 5–10 ha) bordered gallery forest in Nyaituma village. To discourage the spread of bacterial wilt disease the understorey had been left to grow; as a result the plantation was extremely dense, providing chimpanzees with cover. Occasionally they nested in shade trees (e.g. *Ficus exasperata*) within the plantation. Local households engaged in brewing banana beer, and the chimpanzees were particularly attracted by fruits piled in an underground pit to hasten the ripening process prior to pressing (Appendix 4). While the apes visited this plantation throughout the year, evidence of frequent use (feeding traces, dung, nests, and observations) occurred mainly during the September–November low fruiting season. Other fruit cultivars (oranges, jack-fruit, passion fruit) were probably minor dietary items, though consumption may have been underestimated. For example, jackfruit was unlikely to be detected in dung because feeding trace evidence indicated the chimpanzees spat out the large seeds (Plate 10).

Are Fruit Cultivars Fallbacks?

To examine the relationship between consumption of fruit cultivars and forest food availability, I calculated the proportion of different fruit species per dung that were cultivated. Only six cultivars were detected in dung: banana, cocoa, guava, mango, papaya and passion fruit. Cultivated fruit obtained from naturalised or abandoned sources (such as forest cocoa *shambas*) could not be distinguished in dung from that obtained through crop-raiding. The average % fruit species in dung that were cultivated varied significantly across months (Kruskal–Wallis one-way ANOVA, H = 337.52, df = 12, p <0.001). Highest percentages occurred during the low forest fruiting season in September–November (35–38%; mean for all 13 months = 23.3% ± 10.7 SD, range 5.6–

38.0%). Nevertheless, the ripe fruit FAI did not significantly predict monthly variation in mean values (R^2 = 0.165, $F_{1,11}$ = 2.17, p = 0.17). The relationship is apparently obscured by the inclusion of mangos which, unlike the other fruit cultivars considered, were available seasonally. As already noted, mangos were a highly preferred food, eaten in large amounts even when important forest fruit species were fruiting. With mangos excluded, the forest fruit FAI was a significant negative predictor of monthly variation in % fruits in dung that were cultivars (R^2 = 0.517, $F_{1,11}$ = 11.78, p = 0.006) (Figure 5.11).

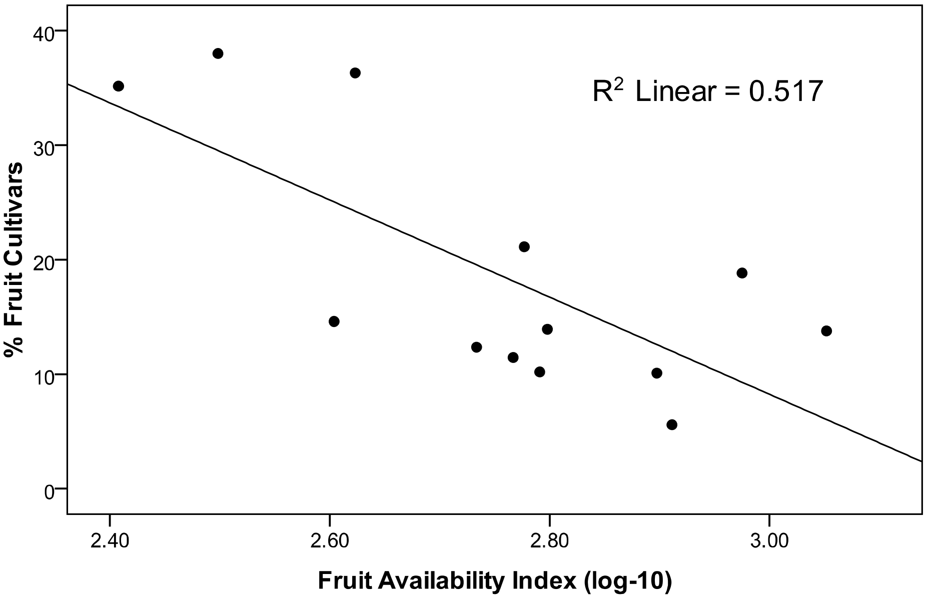

Figure 5.11. Relationship between availability of ripe forest fruits (data are log-10 transformed) and the monthly mean % fruit species in dungs that were non-seasonal cultivars. High monthly values in the top-left of the graph represent Sept–Nov 07, the low fruiting season.

Exploratory correlation analysis indicated two further IVs interacted negatively with this measure of cultivar consumption: mean fruit score, and number of important forest tree fruits dominating monthly dungs. While the overall regression model including all three IVs was highly significant (R^2 = 0.828, $F_{3,9}$= 14.41, p = 0.001), the final model to emerge was not significantly strengthened by the inclusion of ripe fruit FAI or ‘number of important forest tree fruits’, and only mean fruit score was retained (R^2 = 0.769, $F_{1,11}$ = 36.52, p <0.001) (Table 5.5; Figure 5.12). Conversely, the representation of the non-seasonal fruit cultivars in dung was positively correlated with mean abundance scores of both pith ($r_s = 0.714$, $p = 0.006$) and GLFs ($r_s = 0.649$, $p = 0.02$). Chimpanzees ate more fruit cultivars when overall levels of frugivory declined and intake of low quality foliage items increased.

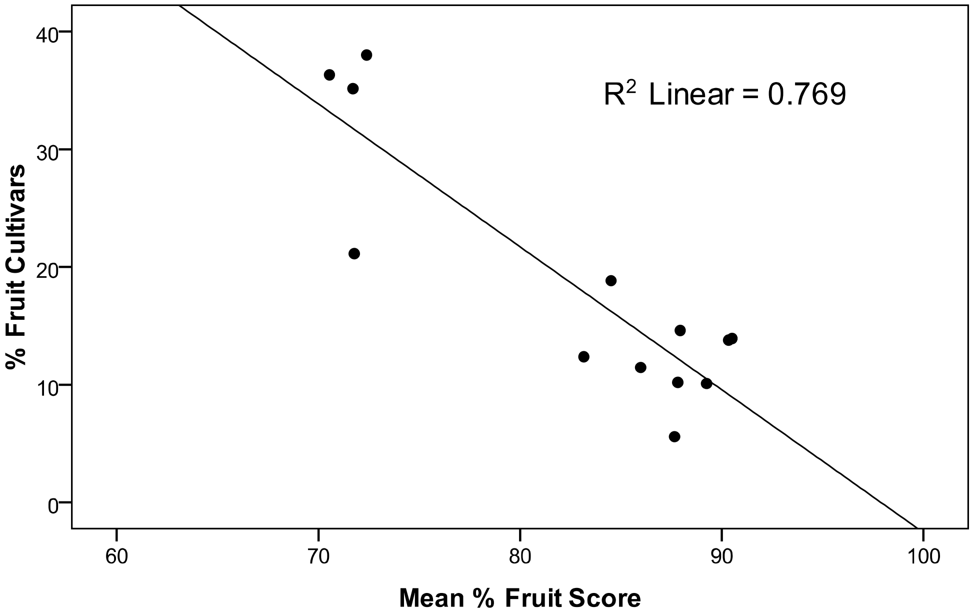

Figure 5.12. Relationship between the monthly mean volume % dungs comprising fruit ('fruit score') and mean % fruit species in dungs that were non-seasonal cultivars.

Cultivated Pith Foods

Chimpanzees fed on the pith of sugarcane, banana, and yam. Since it was not possible to distinguish pith resulting from consumption of cultivars from that of wild plant foods (i.e. THV) in dung, intake was assessed primarily from feeding trace evidence. At Bulindi sugarcane is commonly grown around homesteads and chimpanzees seemed to know the locations of sugarcane gardens across their range. A perennial crop, evidence of sugarcane raiding was recorded in most months of the study (Table 5.2), but consumption intensified during August–December 07. Thirty-two of 41 (78%) independent feeding traces were recorded in these 5-months. The peak period of consumption spans the low fruiting season but more precisely corresponds to the 3½-month interval between ripe fruiting events of *Phoenix reclinata*. At this time chimpanzees frequently ranged within Kiseeta forest feeding on cocoa and young leaves of *Trichilia dregeana* (Chapter 7). They also regularly raided sugarcane from a plantation on the southern edge of the forest (area: ~1500 m^2; K. Hiser, pers. comm. 2009) – the largest within their range. Examination of feeding remains indicated that chimpanzees, like people, often discard the masticated pith after extracting the juice. Remains of banana pith-eating were found mainly between June and December; the apes usually ate the pith from young suckers (Plate 10). Evidence of feeding on yam pith was found once in July.

5.4. Discussion

Diet Composition and Diversity

The diversity of food items recorded in the diet of chimpanzees varies according to study duration, data collection method, time devoted to collecting feeding data, as well as the range of foods available in the habitat (Nishida and Uehara 1983; Tutin and Fernandez 1993b). In this study diet was investigated via systematic dung analysis, supplemented by feeding trace evidence and direct observation of feeding behaviour. Chimpanzees at Bulindi consumed a minimum of 96 plant food items from at least 82 species. Comparative data on the number of plant items and plant species recorded in chimpanzee diets at 17 sites are shown in Table 5.6. Although values are only broadly comparable across sites because some studies excluded foods that were not taxonomically identified or were recorded eaten on a single occasion only, two trends are apparent. First, the number of plant foods recorded is strongly linked to study duration (plant food items: $r_s = 0.864$, $n = 15$, $p < 0.001$; plant species: $r_s = 0.763$, $n = 14$, $p = 0.002$).[8] For the most part, study length can be taken as an index of habituation. At the longest-running sites (Bossou, Mahale, Gombe, Budongo) dietary data are from observations of fully habituated animals. Second, dietary breadth is generally greatest at sites where the primary habitat is rainforest or forest–woodland; the least diverse diets are reported from dry, savanna-dominated habitats with little forest cover (e.g. Hunt and McGrew 2002). The plant diet of chimpanzees at Bulindi is broader than might be expected given the relatively short study, lack of habituation and limited area of forest utilised by the apes. In part this reflects the large sample of dungs analysed, but it may also indicate that the human-modified landscape at Bulindi offers a diversity of plant

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[8] For the correlations study duration was calculated in months, rounded to the nearest 12 mo where duration is cited in years; *n* values are different in the two tests because not all studies provide data on both number of plant food items and species eaten.

foods similar to less-disturbed habitats where chimpanzees are studied. There was no indication that chimpanzees at Bulindi have an impoverished diet. The full range of foods eaten by this population remains unknown: chimpanzee diets show considerable interannual variation (Tutin et al. 1991), and several years of data are required before the dietary repertoire of a community reaches an asymptote (Nishida and Uehara 1983; but see Hunt and McGrew 2002).

Numerically, plant foods at Bulindi comprised mainly fruits (66%), followed by leaves (18%) and piths (9%), with other plant parts (e.g. flowers) rarely recorded as foods. Morgan and Sanz (2006) reported that the mean proportion of dietary items comprising fruits at 12 study sites was 55% (range: 31%–88%). Thus the representation of fruits in the diet at Bulindi is above average, but well within the species-typical range. The proportion of food items that were leaves is similar to the mean value for ten sites (18.7%; calculated from Morgan and Sanz 2006). At long-term sites where chimpanzees are habituated to observation the representation of leaf foods in the diet is often much greater. For example, at Mahale leaves accounted for a larger proportion of food items (35.7%) than fruits (30.5%) (Nishida and Uehara 1983). Chimpanzees at Bossou consumed the leaves of 52 plant species during a 14-month study (Takemoto 2003). At Bulindi the whole leaves of six species (35% of leaf foods) were passed intact in dung and apparently not ingested for nutritional benefit (Wrangham 1995; Huffman et al. 1996). The frequency of whole leaves in dung at Bulindi is higher than in any other population studied to date (McLennan and Huffman, in prep.). Leaf-swallowing is thought to serve a self-medicative function through control of helminth parasite infections (Huffman and Caton 2001). Long-term observations at Mahale revealed the chimpanzees ate 29 species of flower, 19 barks and 12 saps and resins (Nishida and Uehara 1983). Undoubtedly, the diversity of these foods eaten at Bulindi was underestimated. This study confirms the value of faecal analysis for investigating diet where apes are unhabituated, but as previous researchers have noted the diversity of the vegetative component of the diet is underrepresented by this method because non-fruit items are difficult to identify taxonomically in dung (Tutin and Fernandez 1993a; Doran et al. 2002). The inclusion of data from feeding traces and direct observations therefore strengthened the data set.

Table 5.6. Comparison of the number of plant food items and plant species recorded in the chimpanzee diet at 17 sites. Study sites are listed in descending order according to length of dietary study. Where reported, dung sample size and average number of fruit species per dung is given. The Bulindi data are emboldened.

Site	**Country**	**Habitat**	**Length of dietary study**	**Principal Method(s)** [1]	**No. food items**	**No. species**	**Mean no. fruit sp. per dung** [2]	**No. Dungs inspected** [3]	**Reference**
Mahale	Tanzania	Forest–woodland	1965–1981	O	328	198	–	–	Nishida and Uehara (1983)
Bossou	Rep. Guinea	Forest–farmland	1976–1992	O	246	200	–	–	Sugiyama and Koman (1992)
Budongo	Uganda	Mid-altitude forest	1990–2004	O	149	103	–	–	Reynolds (2005)
Gombe	Tanzania	Forest–woodland	1960–1973	O	201	?	–	–	Wrangham (1977)
Lopé	Gabon	Lowland rainforest	96 months	F, T	161	132	2.7	1854	Tutin and Fernandez (1993b**)**
Kahuzi-Biega	DRC	Montane forest	92 months	F, T	137	104	2.7	8070	Yamagiwa and Basabose (2006a)
Ndoki	Rep. Congo	Lowland rainforest	1989–1992	F?	114	108	–	214	Kuroda et al. (1996a)
Mt. Assirik	Senegal	Savanna–woodland	47 months	F, T	60	43	–	?783	McGrew et al. (1988)
Goualougo	Rep. Congo	Lowland rainforest	47 months	O, F	158	116	2.3	497	Morgan and Sanz (2006)
Fongoli	Senegal	Savanna–woodland	38 months	F, O	60	47	–	1007	Pruetz (2006)
Semliki	Uganda	Riverine forest–savanna	≥36 months	O?	33	?	–	72	Hunt and McGrew (2002)
Rubondo Island	Tanzania	Mid-altitude forest	19 months	F	46	46	3	147	Moscovice et al. (2007)
Issa (Ugalla)	Tanzania	Savanna–woodland	≥18 months	F	?	77	–	?	Hernandez-Aguilar (2006)
Bulindi	**Uganda**	**Riverine forest–farmland**	**16 months**	**F**	**96**	**82**	**3.8**	**1436**	**This study**
La Belgique	Cameroon	Lowland rainforest	12 months	T, F	?	80	3.3	135	Deblauwe (2009)
Bwindi	Uganda	Montane forest	12 months	F	60	32	2.1	187	Stanford and Nkurunungi (2003)
Bafing	Mali	Savanna–woodland	10 months	F	40	?	–	71	Duvall (2008b)

[1] O = direct observations, F = faecal analysis, T = feeding traces; in most studies that used indirect methods to study diets of unhabituated or semi-habituated apes, data were supplemented by qualitative direct observations;

[2] Values for Kahuzi and Rubongo are the monthly mean and the median, respectively;

[3] For Mt. Assirik, the number of dungs inspected was not stated but sample size for the same study period was given in an earlier paper (McGrew 1983).

Frugivory

In common with all populations studied to date, chimpanzees at Bulindi were overwhelmingly frugivorous and dung volume was dominated by seeds and other fruit residues in all months. The average number of fruit species per dung at Bulindi is higher than corresponding values reported for several sites (Table 5.6). Inasmuch as number of fruit species in dung reflects the diversity of fruits consumed daily, chimpanzees at Bulindi appear to eat more different fruits per day than other populations. This can be interpreted in two ways: first, the diversity of fruiting plants across the mosaic of habitats at Bulindi might have been relatively high throughout much of the year and thus a variety of different fruits were available to the apes or, second, individual fruit species may have been insufficiently abundant such that chimpanzees needed to exploit a range of fruit sources to meet nutritional requirements, or avoid competition with other animals. Overall, the data do not support the latter explanation because in all months the fruit component of the diet was dominated by 2–5 different species, the residues of which appeared in the majority of dungs; these ‘important’ fruit foods included both exceptionally high density (*Phoenix reclinata*) as well as very low density species (*Caloncoba crepiniana*). During months when ripe *Phoenix* fruits featured prominently in the diet chimpanzees also fed selectively on other less abundant fruits. Further, the chimpanzees regularly supplemented their daily fruit intake from natural sources with cultivated species, many of which were available year-round.

In contrast to overall fruit intake, the diversity of fruits in monthly dungs did not change in accordance with estimated levels of fruit availability. This may be because phenology surveys focused exclusively on forest trees, and did not take into account non-tree fruits and certain cultivars that also provide food for chimpanzees (see below). Moreover, the fruit availability index was disproportionately influenced by *Phoenix* fruiting patterns. Even so, a lack of association between measures of fruit availability and diversity of fruits in chimpanzee dung has been reported elsewhere (Tutin et al. 1991; Kuroda et al. 1996a; Yamagiwa and Basabose 2006a). At Kibale, the diversity of fruits consumed *decreased* when ripe fruit was abundant, apparently because chimpanzees selectively fed on high-quality preferred species (Isabirye-Basuta 1989). Similarly, Kuroda et al. (1996a) report a low diversity of fruit species in dung during the main fruiting season at Ndoki in Congo. A similar inverse relationship was not apparent at Bulindi: for example, during months when forest fruit was abundant – mainly due to the peak fruiting of *Phoenix* palms – dungs contained both the lowest (January–February 2007) and highest (January 2008) average number of fruit species per dung. The low diversity of fruits in dung in January–February 2007 probably reflects the fact that aside from figs and *Phoenix*, other species subsequently identified as important in the diet were not fruiting. During March–April a variety of forest trees fruited concurrently and most dungs contained an assortment of the seeds of several species, all of which were apparently consumed avidly. When few forest tree species were fruiting between September–December chimpanzees maintained relatively high levels of fruit intake and a relatively diverse fruit diet by increasing consumption of non-tree and cultivar fruits. Whether or not overall dietary diversity increased in response to declining forest fruit availability, as was found at Kibale and Budongo (Isabirye-Basuta 1989; Wrangham et al. 1998; Fawcett 2000), is unclear since the range of foliage items eaten is unknown.

Fallback Foods

Preservation of fallback foods may be crucial for the survival of chimpanzees in dynamic habitats such as Bulindi where forest resources are heavily exploited by humans (Chapter 10). Several wild fruits (figs, *Aframomum* spp.) as well as foliage items (young leaves and piths) were identified as probable fallbacks for Bulindi chimpanzees because consumption was inversely related to that of preferred food (fruit) and/or its availability during this study. With the exception of young leaves, which were seldom eaten outside the low fruiting season, these foods can also be regarded as ‘staple’ items in the diet of this community (cf. Marshall and Wrangham 2007).

Wild Fruits

Figs (*Ficus* spp.) were the most commonly eaten fruit, present in 87% of dungs. A similarly high frequency of figs in dung (65–99%) is reported at other sites (Wrangham et al. 1993; Basabose 2002; Tweheyo and Lye 2003; Kagoro-Rugunda and Baranga 2008; Gross-Camp et al. 2009). In some habitats figs have been described as fallback foods for chimpanzees, eaten in increasing quantities when ripe fruit is scarce (Kuroda et al. 1996a; Wrangham et al. 1996; Tutin et al. 1997), whereas at other sites figs are regarded as ‘preferred’ or staple foods because they are eaten year-round during periods of both high and low fruit availability (Newton-Fisher 1999; Pruetz 2006; Gross-Camp et al. 2009; Yamagiwa and Basabose 2009). Basabose (2002) points out that nutrient differences among fig species may influence the importance of figs in the diet at different sites, though this remains to be tested. Fig density is also likely to be a factor. At Bulindi, figs occurred at relatively high densities in forest patches (16.8 stems ha $^{-1}$) and fig residues were present in dungs at high frequencies both in fruit-rich and fruit-poor months. However, fig intake did not increase significantly when availability of other fruits declined. Thus the classification of figs as staple foods would appear to hold for Bulindi. Even so, figs were not 'preferred' fruits since they were not eaten as a function of their availability, which showed moderate temporal variation (Chapter 4). In fact, chimpanzees ate figs in greater quantities when overall fruit intake was reduced and when they ate more fibrous pith. They also ate more figs in months when the diversity of fruits in the diet was low. These results suggest figs were relatively low-ranking fruits. Though eaten on a daily basis, figs served as a seasonal fallback food for Bulindi chimpanzees.

At some sites a single common fruit species plays a key role in sustaining chimpanzee populations throughout the year, but becomes especially important during periods of fruit scarcity. A good example is *Musanga leo-errerae* fruits at Kalinzu Forest in Uganda (Kagoro-Rugunda and Baranga 2008). The continuous availability and abundance of *Musanga* may negate the need for chimpanzees to increase consumption of figs and low-quality foliage during the low fruiting season (Furuichi et al. 2001a). Elsewhere the fruits and pith of the oil palm *Elaeis guineensis*, which are also available year-round, are important fallback items for chimpanzees (Tutin et al. 1991; Yamakoshi 1998; Leciak et al. 2005). While both *Musanga* and the oil palm are absent at Bulindi, the abundant *Phoenix reclinata* palms might fulfil a similar ecological role. These palms produced ripe fruit during 11 of the 14 months in which they were monitored. Yet chimpanzees ate palm fruits in accordance with their availability and regardless of the availability of other forest tree fruits, consistent with this study's definition of a preferred food. *Phoenix* fruits are perhaps best described as a 'preferred staple' food for chimpanzees at Bulindi.

While *Phoenix* fruits are eaten by chimpanzees elsewhere (Wrangham et al. 1994; Hunt and McGrew 2002; Moscovice et al. 2007), they have not previously been ascribed the level of importance to chimpanzee ecology indicated by this study. Probably this reflects the very high density of these palms in the swampy habitat at Bulindi.

Chimpanzees are considered specialist frugivores which exploit low-density food patches such as fig trees (Ghiglieri 1984; Isabirye-basuta 1989). Yet at Bulindi ripe palm fruits were available in continuous patches across large stretches of swamp forest for most of the year. As mentioned previously, this ecological condition may go some way to explaining the widespread occurrence of chimpanzees in small riverine forests in Hoima District (McLennan 2008). Although *Phoenix* palms occur in Budongo, the fruits have not been recorded eaten by chimpanzees (Reynolds 2005). Interestingly, McGrew and Hunt (2002: 45) considered *Phoenix* fruits a likely fallback food for chimpanzees in gallery forest at Semliki, Uganda, "ignored when other items were available". They also report that the Semliki apes consume the pith of the palm frond, but there was no evidence that Bulindi chimpanzees do likewise.

Fruits of wild ginger (*Aframomum* spp.) are eaten by great apes across central and eastern Africa (Izawa and Itani 1966; Suzuki 1969; Sabater-Pi 1979; Wrangham et al., 1994; Doran et al. 2002; Yamagiwa and Basabose 2006a; Kagora-Rugunda and Baranga 2008). At Bulindi consumption peaked in months when availability of tree fruits was at low to intermediate levels, indicating these are probably fallback foods. What prompted the chimpanzees' sudden, intensive consumption of *Lantana camara* fruits during May is unclear. The apes did not feed on these fruits during the low fruiting season, despite their apparent availability, precluding a role as a fallback item. Intriguingly, in 2004 Budongo chimpanzees also fed vigorously on *L. camara* fruits but had not been seen doing so in the preceding decade (Reynolds 2005). Other important wild fruits were seasonally available at Bulindi and consumption was tightly linked to availability.

Foliage

Herbaceous piths and young leaves (but not bark, which was rarely eaten; cf. Nishida 1976) were evidently fallback foods at Bulindi. Piths were eaten throughout the year but intake peaked when fruit availability declined, as was observed at Kibale (Wrangham et al. 1991). Since pith from THV (e.g. *Marantochloa leucantha* and *Pennisetum purpureum*) and cultivars (particularly sugarcane) was not distinguished in dung, the overall importance of THV for chimpanzees at Bulindi is unclear. The distinction may be important. Although of low nutritional density compared to fruit, herbaceous piths are thought to provide chimpanzees with supplementary energy when fruit intake is reduced and are a source of fibre (Wrangham et al. 1991). However, the high sucrose content of sugarcane makes it an especially energy-rich food source.

Chimpanzee populations differ in their propensity to eat leaves when fruit is scarce. Several studies report an inverse relationship between fruit availability or consumption and leaf-eating (Tutin et al. 1991; Kuroda et al. 1996a; Doran 1997; Fawcett 2000). Elsewhere, overall leaf intake does not vary with fruit abundance (Wrangham et al. 1991; Yamakoshi 1998). At some sites, leaves of particular species constitute a staple item in the diet, utilised throughout the year (e.g. *Celtis mildbraedii* at Goualougo; Morgan and Sanz 2006). At Bulindi young leaves were eaten in trivial quantities during most study months, but became a major dietary component during the low fruiting season and more precisely when chimpanzees did not feed on *Phoenix* fruits. Observations suggested the apes selectively fed on emerging leaves of *Trichilia dregeana*. Krief et al. (2006) report that chimpanzees at Kibale eat leaves of a closely-related species, *T. rubescens,* which has antimalarial properties. The authors suggest Kibale chimpanzees may select *T. rubescens* leaves for benefits other than nutrition, and note that other work has demonstrated potentially medicinal properties in *T. dregeana* (i.e. an analgesic effect). However, consumption patterns at Bulindi suggest *T. dregeana* leaves were ingested primarily for nutritional benefit. Notably, the phenology of this species was out of phase with the majority of trees in the community, which exhibited leaf-flushing in January–February (Chapter 4). Further study is required to determine if young leaves of *T. dregeana* are consistently available during low fruiting seasons, thus constituting a reliable fallback food. Chimpanzees appear to select leaves that are high in protein but low in tannins (Takemoto 2003). At Bulindi, chimpanzees might have needed to compensate for a shortfall in protein intake from fruits during the low fruiting season.

Cultivars

Agricultural foods were fully incorporated into the chimpanzees' annual diet; several species were eaten in all or most months and may be regarded as staples (cocoa, guava, papaya, sugarcane). Guava was the most common fruit residue in dungs after figs. While consumption of individual species did not correlate closely with estimated forest fruit availability, chimpanzees tended to increase intake of these cultivars when the fruit component of the diet decreased (cocoa, guava) or when fewer forest tree fruits dominated the diet (papaya). This study highlights the difficulty in quantifying the contribution of agricultural crops in the diets of unhabituated apes due to problems in detecting or identifying seedless fruit pulps and cultivar piths in dungs. For example, the absence of a significant inverse relationship between cocoa feeding and fruit availability – in strong disagreement with qualitative data – indicates that the frequency of cocoa residue in faeces is an unreliable measure of consumption. Chimpanzees fed mainly on unripe pods from forest *shambas* and mature seeds rarely appeared in dung. Examination of feeding remains from ripe cocoa revealed that the large seeds of mature pods were often spat out (Plate 10). This meant that cocoa was usually detected in dung from the partially digested pulp or half-formed seeds of unripe pods, and most reliably when it occurred in large quantities. Therefore the overall frequency of cocoa consumption by chimpanzees at Bulindi is probably considerably higher than faecal data imply. Likewise, consumption of other cultivars (e.g. banana and papaya) was certainly underestimated by dung analysis.

In spite of methodological limitations, the overall representation of fruit cultivars in dungs was strongly associated with reduced frugivory and increased folivory, consistent with this study's definition of a fallback food. (This measure of cultivar consumption excluded mangos which, unlike other cultivated fruits detectable in faeces, were a seasonal, highly preferred food). Increased cultivar consumption during the low fruiting season is supported by behavioural observations and feeding trace evidence, as well as local reports, which plainly indicate that chimpanzees sought agricultural foods and foraged outside of forest patches most frequently when 'important' forest tree-fruits were unavailable. The Bulindi data are therefore in broad agreement with previous studies (Naughton-Treves et al. 1998; Hockings et al. 2009). However, while the data imply that chimpanzees exploited human foods for nutritional benefit when preferred fruits were scarce, the parallel increase in pith intake and, in particular, the sharp rise in leaf-eating, may indicate that consumption of high-quality cultivars was alone insufficient to compensate for nutritional shortfalls associated with decreased intake of major wild fruit species.

Crop-raiding has been defined as "wild animals moving from their natural habitat onto agricultural land to feed on the produce that humans grow for their own consumption" (Sillero-Zubiri and Switzer 2001). But at Bulindi chimpanzee consumption of cultivars was not necessarily in the context of crop-raiding. In particular, chimpanzees habitually ate cocoa from abandoned forest *shambas* and raided cocoa from village sources much less frequently. These forest shambas were established *within* the chimpanzees' natural habitat. Since forest cocoa was no longer guarded its consumption is comparable to that of other wild foods. Similarly, mangos were sometimes obtained from trees in regenerating habitat rarely visited by people. Because consumption of cultivars from guarded crops as opposed to abandoned or unguarded sources could not be distinguished in dung the frequency of crop-*raiding* could only be qualitatively assessed (cf. Hockings et al. 2009). But there is little doubt that crop-raiding was a daily activity of chimpanzees in some months, particularly during mango season and the low fruiting season.

Methodological Considerations

Tree-fruits are generally considered the most important fruit sources for chimpanzees, yet in some months the fruits of shrubs, vines and herbs constituted a major part of the fruit diet at Bulindi (e.g. *Monanthotaxis ferruginea* between November 2007 and January 2008).[9] Since non-tree life forms were not sampled in vegetation or phenology surveys their contribution to overall forest food availability is unknown. Several non-tree fruits identified as 'important' for chimpanzees were locally abundant (e.g. *Aframomum* spp. in swamp forest, *Dovyalis macrocalyx* in mixed forest, *Lantana camara* in open, heavily logged areas, and *Monanthotaxis ferruginea* and *Rubus pinnatus* in ecotone forest). When available these foods may have contributed considerably to overall fruit biomass in forests. Thus, future studies of forest food availability at Bulindi should include non-tree species.

Inter-site Differences in Plant Foods Eaten

The extent to which particular plant foods are utilised may differ between study sites (Nishida et al. 1983). For example, the fruits of several monitored species that are seasonally important for chimpanzee elsewhere were seemingly ignored at Bulindi (e.g. *Harungana madagascariensis* at Mahale and Gombe [Matsumoto-Oda 2002; Chepstow-Lusty et al. 2006]; *Teclea nobilis* at Kalinzu and Kibale [Tashiro et al. 1999; Emery-Thompson and Wrangham 2008]; and *Croton macrostachyus* at Budongo

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[9] See also Itoh and Nishida (2007) and Moscovice et al. (2007) for the importance of *Saba* lianas to Mahale and Rubondo chimpanzees, respectively.

[Newton-Fisher 1999]). Of these, *Harungana, Teclea* and *Croton* all fruited during this study but the seeds never appeared in chimpanzee dung.[10] Similarly, seeds of *Maesopsis eminii* and *Pycnanthus angolensis*, which are common fruit foods for chimpanzees at Budongo (Reynolds 2005) and Mahale (Takasaki 1983b), respectively, each occurred in a single dung only at Bulindi. In the cases of *Teclea* and *Maesopsis*, phenology specimens exhibited only a light fruiting during the study which could explain why they were not fed on by chimpanzees. But why other palatable and, at some sites, preferred fruits should be ignored is unclear. While potential cultural factors cannot be ruled out, chimpanzee fruit choice at a given time will be influenced by interactions with other available foods in the habitat (Boesch et al. 2006). Foraging habits of competitors may also be a factor (i.e. if fruits are eaten by other animals when unripe).

In addition to wild foods, the apes seemingly ignored several cultivars grown locally that are eaten by chimpanzees elsewhere. These include pineapple (eaten at Bossou), maize fruit and/or pith (Bossou, Kahuzi, Kibale and Mahale), rice pith (Bossou, Kanka Sili), millet (Kanka Sili), cassava tubers (Bossou, Rio Muni), and yam tubers (Bossou) (Dunnett et al. 1970; Sabater-Pi 1979; Nishida and Uehara 1983; Yamagiwa et al. 1992; Naughton-Treves et al. 1998; Hockings et al. 2009). In particular, chimpanzees at Bulindi have ample opportunity to eat cassava, maize and rice since these are important food crops, common throughout the chimpanzees' range, yet no evidence suggested the apes fed on them. Elsewhere in Hoima chimpanzees reportedly raid maize (McLennan 2008). In dynamic human-modified environments chimpanzee dietary traditions are likely to be in a state of flux. At Bulindi the importance of cultivars in the diet, and the range of human foods eaten, is almost certainly rising. According to local residents the apes have eaten mangos and bananas growing alongside forest, and cocoa inside the forest, for many years. But chimpanzees entering village areas looking for food is apparently a recent phenomenon (Chapter 9). Increased exposure to human foods is likely to lead to the incorporation of new items in the diet. For example, prior to 2007 oranges were apparently not eaten by the chimpanzees. Takasaki (1983a) provides a similar example in which chimpanzees at Mahale discovered mangos. At Budongo, chimpanzees of the habituated Sonso community were seen feeding on maize for the first time in 2007, which they may have discovered in the course of raiding mangos (F.

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[10] However, another species of *Croton* (*C. sylvaticus*) was eaten.

Babweteera, pers. comm., 2007).[11] Perhaps prior to recent extensive deforestation at Bulindi, sufficient food availability in riverine forests meant the chimpanzees had little need to experiment with unfamiliar human foods growing outside the forest. With ongoing forest clearance locally the importance of human foods in the chimpanzee diet at Bulindi is set to increase.

Summary

1. The plant food diet of chimpanzees at Bulindi was examined via systematic faecal analysis, supplemented by evidence from feeding traces and opportunistic observations of feeding behaviour. Diet composition and breadth was overall similar to other studied populations.
2. Chimpanzees at Bulindi were highly frugivorous. Fruits accounted for the majority of plant foods and dungs were dominated by fruit residues in all months. ‘Important’ fruit species were identified, defined as those detected in the majority of dungs in at least one month or in >10% of all dungs collected.
3. The chimpanzees supplemented their natural diet with a variety of cultivars, of which several (cocoa, guava, mango, papaya) were among the most important fruit foods for this community. Important fruits included species that were available seasonally, for extended periods or year-round, and included trees, shrubs, vines and herbs.
4. Overall fruit intake decreased during three months when most important forest tree fruits were unavailable, particularly the superabundant *Phoenix* palm. At this time the apes pursued a mixed strategy of increasing consumption of high quality items such as figs and cultivars whilst exploiting low quality, but more abundant, foliage foods (leaves and herbaceous piths). Proposed fallback foods for this community include both wild and cultivated species.

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[11] Webber (2006) recorded one instance of chimpanzee damage to maize in a village bordering Budongo in 2004, but it was unclear if the individual(s) concerned were from Sonso or an unhabituated neighbouring community (A. Webber, pers. comm. 2010).

CHAPTER 6 – DIET & FEEDING ECOLOGY.

II. ANIMAL FOODS

6.1. Introduction

Animal food is a high-quality resource, rich in protein, fat and energy as well as various vitamins and minerals (Hladik 1977; Stanford 1999; Deblauwe and Janssens 2008; Raksakantong et al. 2010). Many primates supplement a predominantly plant based diet with insect and/or vertebrate prey (e.g. Tutin et al. 1997; McGrew 2001; Furuichi 2006), including all the great apes (Tutin and Fernandez 1992; van Schaik et al. 2003; Hohmann and Fruth 2008). Animal foods are eaten by chimpanzee populations across Africa to varying degrees (McGrew 1983, 1992). For example, insects are a regular component of the diet at some sites (Uehara 1986; Tutin and Fernandez 1992; Deblauwe and Janssens 2008), but elsewhere insectivory is relatively infrequent (Reynolds 2005). As discussed in the previous chapter, chimpanzee diets show seasonal variation as the relative contribution of preferred foods (i.e. ripe fruits) and lower-quality foliage foods in the diet fluctuate according to fruit availability. Few studies have assessed the nutritional aspects of chimpanzee insectivory, but there is some evidence that chimpanzees increase consumption of certain taxa when fruit intake is reduced (Deblauwe 2009). On the other hand, seasonal variability in consumption of some prey species may be determined by the insect's life-cycle (Matsumoto-Oda 2002).

The most commonly exploited invertebrates are social insects: ants, termites and honey-making bees. Chimpanzees' use of tools to harvest these prey has received considerable attention from fieldworkers (e.g. McGrew 1974; Uehara 1982; Boesch and Boesch 1990; Sanz and Morgan 2009). Where environmental factors can be ruled out, inter-site differences in techniques employed to obtain insects seem to reflect cultural traditions (McGrew 1992; Schöning et al. 2008). Across sites increased levels of insectivory are seen in populations that habitually employ tools to harvest insect prey or access honey (McGrew 1992). Tool-use may facilitate greater access to high-quality insect fallback foods in such populations during periods of fruit scarcity (Yamagiwa and Basabose 2009). Chimpanzees in the northern part of the Rift Valley in Uganda, at Budongo, Kibale and Semliki, stand out among studied populations in having meagre overall tool kits (Hunt and McGrew 2002; Reynolds 2005; Sherrow 2005; Watts 2008; Gruber et al. 2009). Insectivory appears to be uncommon at all these sites. Given Bulindi's geographical location – south of Budongo and north of Kibale and Semliki – tool-use in extractive insect foraging was expected to be similarly rare or absent.

As with insectivory, predation on vertebrates – especially arboreal monkeys – is a common activity at some sites (Goodall 1986; Boesch and Boesch-Achermann 2000; Hosaka et al. 2001; Watts and Mitani 2002), but occurs less often at others (Sugiyama and Koman 1987; Newton-Fisher et al. 2002; Morgan and Sanz 2006). Overall predation frequencies appear to be largely dictated by the presence or absence of particular prey species, but other factors such as the hunting 'culture' of the chimpanzee population may also play a part. In areas where chimpanzees are forced to live in close proximity with humans this carnivorous tendency has meant young children occasionally fall victim to chimpanzee predation (e.g. Wrangham et al. 2000; Kamenya 2002).

The aims of this chapter are to:

1. Describe the range of animal foods eaten by chimpanzees at Bulindi. This chapter expands on the preceding chapter, which focused on plant foods; together they present a complete list of known foods in the Bulindi chimpanzee diet;
2. Examine seasonality in insectivory and determine whether insect feeding is related to patterns of fruit availability;
3. Present evidence for tool-use in insect foraging by Bulindi chimpanzees;
4. Assess the frequency of meat-eating in this population.

6.2. Methods

During this study chimpanzees were never observed feeding on animal foods or using tools for extractive foraging. Thus data come from faecal analysis, supplemented with information from feeding traces. Insects have chitinous exoskeletons that are indigestible to chimpanzees and thus detectable in dung. Likewise, vertebrate body parts including bones, hair, teeth and skin may pass through the gut intact (Tutin and

Fernandez 1993a). Faecal analysis therefore provides information on frequency and seasonality of insectivory and meat-eating (McGrew 1983; Uehara 1986; Tutin and Fernandez 1992; Basabose and Yamagiwa 1997; Deblauwe 2009). A drawback to the method is that soft-bodied invertebrates such as insect larvae may leave no recognisable trace in dung at all (Deblauwe 2009). The methods used to collect and process fresh chimpanzee faecal samples for analysis were described in detail in the previous chapter. The dried undigested contents of dungs were inspected for animal matter; insect or bone fragments were stored dry or preserved in ethanol for identification. Supplementary data on honey-eating and associated tool-use were collected opportunistically at subterranean hives of stingless bees (*Meliponula* spp.) in areas frequented by chimpanzees.

6.2.1. Data Analysis

The analysis is restricted to dungs collected over 13 months from January 07 to January 08. The number of independent dungs inspected was 1436. Monthly sample size was shown in Figure 5.1. A list of animal food items consumed by chimpanzees during the study period was compiled from faecal data and information from feeding traces. Animal prey species are listed by taxa; ant and stingless bee taxonomy follows Taylor (2007) and Eardley (2004), respectively. Insect remains in dung, as well as live-caught insects (e.g. bees from nests targeted by chimpanzees for honey), were identified by specialists at the National Agricultural Research Organisation, Kampala, and the Natural History Museum, London.

A ripe fruit availability index (FAI) based on ranked scores of fruit crop size was calculated as described in Chapter 4. Monthly fruit intake was indexed as the mean % volume of fruit in dungs (Chapter 5).

Statistics

Correlation and regression analysis were used to assess the association between the frequency of monthly dung samples containing invertebrates and variables including rainfall, fruit availability and measures of dietary composition (e.g. fruit intake). ‘Consumption’ of particular insect prey is measured as the % of monthly dungs containing the item. Regression analysis was performed to examine the relationship between a dependent and one or more independent (predictor) variables, whereas correlations were used when variables were not designated as dependent or independent. Independent variables (IVs) used in multiple regressions were rainfall, fruit availability, and fruit intake. The latter variable was included since it was a particularly strong negative predictor of the consumption of several plant foods proposed as fallback foods for Bulindi chimpanzees (Chapter 5). Rainfall data were unavailable for January 08. For this month I used mean rainfall in 2001–7 to increase the sample size and improve the power of the test. In these preceding seven years January was consistently dry (mean 27.4 mm ± 14.4 SD, range: 5.3–47.0 mm), and January 08 followed this pattern. I employed the backwards stepwise method in multiple regressions, as outlined in Chapter 5. Variables expressed as percentages were converted to proportions and transformed to arcsine square roots, unless all values fell below 30%, in which case standard square root transformations were applied (Ahrens et al. 1990). The residuals of dependent variables were tested for normality with Kolmogorov–Smirnov and Shapiro–Wilk tests (Field 2005). The distribution of one variable used in correlations remained non-normal following transformation, and non-parametric Spearman rank coefficients were employed throughout. The analysis was performed using SPSS version 17.0. All tests are two-tailed and significance was set at $p < 0.05$.

6.3. Results

6.3.1 Insectivory

Insects were the most commonly eaten animal prey during the study (Table 6.1). Of at least 21 taxa consumed the majority were from a single order, Hymenoptera (ants and bees; wasps were not eaten).[1] Insect remains (including Apian produce) occurred in 15.1% of dungs and in all months (average monthly mean: 14.8% ± 10.3 SD, range 2.2–32.9%). Inter-monthly variation in the frequency of insects in dung was significant ($\chi^2 = 105.44$, $df = 12$, $p < 0.001$). Seasonal peaks in consumption were observed during June–July and September–October 07, and January 08, whereas few dungs contained insects between January–May 07 (Figure 6.1). Despite this apparent seasonality the overall effect of rainfall, ripe fruit availability and fruit intake on insect consumption was non-significant ($R^2 = 0.126$, $F_{3,9} = 0.43$, $p = 0.74$), and none of the IVs were individually

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[1] Tiny fig wasps (Agaonidae), ingested in the course of feeding on figs, were not considered insect prey.

retained in a significant model. Because monthly changes in the frequency in dungs of ants and bees – the two main categories of insect prey – were uncorrelated (r_s = -0.039, p = 0.90), consumption patterns for these two major insect taxa were examined separately.

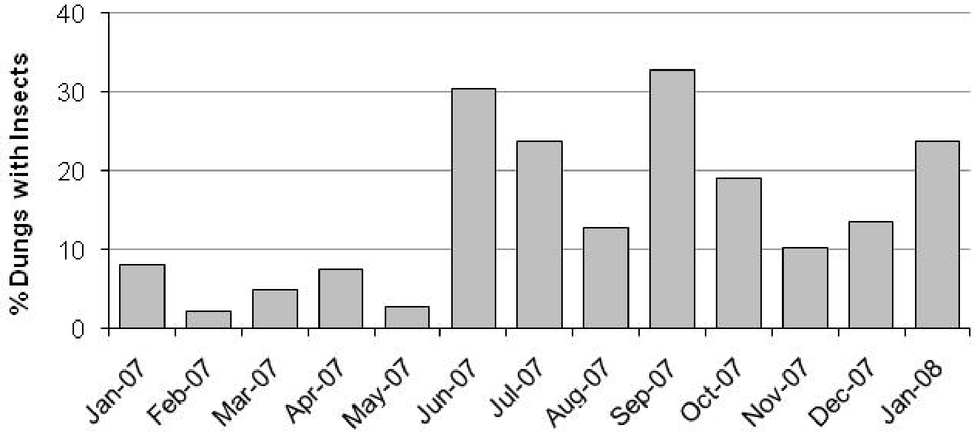

Figure 6.1. Monthly variation in frequency of insect matter in dung.

Ants (Formicidae)

Ants were present in 10.2% of dung specimens and appeared in dungs in all months except January–March, at the start of the study, though other insect taxa were eaten during that period (Table 6.1). Of at least 14 ant species found in dung only the weaver ant (*Oecophylla longinoda*) was eaten frequently (8% of all dungs). This species was not detected in faeces prior to April 07 but was observed in all subsequent months at varying frequencies. Consumption peaked sharply in June–July and again in January 08 (Figure 6.2), but change in the proportion of monthly dungs containing the ants was unrelated to rainfall, fruit availability, or fruit intake (R^2 = 0.074, $F_{3,9}$ = 0.24, p = 0.87). Intriguingly, the proportion of dungs with weaver ants was positively and significantly correlated with the presence of whole undigested leaves (r_s = 0.744, p = 0.004; Figure 6.3), which chimpanzees swallowed for presumed self-medicative purposes (Chapter 5).

Table 6.1. Animal prey in the diet of Bulindi chimpanzees, Jan 07–Jan 08.

Taxa [common name]	**Criteria** [1]	**No. dungs (N = 1436)**	**% dungs**	**Months in which prey item was recorded eaten** [2]												
				Ja 07	**Fb**	**Mr**	**Ap**	**My**	**Jn**	**Jl**	**Ag**	**Sp**	**Ot**	**Nv**	**Dc**	**Ja 08**
Class Insecta		**217**	**15.11**													
Order Diptera																
Ceratitis sp. [fruit fly]	F	1	0.06			x										
Order Hemiptera																
Graptostethus sp. [seed bug]	F	1	0.06	x												
Order Hymenoptera																
Family Apidae [3]		**74**	**5.15**													
Apis mellifera [honey bee]	F, T	35	2.44			x	x	x	x	x ●		x	x ●			
Meliponula (*Meliplebeia*) *lendliana* [stingless bee]	F, T	26	1.81				x		●?	x	x ●	x ●	x ●	x ●	x ●	
Xylocopa sp. [carpenter bee]	F, T	13	0.91	x	x		x						x	x	x	x ●
Family Formicidae [ants]		**147**	**10.24**													
Atopomyrmex mocquerysi	F	4	0.28				x			x		x				
Camponotus (Myrmopelta) vividus [wood-boring ant]	F	1	0.06									x				
Crematogaster (Atopogyne) buchneri	F	4	0.28									x			x	
Crematogaster (Atopogyne) depressa	F	1	0.06										x			
Dorylus sp. [driver ant]	F	3	0.21												x	
Monomorium sp.	F	1	0.06				x									
Myrmicaria natalensis subsp. *eumenoides*	F, T	4	0.28										x ●			
Odontomachus troglodytes	F	5	0.35				x					x			x	x
Oecophylla longinoda [weaver ant]	F	115	8.01				x	x	x	x	x	x	x	x	x	x
Pheidole sp.	F	8	0.56									x			x	
Polyrhachis sp.	F	1	0.06				x									
Tetramorium sp.	F	1	0.06												x	
? Oligomyrmex sp.	F	1	0.06										x			
Unknown *spp.* (subfamily Myrmicinae)	F	6	0.42											x	x	
Family Halictidae																
Unknown sp. [sweat bee]	F	1	0.06													x
Order Odonata																
Unknown sp. [dragon fly]	F	1	0.06	x												
	No. insect sp. in monthly dung sample:			3	1	2	8	2	2	4	2	8	7	4	9	4
	% monthly dungs with insects:			8.2	2.2	4.9	7.5	2.8	30.4	23.7	12.8	32.9	19.1	10.3	13.5	23.7

Cont. overleaf

Table 6.1 *cont.*

Taxa [common name]	**Criteria** [1]	**No. dungs (N = 1436)**	**% dungs**	**Months in which prey item was recorded eaten** [2]												
				Ja 07	**Fb**	**Mr**	**Ap**	**My**	**Jn**	**Jl**	**Ag**	**Sp**	**Ot**	**Nv**	**Dc**	**Ja 08**
Class Aves																
Order Galliformes																
Gallus gallus [domestic chicken]	F, T	3? [4]	0.21?			x									●	
Class Mammalia																
Order Rodentia																
Unknown sp. [small rodent]	F	1	0.06				x									

[1] Criteria: F = Faecal Specimen, T = Feeding Trace;

[2] x = indicates taxa seen in dung during the month; ● = indicates feeding trace evidence was found during the month: for *Apis* bees feeding remains were honeycombs, while for *Meliponula* and *Xylocopa* bees feeding traces were scored when there was clear evidence that chimpanzees had targeted a nest (i.e. with tools) even if honey feeding remains were not present;

[3] Bee remains in faeces included adults, pupae and bee's wax; note that *Meliponula* bees found in dung may comprise >1 form or species (A. Lugoloobi, pers. comm. 2007); however, adult bees recovered live from three subterranean nests targeted by chimpanzees for honey were all *Meliponula* (*Meliplebeia*) *lendliana*;

[4] Skin and tissue in dung believed to be chicken but not confirmed.

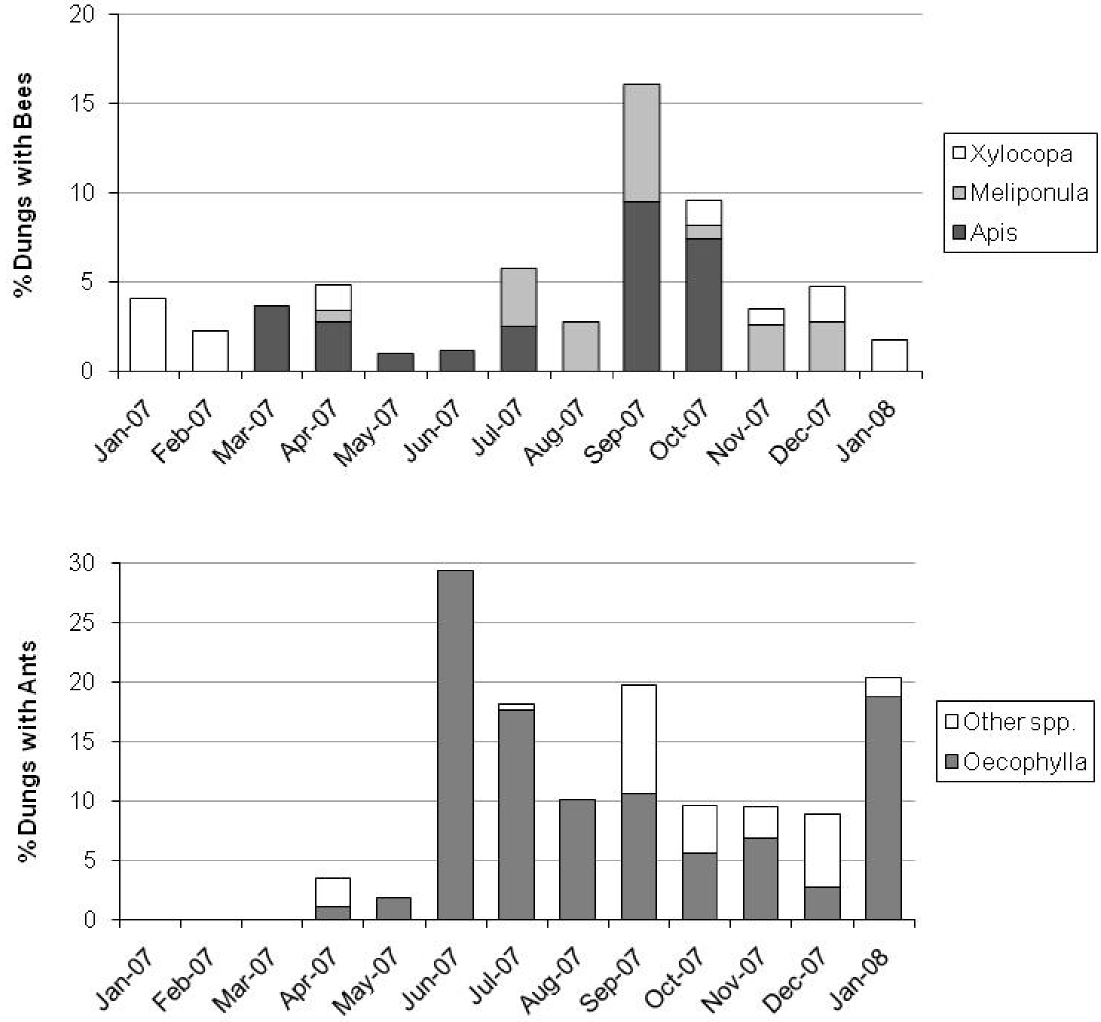

Figure 6.2. Monthly variation in the proportion of faecal specimens containing ants (lower chart) and bees and/or their produce (upper chart). The representation of the most common taxa in the monthly figures is shown. September–November was the low fruiting season in Bulindi forests.

Other ant species were eaten infrequently. No other taxa occurred in >1% of dungs; in some instances ingestion may have been inadvertent (e.g. eaten with fruit or foliage). When species were lumped, non-weaver ants were eaten mainly between September–December during the low fruiting season (Figure 6.2), but the occurrence in monthly dungs was not predicted by fruit availability or fruit intake ($R^2 = 0.106$, $F_{2,10} = 0.59$, $p = 0.57$). There was a positive correlation between proportion of dungs containing non-weaver ants and mean abundance of green leaf fragments ($r_s = 0.577$, $p = 0.04$). Monthly frequencies of weaver ant and non-weaver ants in dung were uncorrelated ($r_s = 0.247$, $p = 0.42$). Thus chimpanzee ingestion of weaver ants was distinct from other ant-eating.

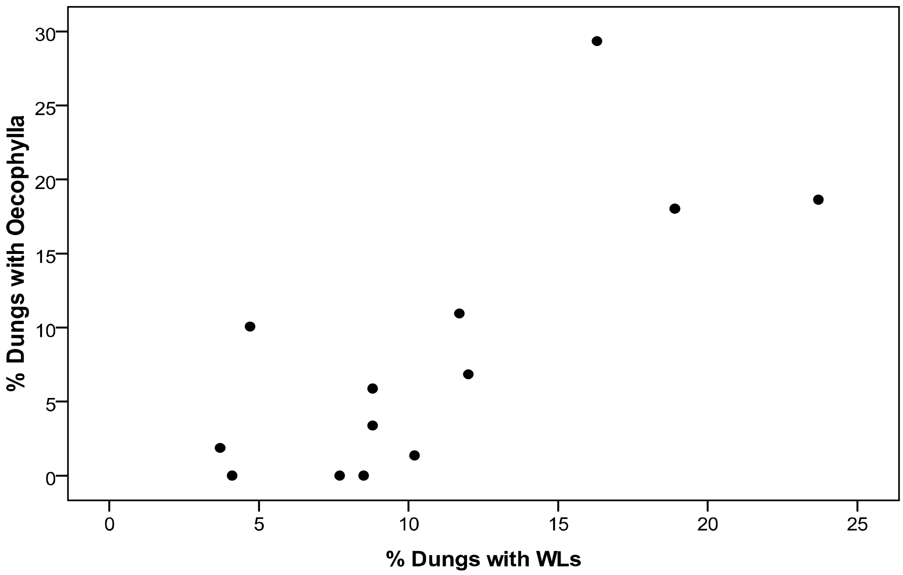

Figure 6.3. Correlation between the proportion of monthly dungs containing whole swallowed leaves (WLs) and the proportion containing fragments of weaver ants (*Oecophylla longinoda*).

There was no evidence that chimpanzees at Bulindi use tools to harvest ant prey. In one case, feeding trace evidence indicated ants were acquired by hand. On 23 October 2007 four adult males travelled from Kiseeta forest to Kaawango forest, crossing the main Hoima road at Bulindi trading centre. Ten minutes after they crossed we encountered them abruptly in overgrown gardens behind the trading centre. Knuckle and finger marks showed they had been digging in a small patch of recently tilled soil. *Myrmicaria natalensis* (subsp. *eumenoides*) ants and passages presumably leading to a subterranean nest were visible in the disturbed soil. No tools (e.g. digging sticks or probes) were present. These same ants appeared in four dungs during that month.

Bees (Apidae)

Apian remains (including adult workers, pupae, larvae and bees wax) appeared in 5.2% of dungs and in all months. While insect matter seldom accounted for >5% of dung volume, the residue of a honey meal occasionally constituted a considerable portion of dung contents. Three taxa of honey-making bee were ingested: African honey bees (*Apis mellifera*), stingless bees (*Meliponula* [subgenus *Meliplebeia*] spp.) and carpenter bees (*Xylocopa* sp.). Seasonal differences in predation on these taxa were apparent. *Apis* bees and associated produce were present in dungs in March–October, with consumption peaking in September–October, while *Meliponula* bees were eaten mainly from July to December (Figure 6.2). In contrast, *Xylocopa* fragments appeared in faeces primarily during the December–February dry season, when *Apis* and *Meliponula* were rarely eaten. Accordingly, changes in the monthly frequency of *Xylocopa* fragments in dung was negatively predicted by rainfall (R^2 = 0.469, $F_{1,11}$ = 9.72, p = 0.01). *Apis* and *Meliponula* were considered together because of the strong temporal overlap in consumption. There was a significant overall effect of rainfall, fruit availability and fruit intake on consumption of these taxa (R^2 = 0.591, $F_{3,9}$ = 4.33, p = 0.04). However, the final regression model to emerge was not significantly strengthened by the inclusion of either fruit availability or intake, and only rainfall was retained (R^2 = 0.511, $F_{1,11}$ = 11.52, p = 0.006). Chimpanzees preyed on these bees most often during rainy months.

Tool-Use for Honey Gathering

On 13 occasions between June and December 07 indirect evidence was found that chimpanzees used tools to excavate subterranean nests of *Meliponula* bees to obtain honey (Plate 11). This corresponds to the period when *Meliponula* bees appeared in dungs together with bee wax (Table 6.1). Stick tools were found in association with confirmed (n = 6) or presumed (n = 2) *Meliponula* nests located along chimpanzee trails, including one nest located inside a termite mound. In each case chimpanzees were nearby and/or signs of recent chimpanzee activity near the tool-use site were evident (dung, night nests, knuckle prints). Chimpanzees used sticks to dig vertically in the ground (or obliquely into the termite mound) to a maximum depth of 45 cm. Three hives were targeted by chimpanzees on ≥2–4 separate occasions. Worker bees collected at three nests were subsequently identified as *M. (Meliplebeia) lendliana*. In three other instances during the same period shallow holes were found, each in association with a single stick, but no traces of honey or bee's wax were evident and our excavations revealed no presence of bees (i.e. tunnels leading to chambers where honey is stored) or other insects in the soil. These cases may represent abortive attempts to locate subterranean hives.

In total 44 stick tools were found in association with dug holes. In most cases sticks had been modified several times (i.e. stripped of twigs, leaves and often bark, and clipped to length), and manufactured from shrubs, saplings or small trees growing in the immediate vicinity of the digging site. The tools included sturdy digging sticks (‘perforators’; Boesch et al. 2009), which had one or both ends encrusted with soil, and more slender sticks largely devoid of soil. These latter tools may have functioned to probe narrow entrance tunnels, and possibly to extract (‘dip’) honey from the subterranean chambers, though honey traces were not visible on them. Three times chimpanzees appeared to have dug up underground nests and obtained honey by hand without tools since none were found in the vicinity of the nest site.

Circumstantial evidence of a second context to tool-use in extractive foraging by chimpanzees at Bulindi involved carpenter bees (*Xylocopa* sp.). In January 08 nine sticks were discovered immediately below an occupied *Xylocopa* nest, 25 cm above the ground in the dead branch of a small *Oxyanthus speciosus* tree. Seven of the sticks originated from a single branch of a neighbouring *Lovoa trichilioides* tree, which had been detached, stripped of bark and snapped into several sections. Two adjoining sections had been further split lengthwise to produce narrower tools. One or both ends of all sticks fitted the bees’ three entrance holes (18, 17 and 17 mm diameter, respectively). Inside the nesting branch hollowed chambers housed several adults, larvae and honey (Plate 12).

Miscellaneous Insects

An intact fruit fly (*Ceratitis* sp.) and an intact seed bug (*Graptostethus* sp.) each appeared in a single dung specimen. Other insect remains seen in dung included the wing of a dragon fly (Odonata) and the head of a sweat bee (Halictidae). Whether such miscellaneous taxa were ingested incidentally or actively is unknown.

No evidence indicated the chimpanzees ate termites. Twice, freshly disturbed termite mounds (*Pseudacanthotermes* sp. and *Macrotermes* sp.) were seen with chimpanzee finger and knuckle marks in the soil. On a third occasion, two shallow cavities (~2 inches deep) had been made along a fissure in a woodland path earlier traversed by chimpanzees; imprints clearly showed the holes were excavated with fingers. Termites (*Macrotermes* sp.) were recovered from the disturbed soil indicating the presence of a subterranean nest. Since termites never appeared in faeces, one explanation is that in each of these cases the chimpanzees were seeking termite clay for consumption. Lumps of soil were three times seen in dungs (0.2%), the origin of which is unknown.

6.3.2. Carnivory

Evidence of meat-eating was sparse. Only four dungs (0.28%) contained vertebrate remains. On 1 March 07 three dungs collected in Kiseeta forest contained varying amounts of skin and tissue that appeared to be chicken (*Gallus gallus*); a local pit-sawyer claimed that chimpanzees had taken a chicken from a nearby homestead the previous day. Additional evidence came from feeding traces. In December 07 the remains of a chicken kill were discovered in Katigiro in association with fresh night nests; a noisy party of chimpanzees were <100 m away. The carcass may have been divided as blood and feathers were found at two sites separated by 30 m. Residents at a household bordering the forest patch complained they had lost a chicken to chimpanzees the previous evening. Notably, no dung specimens collected from Katigiro that day or the next contained bones, skin or tissue. Several villagers claimed the apes also preyed on goats or pigs but evidence of this was not seen during the study.

Mammalian remains consisting of the fur and bones of an unidentified small rodent were present in one dung specimen (0.07%) collected in April 07. No evidence indicated that chimpanzees hunted and ate other primates despite the presence of suitable prey (e.g. *Colobus guereza*). One faecal specimen contained a clump of black hairs, but these appeared to be chimpanzee rather than *C. guereza*. Two non-fatal attacks on human children by chimpanzees occurred during 2007. In neither case did the attacking ape eat from the victim or inflict a fatal bite and these incidents were probably motivated by aggression rather than predation (Appendix 5).

6.4. Discussion

Insectivory

Insects – principally ants and bees (and their produce) – were eaten regularly in some months, occurring in 15% of dungs. Compared to some sites this is a low overall frequency. For example, at Mahale in Tanzania 49% of dungs contained insects (Uehara 1986), while at La Belgique in Cameroon 88% of dungs included insect matter (Deblauwe and Janssens 2008). Nevertheless, insect-eating at Bulindi occurs more often than in other studied communities in the northern part of Uganda's Rift Valley, where insectivory is notably uncommon. At Budongo invertebrates appeared in only 2.5% of 161 dungs (Fawcett 2000) and insectivory is observed infrequently (Reynolds 2005). At Kibale *none* of >1200 dungs from two communities were said to contain insects (Wrangham et al. 1991), though limited insectivory has since been witnessed (Watts 2008). West of Kibale, at Semliki, insect-eating is rare or absent (Hunt and McGrew 2002). Thus, insectivory at Bulindi is more frequent than expected based on geographical location.

Seasonality

There was little indication that chimpanzees at Bulindi ate more insects in response to declining food availability or reduced fruit intake. The main ant species eaten at Bulindi was the weaver ant *Oecophylla longinoda*. These ants are a common insect prey for some chimpanzee and gorilla populations (McGrew 1992; Tutin and Fernandez 1992; Deblauwe and Janssens 2008), but have not previously been reported in the diet of Ugandan chimpanzees. Consumption of *Oecophylla* was concentrated at the start of the rainy season at Assirik (Baldwin 1979 cited in McGrew 1992) and Gombe (Goodall 1986), but was unrelated to rainfall at Bulindi. Neither was *Oecophylla* eating related to fruit availability or fruit intake, which is consistent with findings from La Belgique (Deblauwe 2009). In parts of Australia and Asia weaver ants are believed to have medicinal properties and are used by local people to treat a range of common maladies including gastrointestinal upsets (Devanesen 2000; Oudhia 2002). At Bulindi, the proportion of dungs containing weaver ants was highest in months when intact and undigested leaves – swallowed whole for presumed medicinal purposes (Huffman et al. 1996) – also appeared in dungs at high frequencies. Deblauwe (2009) also speculated that ingestion of weaver ants by chimpanzees at La Belgique could have a medicinal function, but did not report an association with medicinal plant use. The possibility that Bulindi chimpanzees consume these ants for therapeutic rather than nutritional benefit warrants further investigation.

Chimpanzees ate non-weaver ants during months when they fed heavily on young leaves, which are a fallback food at Bulindi (Chapter 5). Deblauwe (2009) suggested that termites and ants provide chimpanzees at La Belgique with supplementary protein and energy during periods of fruit scarcity when the apes increasingly rely on low-quality foliage including leaves. But it is unlikely that non-weaver ants were eaten in sufficient quantities at Bulindi to constitute a high-quality fallback food (cf. Yamagiwa and Basabose 2009). Moreover, the chimpanzees apparently ignored termites despite the potential nutritional importance of these insects (Deblauwe and Janssens 2008). Though suitable taxa were widespread (e.g. *Pseudacanthotermes* sp. and *Macrotermes* sp.), the remains (e.g. mandibles) never appeared in dung and 'fishing' tools were not found at the base of epigeal nests in areas habitually used by chimpanzees. Perhaps the need to compensate for a nutritional shortfall when fruit intake was reduced was negated somewhat by the chimpanzees' access to high-energy agricultural crops. Alternatively, the total absence of evidence of consumption may simply indicate Bulindi chimpanzees do not regard termites as food.

Unlike ant-eating, which was unrelated to rainfall, there was a seasonal pattern to honey consumption. The occurrence in dungs of *Apis* and *Meliponula* bees and their produce increased during the low fruiting season when overall fruit intake was reduced, yet the independent effect of fruit availability and intake was non-significant when rainfall was controlled for. Whereas these taxa were eaten in rainy months, carpenter bees (*Xylocopa* sp.) appeared in dungs mainly during the December–February dry season. These results imply that honey-eating may be related to the life-cycle of the bees. Even so, honey constitutes an energy-rich food that was consumed at highest frequencies in the low fruiting season (Figure 6.2).

Inter-Site Differences in Ant-Eating

Many of the identified ant genera recovered from chimpanzee dung at Bulindi are eaten by chimpanzees elsewhere (*Camponotus*, *Crematogaster, Dorylus, Monomorium, Oecophylla, Pheidole, Polyrhachis, Tetramorium*; e.g. Nishida and Uehara 1983; Deblauwe and Janssens 2008). However, several may be new records for chimpanzees (*Atopomyrmex, Myrmicaria, Odontomachus*). Inter-populational differences in ant-eating are not always explainable by the mere presence or absence of particular taxa and may reflect cultural traditions (McGrew 1983, 1992; Schöning et al. 2008). For example, some chimpanzees manufacture vegetative probes to 'fish' arboreal wood-boring ants (*Camponotus* spp.) from cavities in tree trunks (Nishida 1973; Tutin et al. 1995; Fowler and Sommer 2007). While quantitative data on ant abundance are lacking, species preyed upon elsewhere (*C. brutus* and *C. vividus*) occurred at Bulindi, yet a single minor worker of *C. vividus* was found in just one dung specimen. Similarly, chimpanzee consumption of driver ants (*Dorylus*, subgenus *Anomma*) occurs at sites across Africa (McGrew 1992; Schöning et al. 2008), and use of tools to avoid the ants' painful bites ('ant-dipping') is well-documented in some populations (McGrew 1974; Hashimoto et al. 2000; Fowler and Sommer 2007; Möbius et al. 2008; Sanz et al. 2010; Schöning et al. 2008). These ants appear to be eaten in appreciable amounts only by chimpanzees that employ tools to harvest them. In Uganda, only chimpanzees at Kalinzu in the southwest of the country have been found to dip for driver ants (Hashimoto et al. 2000). Further north along the Rift Valley *Dorylus* consumption has not been reported (Reynolds 2005; Watts 2008). Indeed, the Budongo chimpanzees have not been recorded eating ants at all (Reynolds 2005). At Bulindi, at least one suitable prey species (*D. (Anomma) wilwerthi*) was seemingly widespread but small numbers of *Dorylus* ants turned up in only three dung specimens (in December 07), and may have been incidentally ingested. McGrew (1992: 159) noted that no ant species that require digging up from subterranean nests are known to be eaten by chimpanzees. Consumption of *Myrmicaria natalensis* at Bulindi apparently represents an exception to this pattern.

Tool-Use

At first sight, the chimpanzees' apparent disinterest in certain insect taxa (termites and *Camponotus* and *Dorylus* ants), which are harvested with the aid of tools at some sites, is consistent with findings from elsewhere in the northern half of Uganda's Rift Valley where tool-use in extractive foraging is minimal and toolkits are overall small (Reynolds 2005; Sherrow 2005; Watts 2008; Gruber et al. 2009). Therefore the finding that Bulindi chimpanzees use tools to dig for honey stored in the underground hives of *Meliponula* bees is noteworthy. Honey-digging has been recorded at a number of sites (Yamagiwa et al. 1988; Fay and Carroll 1994; Deblauwe 2006; Fowler and Sommer 2007; Boesch et al. 2009), but seems largely confined to Central African populations. It has not previously been reported for any Ugandan population, including at nearby Budongo where the chimpanzees do not use sticks in feeding (Gruber et al. 2009).[2] Evidence of the behaviour was found on 11 occasions, suggesting it may be a habitual activity in this community. By using tools to dig for honey the chimpanzees might have increased their access to a high-quality food item during the low fruiting season

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[2] Although chimpanzees at Bwindi use tools to obtain honey from subterranean stingless bee nests (Stanford et al. 2000), evidence of digging was not seen (C. Stanford, pers. comm.. 2010).

(Yamagiwa and Basabose 2009). At present, the origin of honey-digging by chimpanzees at Bulindi can only be speculated upon. Intriguingly, local humans sometimes use hoes or *pangas* to dig out honey from subterranean *Meliponula* hives, including those along chimpanzee trails, raising the possibility that the apes learnt this behaviour from people. *Meliponula* bees also nest in tree cavities (Kajobe 2007) but it is not known if chimpanzees targeted arboreal nests. Further investigation is also needed to determine if Bulindi chimpanzees use tools to obtain honey from arboreal *Apis* hives, as is observed at some sites (e.g. Fay and Carroll 1994; Boesch et al. 2009; Sanz and Morgan 2009).

Circumstantial evidence strongly suggested that the chimpanzees also use stick tools in predation on carpenter bee (*Xylocopa* sp.) nests, perhaps as probes for determining the presence of adult bees. Relative to *Apis* and *Meliponula* predation, records of chimpanzees feeding on *Xylocopa* bees and honey are few (Uehara 1982; Sugiyama and Koman 1987; Boesch and Boesch 1990; Gruber et al. 2009), but indicate the principal target was most likely honey and/or larvae. Even so, fragments of adult bees in dung at Bulindi demonstrate the adults are not ignored. Boesch and Boesch (1990: 89) provide an account of *Xylocopa* predation involving tools at Taï in West Africa: a chimpanzee "first tests for the presence of adults by probing the nest entrance with a stick. If present, adult bees block the entrance with their abdomens, ready to sting. The chimpanzee then disables them with the stick to make them fall out and eats them rapidly. Afterwards, the chimpanzee opens the branch with its teeth to obtain the grubs and the honey". If a similar technique is employed at Bulindi, it appears that on the occasion reported here chimpanzees were unsuccessful since the bee nest was both intact and occupied.

Carnivory

The faecal data imply a low rate of meat-eating at Bulindi during the study relative to most other sites (Table 6.2). There was no evidence of monkey predation whatsoever. Chimpanzees preferentially target red colobus monkeys (*Piliocolobus* spp.) wherever the two co-occur, and monkey hunting is particularly prevalent among such populations (Gombe: Goodall 1986; Kibale (Ngogo): Watts and Mitani 2002; Mahale: Hosaka et al. 2001; Taï: Boesch and Boesch 1989). Although red colobus are absent at Bulindi, as in most Ugandan forests, all four species of monkeys sympatric with the chimpanzees

(Black and white colobus, tantalus [or vervet] monkey, blue monkey and olive baboon) have been recorded as prey for chimpanzees elsewhere in East Africa (Nishida and Uehara 1983; Goodall 1986; Newton-Fisher et al. 2002; Watts and Mitani 2002). In Uganda, black and white colobus (*Colobus guereza*) are the main prey species at nearby Budongo (Newton-Fisher et al. 2002) and probably also at Semliki (Hunt and McGrew 2002). These monkeys are common at Bulindi but few interactions between the two species were witnessed; on at least one occasion colobus monkeys were seen resting in the same tree as chimpanzees and did not appear fearful. The lack of evidence for monkey hunting at Bulindi is therefore not attributable to an absence or scarcity of suitable prey. Neither is it attributable to demographic factors: hunting is predominantly an activity of adult male chimpanzees, yet at least six adult males were present at Bulindi (Chapter 8). Nevertheless, the findings should be interpreted with caution. At Taï chimpanzees regularly hunt monkeys but faecal analysis was an unreliable indicator of hunting frequency (Boesch and Boesch 1989). At Bulindi, hunters from Nyakakonge claimed to have seen *C. guereza* carcasses in the forest which they attributed to chimpanzee predation. Thus it may be too soon to rule out monkey hunting by this population. Regardless, this study did find evidence that the apes occasionally prey on domestic poultry that range freely around homesteads bordering forest. One possibility is that chickens have become the main prey item for these chimpanzees, since they are presumably easier to catch than arboreal monkeys. Although two chimpanzee attacks on young children were documented in this study, these did not appear to be predatory-motivated.

Summary

1. Faunivory by Bulindi chimpanzees was investigated via faecal analysis. Animal foods accounted for a minimum of 26 food items (comprising ≥21 insect taxa, produce from three genera of bee, and two vertebrates), bringing the total number of plant and animal foods in the diet of chimpanzee at Bulindi to 122.
2. Insect-eating occurs more frequently at Bulindi compared to nearby populations (e.g. Budongo and Kibale). Ants (particularly weaver ants) and bees (honey) were the main insect foods; chimpanzees ignored termites.

Table 6.2. Frequency of vertebrate and/or mammalian remains in chimpanzee faecal specimens at various sites (listed alphabetically). The Bulindi data are emboldened. A dash indicates that the value was not reported.

Study Site	Country	Sample period (months)	No. dungs inspected	Vertebrate remains (% dungs)	Mammalian remains (% dungs)	Reference
Bossou	Guinea	?	>300	0.0	0.0	Sugiyama and Koman (1987)
Budongo	Uganda	10	161	–	0.0	Fawcett (2000)
Bulindi	**Uganda**	**13**	**1436**	**0.3**	**0.1**	**This study**
Bwindi	Uganda	12	187	–	4.3	Stanford and Nkurunungi (2003)
Gombe	Tanzania	42	1963	–	5.8	McGrew (1983)
Kahuzi	DRC	13	1551	–	1.0	Basabose and Yamagiwa (1997)
Kalinzu	Uganda	10	371	–	2.4	Hashimoto et al. (2000)
Kasakati	Tanzania	15	174	–	0.6	Suzuki (1966)
Kibale (Kanyawara)	Uganda	~40	839	2.9	–	Wrangham et al. (1991)
Kibale (Ngogo)	Uganda	~40	416	2.9	–	Wrangham et al. (1991)
Lopé	Gabon	96	1854	–	1.7	Tutin and Fernandez (1993b)
Lui Kotale [1]	DRC	12	458	6.6	–	Hohmann and Fruth (2008)
Mahale (K group)	Tanzania	17	507	0.2	–	Uehara (1986)
Mahale (M group)	Tanzania	6	1053	5.9	–	Uehara (1986)
Mt. Assirik	Senegal	43	783	–	1.8	McGrew (1983)
Ndoki	Republic of Congo	16	214	3.7	–	Kuroda et al. (1996b)
Semliki	Uganda	?	72	2.8	–	Hunt and McGrew (2002)
Taï	Côte d'Ivoire	~24	381	0.3	0.0	Boesch and Boesch (1989)

[1] Data from Lui Kotale are for bonobos (*Pan paniscus*).

3. Honey-eating occurred most frequently in the rainy season when fruit availability was low, but little evidence suggested that insects are fallback foods overall.
4. Chimpanzees at Bulindi use stick tools to dig up underground bee nests. This behaviour has been recorded in Central Africa but has not previously been reported for Ugandan chimpanzees. Evidence of regular tool-use in extractive foraging sets these chimpanzees apart from nearby populations elsewhere in the northern part of Uganda’s Rift Valley.
5. There was a low incidence of vertebrate remains in dung compared to other sites, and no evidence of predation on monkeys. Instead, chimpanzees occasionally preyed on domestic chickens.

CHAPTER 7 – HOME RANGE, NEST GROUPS & PATTERNS OF RANGE USE

7.1. Introduction

Studies of home range size and seasonal range use patterns are necessary for understanding the behavioural ecology of a species and for informing effective conservation strategies that take into account a population's spatial needs and habitat requirements (Irwin 2008; Graham et al. 2009; Houser et al. 2009; Wartmann et al. 2010; White et al. 2010). An animal's home range has been defined as the area traversed during "its normal activities of food-gathering, mating and caring for young" (Burt 1943: 351). In practice, primate home ranges are often regarded as the total area used by an individual or group during a specified time period (typically one to several years; e.g. Robbins and McNeilage 2003; Basabose 2005; Ren et al. 2009). Chimpanzees live in 'communities' that vary in size from less than 20 to approximately 150 individuals, and comprise multiple males and females that interact with one another and share a common home range (Goodall 1986; Nishida 1990; Boesch and Boesch-Achermann 2000; Watts and Mitani 2002; Sugiyama 2004; Reynolds 2005). Since chimpanzees aggressively defend their home range from conspecific strangers, their ranges are commonly referred to as territories (Herbinger et al. 2001; Amsler 2009). Here I use the more general term 'home range' because the nature and extent of interactions between Bulindi chimpanzees and their closest neighbours are not yet established.

The size of chimpanzee home ranges vary greatly among sites. In general, ranges in forested habitats are <30 km^2 (and usually <20 km^2) (Hasegawa 1990; Herbinger et al. 2001; Newton-Fisher 2003; Basabose 2005; Amsler 2009), but chimpanzees in arid savanna environments range over considerably larger areas (>50 km^2; Baldwin et al. 1982; Pruetz and Bertolani 2009). A definitive calculation of range size in savanna habitat remains to be made, however, owing to difficulties in locating and habituating apes in this environment (but data from the Fongoli site in Senegal are likely forthcoming; see Pruetz and Bertolani 2009). Differences in range size among habitats primarily reflect variation in the distribution of food and forest cover, and access to water (Baldwin et al. 1982; Hunt and McGrew 2002; Basabose 2005; Pruetz and Bertolani 2009). Within habitats, the home range of individual communities are fluid, expanding and contracting over time in response to an interplay of factors including food availability, community size, number of adult males, and the relative size and strength of neighbouring communities (Goodall 1986; Lehmann and Boesch 2003; Williams et al. 2004; Amsler 2009). Consequently, the total area used by a community over multiple years tends to be larger than the annual range (Basabose 2005).

Many animals do not use their home ranges evenly. Instead, activities are often concentrated within a particular portion of the range, which may be especially rich in resources (Samuel et al. 1985). It is therefore useful to distinguish a heavily utilised 'core area' from infrequently visited peripheral areas (primates: e.g. Robbins and McNeilage 2003; Harris and Chapman 2007; Irwin 2008; Agostini et al. 2010; Wartmann et al. 2010). Although the method used to calculate core area has varied among studies, chimpanzee core areas usually comprise ≤35% of the total home range (Lehmann and Boesch 2003; Yamagiwa and Basabose 2006b; Amsler 2009). At some sites, chimpanzees show seasonal variation in their use of particular regions or habitats within their range (Matsumoto-Oda 2002; Poulsen and Clark 2004; Tweheyo and Lye 2005). These studies indicate that ranging patterns are influenced by the spatial distribution of resources at different times of the year. However, other studies report no major seasonal shift in activity centre (e.g. Herbinger et al. 2001).

Seasonal fluctuations in food availability have also been linked to patterns of chimpanzee sociality. Chimpanzees exhibit a fission–fusion social organisation: community members form temporary associations known as 'parties' of varying size, composition and duration that feed, travel and socialise together (Goodall 1986; Sakura 1994; Anderson et al. 2002). Temporal variations in party size are observed across a range of habitats (Doran 1997; Matsumoto-Oda 2002; Reynolds 2005; Pruetz and Bertolani 2009). At some sites this variability corresponds to seasonal changes in food distribution and density (Wrangham 1977; Chapman et al. 1995; Itoh and Nishida 2007). For example, chimpanzees may feed and travel in smaller parties during periods of fruit scarcity to avoid costs associated with feeding competition (Wrangham 1977, 2000). Other studies have shown that the presence of estrous (i.e. sexually swollen) females interacts with, or acts independently of, food availability to increase party size (Wrangham 2000; Hashimoto et al. 2001; Anderson et al. 2002; Mitani et al. 2002;

Reynolds 2005). In common with other great apes, chimpanzees build nests in which to sleep at night (Fruth and Hohmann 1996). Where chimpanzees are not well habituated and visual observations are limited, the size of nest groups has been used as an indirect measure to examine seasonal changes in foraging group size (Furuichi et al. 2001b; Hohmann et al. 2006; Moscovice et al. 2007). Supporting the hypothesis that food availability limits party size, nest group sizes were larger when fruit was abundant at Kalinzu and Gashaka (Furuichi et al. 2001b; Hohmann et al. 2006); however, a similar relationship was not apparent at Rubondo Island (Moscovice et al. 2007).

The abovementioned studies were conducted at sites with low levels of human disturbance. Little is known about the home range requirements and ranging patterns of chimpanzees in landscapes dominated by people. For example, the fragmented distribution of resources may force apes to range widely to find sufficient food to meet their energy requirements. Alternatively, ranging may be restricted by human activities. At Bossou, chimpanzees range over an area of approximately 15–20 km^2 that includes cultivated fields and villages, but confine most of their activities to a small forested core area (Sugiyama 2004; Hockings 2007). Although this community is semi-isolated from neighbours as a result of agricultural expansion, the apes occasionally make excursions to forest patches far outside of their normal range (Ohashi 2006), suggesting that agricultural landscapes may not inhibit ranging *per se*. However, features of the human environment such as busy roads and the presence of hostile humans in village areas present novel risks for chimpanzees, which might influence grouping patterns (Sakura 1994; Hockings et al. 2006; Hockings 2007). At Bossou, road-crossing parties were larger than parties within the forest (Sakura 1994), and parties tended to be larger when the apes fed on crops compared to wild fruits (Hockings 2007). Similarly, Wilson et al. (2007) found that chimpanzees formed larger parties when crop-raiding along the border of Kibale NP compared to when they were inside their core area. These studies imply that chimpanzees respond to human-induced danger with increased group cohesiveness.

The aims of this study were as follows:

1. Map the home range of chimpanzees at Bulindi and estimate range size and core area;
2. Assess the influence of food availability and diet on grouping patterns, using the size of nest groups as a proxy for party size;

3. Examine the distribution of nests in individual forest patches in relation to the availability and spatial distribution of major foods;
4. Determine seasonal patterns of range use by the chimpanzees.

7.2. Methods

7.2.1. Data Collection

Mapping Home Range

A precise measure of a community's range size requires long-term data on the ranging of habituated individuals. However, home range size can be reasonably approximated in the absence of fully habituated subjects by mapping the locations of sightings as well as indirect signs such as nests (Baldwin et al. 1982; Nkurunungi and Stanford 2006). At the start of this study chimpanzees at Bulindi were unhabituated, necessitating the use of indirect indicators to map home range. Between October 2006 and January 2008 GPS readings were taken of locations of nests, fresh faeces and direct encounters with the apes. Readings were also taken for fresh feeding traces where these occurred in the absence of other indicators. Local people could often provide precise information on routes taken by chimpanzees travelling between forest patches (e.g. habitual crossing points), and select localities were georeferenced. Whenever we received reports of chimpanzees in village areas or peripheral parts of the range outside of main forest patches, these were followed up. For example, when chimpanzees were reported within the 26 km^2 Kandanda–Ngobya Forest Reserve (FR), east of the riverine forests, we searched locations where they had been sighted for recent sign. If no evidence was found but local information was deemed reliable, the position was treated as an unconfirmed but probable part of the home range.

A disadvantage to mapping the range of unhabituated apes is the possibility of ascribing nests made by neighbouring chimpanzees to the study community (Nkurunungi and Stanford 2006). However, the chimpanzees that range within the Bulindi area comprise a single community, and most adults were identified during the study (Chapter 8). Other chimpanzees were present along the Waki River (>5 km northwest of Bulindi) and around Kasongoire FR (>5 km northeast of Bulindi) (McLennan 2008), but no evidence suggested individuals from these communities entered the study area during the research period. A number of local sightings of apes north of the confirmed range of the chimpanzees suggested these apes had most likely travelled from Bulindi, and not from further north. Nevertheless, since these sightings could have been of neighbouring apes they were disregarded. There was no evidence of the existence of neighbouring communities to the east and south of the study area, and all chimpanzee sign encountered within the hills of Kandanda–Ngobya FR (hereafter 'Kandanda') were assumed to be of the Bulindi study community.

Nest Group Size

Although some habituation occurred during the study, direct observation of chimpanzees was limited to a variable number of opportunistic or chance encounters each month. In many encounters party size could not be counted due to poor visibility in dense undergrowth (Chapter 8). I therefore used data on nest group size in order to assess monthly changes in grouping patterns. A drawback to this approach is that while nest groups reflect late evening and early morning party size, they do not necessarily correspond to daytime party size (Yamagiwa et al. 1996; Ogawa et al. 2007). Three age classes of nests were distinguished based on Tutin and Fernandez (1984): *Fresh nests* were less than two days old with only green healthy leaves and, typically, dung and urine below. *Recent nests* were two days to about two weeks old and contained wilted green and browning leaves. Disintegrating nests or those consisting solely of brown, dried leaves were *old*. Only data on fresh and recent nests – for which the date of construction was known or could be approximated – are presented here. In addition to night nests, chimpanzees occasionally build day nests for resting. Although day nests are usually small and weakly constructed relative to night nests (Brownlow et al. 2001), direct observation of day nest building at Bulindi showed that some day nests were indistinguishable from night nests. Therefore day and night nests were not differentiated in this study.

A *nest group* is a close spatial aggregation of same-age nests, assumed to have been built on the same night (Fruth and Hohmann 1996). The nest group size corresponds to the number of weaned individuals in the night-time party, since dependent offspring share their mother's nest. Previous authors have variously considered all same-age nests separated from the nearest nest by an arbitrary maximum gap of 20–50 m to belong to the same nest group (Furuichi et al. 2001b; Basabose and Yamagiwa 2002; Morgan et al. 2006; Moscovice et al. 2007; Ogawa et al. 2007). In this study, a nest group is defined as all nests made on the same evening and found within 30 m from the nearest other nest (following Furuichi et al. 2001b). In a study of nest groups in bonobos (*Pan paniscus*), Mulavwa et al. (2010) found that 30 m was an appropriate cut-off value since the frequency of nest groups in which the largest gap among nests exceeded 25 m was considerably lower than in the 10–15, 15–20 and 20–25 m classes. At Bulindi, the sizes of only a small proportion of nest groups were likely underestimated using this method. Although we attempted to locate all nests in a group, nest group sizes may have been underestimated in dense vegetation if some nests were undetected. I did not determine nest group size if there was reason to suspect a cluster of same-age nests was built on >1 night, as when chimpanzees nested at the same site on consecutive nights, or if there was uncertainty regarding re-use of older nests.

Nests were located opportunistically and by searching areas where chimpanzees were heard or seen. Phenology surveys provided an opportunity to encounter nests in each of the main forest patches in the absence of specific knowledge of recent use by chimpanzees. Since the phenology trail was walked fortnightly (Chapter 4), each forest was visited twice per month regardless of whether or not chimpanzees were known to have used it. While phenology trails passed extensively through patches, one area habitually utilised by the apes was not covered by phenology surveys. This was the Nyakakonge sector of Mparangasi–Nyakakonge, which was permanently wet and difficult to access. Nests were recorded in this part of the forest only when intermittent visits were made. Likewise, small forest patches outside the main fragments, such as in Kandanda, were visited on an irregular basis.

7.2.2. Data Analysis

Estimation of Home Range Size

GPS readings of the locations of all nests, dung, and encounters, together with selected locations of feeding traces, trails and road-crossing points, were entered into a geographic information system (ArcGIS version 9.3). Home range size was estimated using the 100% minimum convex polygon (MCP) method, which links external points to create the smallest area polygon encompassing all locations; the polygon's area is then calculated. I employed this simple method because, unlike statistical techniques such as kernel analysis, it does not require independent data points such as can be obtained through systematic sampling during follows of habituated animals (Newton-Fisher 2003; Amsler 2009), and is appropriate for presence-only data. Although the MCP method has well-known limitations, for example its sensitivity to outlying locations may result in overestimation of range size (Harris et al. 1990; Burgman and Fox 2003; Pimley et al. 2005; Grueter et al. 2009; but see Boyle et al. 2009), it is widely used in primate ranging studies (e.g. Robbins and McNeilage 2003; Harris and Chapman 2007; Ren et al. 2009; White et al. 2010; chimpanzees: Herbinger et al. 2001; Newton-Fisher 2003; Lehmann and Boesch 2003; Wilson et al. 2007; Amsler 2009), and is comparable across studies (Harris et al. 1990).

Because the polygon may include areas never visited by the animal, Grueter et al. (2009) recommended adjusting the MCP method by superimposing a grid over the polygon and clipping out cells that are never entered or constitute unsuitable habitat. This is a variation of the standard grid cell method wherein home range size is calculated from the number of cells visited (Hasegawa 1990; Basabose 2005). While at Bulindi ‘unsuitable’ parts of the polygon might conceivably include areas of busy human activity such as villages, schools and trading centres, chimpanzees made forays into village areas across the study site (and were once seen by residents at dawn eating figs at the main Bulindi trading centre); therefore all areas encompassed by the MCP were considered potentially suitable for the apes. Since follows of chimpanzees were not undertaken, knowledge of their travel routes outside of most frequently used areas was limited, and evidence of their use of peripheral locations (e.g. in Kandanda) came mainly from a small number of widely distributed nest sites. The standard grid cell method would therefore underestimate range size since many outer cells would be blank. Grid cell methods were thus not applied.

Three MCPs were calculated: the first encompassed 100% of locations for which there was direct evidence of use by chimpanzees (*confirmed range*); a second incorporated several outer locations apparently visited by the chimpanzees, according to reliable local information, but for which supporting evidence (e.g. nests, dung) was not found (*probable range*). While the 100% MCP method returns an estimate of the total area utilised by the chimpanzees during the study, it provides no information about the intensity of use of different parts of the range. A third polygon was therefore calculated to estimate *core area* size. Chimpanzee researchers have variously defined core area as that part of the range including 50%–80% of locations (e.g. Herbinger et al. 2001;

Amsler 2009), but since the Bulindi data were not derived from independent data points this method was not applicable. Instead, I defined core area as those parts of the range utilised by chimpanzees in ≥7 months between December 06 and December 07 (i.e. >50% months), when all main forests were visited twice monthly for phenology surveys. Further to information from dung, sightings and vocalisations, 'use' required that chimpanzee parties nested in the forest patch on ≥1 night during the month; at times travelling parties passed quickly through forest patches apparently without foraging.

Food Availability

Chimpanzee nesting and ranging patterns were assumed to be influenced by food species that constitute a regular component of the diet at particular times of the year (Furuichi et al. 2001a; Basabose and Yamagiwa 2002). I therefore modified the monthly forest fruit availability index (FAI) calculated in Chapter 4 by excluding eight phenology species for which there was no evidence of consumption by chimpanzees during this study. Also excluded were three species eaten at negligible frequencies, for which patterns of availability were presumed to have exerted no influence on grouping and range use by chimpanzees. (These were *Macaranga schweinfurthii*, *Maesopsis eminii* and *Pycnanthus angolensis*, the residues of each occurred in just 1–2 dung specimens). Four fig species which were not confirmed eaten were retained, however, because circumstantial evidence (e.g. discarded fig 'wadges' and/or fresh nests in the vicinity of fruiting trees) strongly suggested chimpanzees did eat the fruits when available. The retained species (*n* = 19) comprised nine figs and ten non-figs, including seven that were categorised as 'important' food species based on faecal analysis (see Chapter 5) (Table 7.1).

In previous analyses I used a monthly FAI derived from visual estimates (ranks) of ripe fruit crop size. (The methods employed to measure food availability at Bulindi were described in Chapter 4). For this chapter a simpler measure based on presence/absence of ripe fruit was used. This was because separate FAIs were also calculated for individual forest patches to determine if seasonal variation in food availability among patches influenced their use by chimpanzees (see below). As described in Chapter 4, phenology trees were distributed along a fruit trail that included forest patches across Bulindi, and in most cases the sample of trees of each species per patch was too small to calculate individual FAIs using ranked data. Instead, for each species the overall proportion of monitored individuals with fruit was assumed representative of the proportion of fruiting specimens within individual patches. For consistency, presence/absence data were also used to calculate the overall (habitat-wide) FAI of chimpanzee foods. While the magnitude of peaks and troughs in seasonal food availability may be less apparent with presence/absence data compared with ranked data, FAIs derived from both measures were in fact highly correlated (Chapter 4).

The monthly forest fruit availability index of chimpanzee foods (CF_m) is calculated as:

$$CF_m = \sum_{k=1}^{n} P_{km} \times D_k \times S_k$$

where P_{km} denotes the proportion of individuals with ripe fruit in species k during month m, D_k denotes the density (stems ha $^{-1}$) of adult trees of species k, and S_k is the mean size in centimetres DBH of adult trees of species k (e.g. Fawcett 2000; Mitani et al. 2002).

Table 7.1. Tree species included in the fruit availability index of known chimpanzee foods. For non-figs, the main period of consumption during 2007 is listed as indicated by faecal analysis; figs were eaten at a high frequency year-round but it was not possible to distinguish species in the dung.

Phenology Species	**Main period of consumption**
Non-figs	
1. Annona senegalensis Pers.	Aug
2. Antiaris toxicaria Leschen. *	Mar–May
3. Morus mesozygia Stapf *	Mar
4. Parkia filicoidea (Welw. ex) Oliv. *	Apr–May
5. Phoenix reclinata Jacq. *	Jan–May, Jul–Aug
6. Pseudospondias microcarpa (A. Rich.) Engl.*	May–Jul
7. Psidium guajava L. [guava tree] *	Year-round (Sept–Oct peak)
8. Sterculia dawei Sprague	Aug
9. Theobroma cacao L. [cocoa tree] *	Year-round (Aug–Nov peak)
10. Zanha golungensis Hiern	May
Figs	Year-round
1. Ficus exasperata Vahl	
2. Ficus glumosa Del.	
3. Ficus mucuso Ficalho	
4. Ficus natalensis Hochst.	
5. Ficus ovata Vahl	
6. Ficus sansibarica Warb.	
7. Ficus sur Forssk.	
8. Ficus vallis-choudae Del.	
9. Ficus variifolia Warb.	

* Indicates species categorised as ‘important’ in the diet (i.e. occurring in ≥50% of dungs in at least one month or >10% of the total dung sample; see Chapter 5).

The densities of tree species included in the FAI of chimpanzee foods varied considerably among forest patches (Appendix 1). Individual FAIs for the five riverine forests (Kyamalera, Kyamusoga, Kiseeta, Kaawango and Mparangasi–Nyakakonge) were calculated by substituting species density per patch for overall density. The adult density of particular species in individual forests was sometimes unknown if the species was not recorded during the tree survey of the patch or was represented by immature specimens only. But if adult individuals were known to occur, I assigned the species a density half that of the lowest recorded species in the patch. The number of species comprising the FAI for individual patches varied from 12–15 because certain species were absent from each forest. A separate FAI could not be calculated for Katigiro because few monitored species occur in ecotone habitat (Chapter 3); thus Katigiro was excluded from the analysis of the influence of food availability on forest patch use.

To examine nesting patterns in relation to food availability I used a subset of data collected between December 2006 and December 2007, when phenology data were also collected.[1] All analyses were performed on this subset of data unless otherwise indicated. Months were grouped according to whether forest fruit availability was at high or low levels to assess whether nest group size varied according to seasonal food abundance. High and low fruit availability months were identified by standardising the monthly FAI scores as Z-values: high fruit months were those with scores above the mean (positive values) while low fruit months were those with scores below it (negative values). Defined in this way, December–April and June–August had high fruit availability and May and September–December had low fruit availability (Figure 7.1).

As noted above, the size of nest groups was not always determined. In particular, nests recorded in April were often in groups of undetermined size because chimpanzee parties nested repeatedly in a narrow strip of swamp forest in Kyamalera; the concentration of similarly-aged nests (including nests that were probably re-used) frequently made nest group counts impractical. Consequently, data for April are biased against large-sized nest groups, and I excluded this month in analysis of nest group size.

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[1] Though phenology was also recorded in January 08, too few nests were recorded in that month to include in the analysis (*n* = 6).

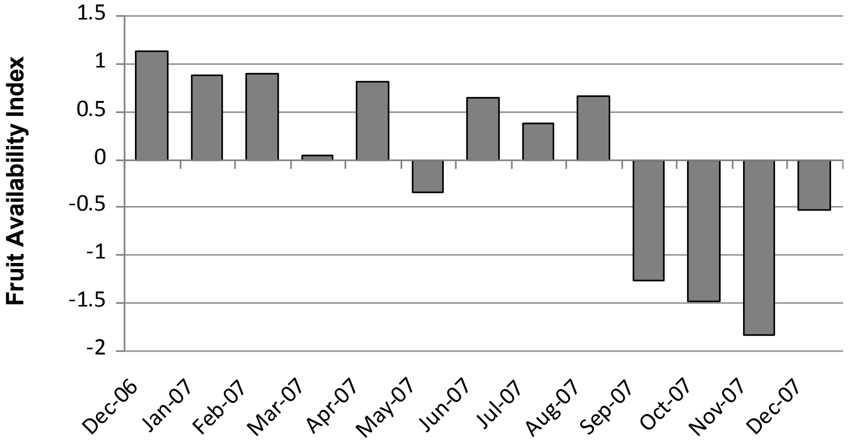

Figure 7.1. Monthly availability of ripe forest fruit shown as standardised Z-values (Dec 06–Dec 07). The mean monthly value is 0. Only known chimpanzee foods are included in the index. Positive values are categorised as months of high fruit availability; negative values are months of low fruit availability.

Range Use

The geographic coordinates of nests, dungs and chimpanzee encounter sites recorded monthly were entered into ArcGIS and plotted on maps of the study area to depict monthly patterns of range use graphically. Recent nests encountered in the initial days of a month were attributed to the preceding month. While chimpanzees were heard vocalising most days, the locations of parties were not georeferenced unless a documented encounter ensued. Prior to June 07 not all dungs collected by field assistants were georeferenced.

Nests were used as a proxy for forest use. Though chimpanzees sometimes travelled between forest patches late in the afternoon and evening prior to nesting, in any month forests frequently used by the apes during the daytime were generally where nest sites were also located. Thus, intra- and inter-forest variation in the number of nests recorded each month is assumed to reflect real differences in intensity of use. Two measures of use were calculated for each of the five riverine forest patches: (i) the proportion of nests recorded per month as a percentage of the total number of nests recorded in the patch; and (ii) the percentage of the total monthly sample of nests recorded across the apes' range that occurred in the patch. Whereas the first measure is used to evaluate monthly changes in the intensity of use within patches, the second provides a measure of use relative to other forest patches. Nests that were recorded in gardens outside of forest but in proximity to a main patch were assigned to that patch for the analysis.

Statistics

The Mann–Whitney *U* test was used to test the null hypothesis that median nest group size did not differ between months of high versus low fruit availability. I used regression analysis to examine the relationship between dependent variables and one or more independent (predictor) variables. Simple regression was used to test the effect of availability of chimpanzee fruit foods on monthly nest group size. Since the overall availability of all phenology species was found to correlate negatively with the proportion of non-seasonal fruit cultivars (banana, cocoa, guava, papaya, passion fruit) in dung (Chapter 5), nesting patterns might be influenced by consumption of these cultivars. I therefore performed a multiple regression with the monthly FAI of chimpanzee foods and mean % fruit cultivars in dung as independent variables (IV) to assess their simultaneous and individual effect on nest group size. A multiple regression was also conducted to determine the effects of chimpanzee food availability and non-seasonal cultivar consumption on monthly variation in % nests recorded within each of five riverine forests. In each analysis three IVs were entered into the model: the FAI for the individual forest patch, the overall (habitat-wide) FAI, and mean % fruit cultivars in dung. Since dung data were unavailable for December 06, all analyses that include this measure of cultivar consumption as an IV are for the period January–December 07.

In all multiple regressions the backward stepwise method was employed, as outlined in Chapter 5. The residuals of dependent variables were inspected for normality using Kolmogorov–Smirnov and Shapiro–Wilk tests. If non-normality was confirmed by either test, log-10 transformations were applied to IVs (Chen et al. 2003; Field 2005). Variables expressed as percentages were converted to proportions and transformed to arcsine square roots unless all values fell below 30%, in which case standard square root transformations were applied (Ahrens et al. 1990). In all tests collinearity statistics generated in SPSS indicated no problems associated with collinearity or multicollinearity, and the Durbin–Watson statistic showed that the assumption of independent errors was met. The analyses were performed with SPSS Version 17. All tests were two-tailed and $p < 0.05$ indicated significance.

7.3. Results

7.3.1. Home Range Size and Core Area

The chimpanzees had a *confirmed* range of 21.0 km^2 during October 06–January 08, and a *probable* range of at least 24.6 km^2, if unconfirmed locations where local people reported seeing chimpanzees travelling from Bulindi are included (Figure 7.2). These are minimum estimates: for example, the extent of the chimpanzees' ranging within Kandanda is unknown but is almost certainly greater than suggested by positions of nest sites. The estimated core area was 4.6 km^2, equivalent to 22% of the confirmed range (or 19% of the probable range). This core area included all the main forest patches, except Kaawango (Figure 7.2).

7.3.2. Nest Group Size and Food Availability

A total of 1247 fresh or recent nests were recorded. Mean nest group size was 3.1 ± 2.6 SD (range: 1–15; n = 296 nest groups for which number of nests was determined). This value is close to the average size of chimpanzee nest groups recorded across a range of habitats at 14 other sites (mean = 3.3 ± 1.3; Table 7.2). During the 13-month period when both phenology and nest data are available (December 06–December 07; n = 1094 nests), an average of 84 nests were recorded monthly (range: 44–118) and mean nest group size was equivalent to that for all study months (3.2 ± 2.6). While nest group size did not vary significantly across months (Kruskal–Wallis test: $H = 15.85$, $df = 12$, $p = 0.20$), nest groups were significantly larger in months of low fruit availability compared with months when fruit availability was high (median size: low = 3.0; high = 2.0; Mann–Whitney: $U = 5106.5$, $p = 0.013$) (Figure 7.3). The highest mean nest group size was recorded in November 07 (= 5.0), when availability of ripe fruits was at its lowest point in the study. The monthly FAI of chimpanzee food species was a significant negative predictor of nest group size ($R^2 = 0.575$, $F_{1,11} = 13.55$, $p = 0.004$).

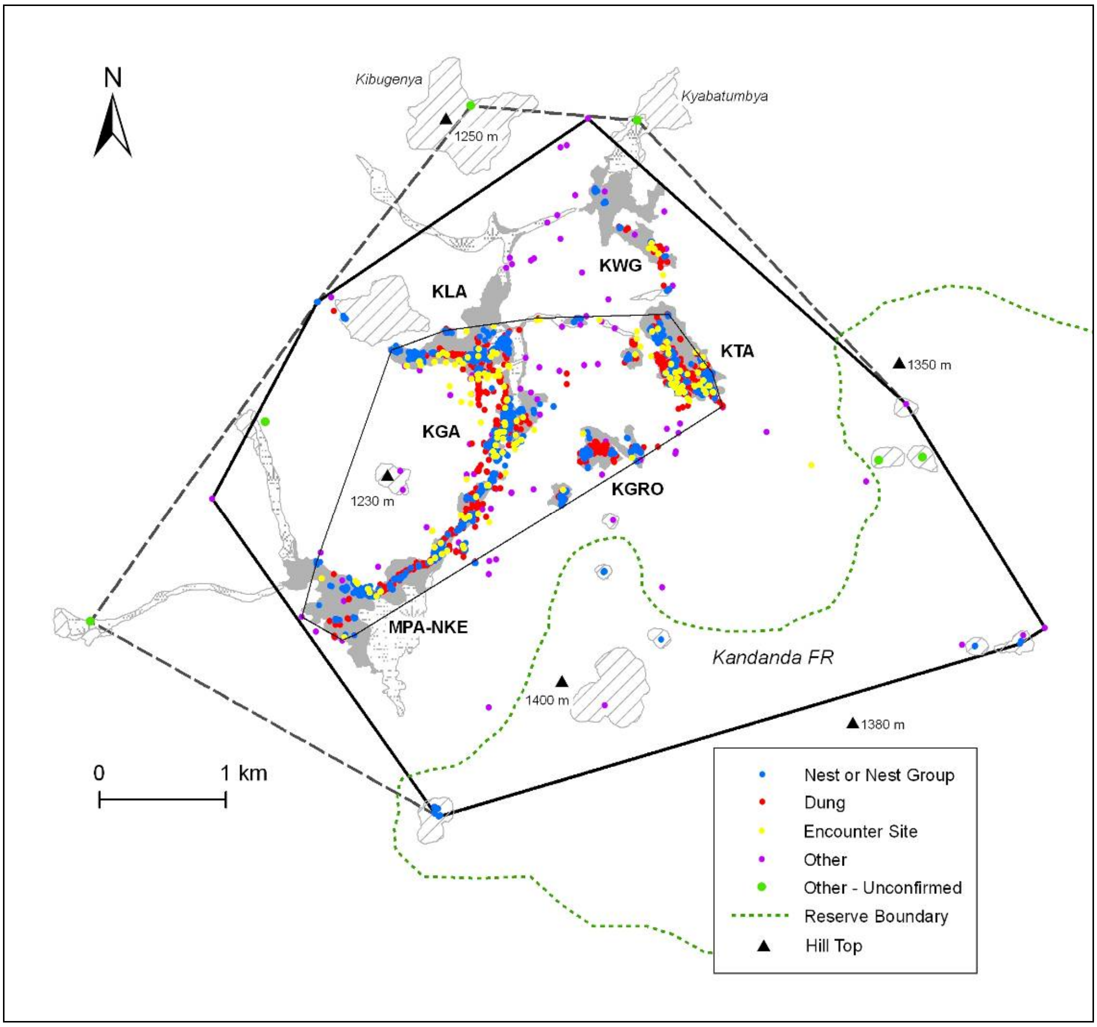

Figure 7.2. Home range of Bulindi chimpanzees based on GPS readings of nests, dung and encounter sites (Oct 06–Jan 08). 'Other' positions are the locations of feeding traces, crop-raiding events and chimpanzee trails. 'Unconfirmed' positions are several outlying sites where chimpanzees were locally reported, but for which evidence was lacking. Home range polygons were calculated via the minimum convex polygon (100%) method: *confirmed* range (thick middle polygon; 21.0 km^2); *probable* range including the unconfirmed locations (dashed outer polygon; 24.6 km^2); *core area* (thin inner polygon; 4.6 km^2). Main forest patches (grey fill): KLA = Kyamalera, KGA = Kyamusoga, KTA = Kiseeta, KWG = Kaawango, MPA–NKE = Mparangasi–Nyakakonge, KGRO = Katigiro. Hatched areas represent patches of forest or forest–woodland in peripheral parts of the range. The Kandanda–Ngobya FR boundary is an approximation.

Table 7.2. The average size of chimpanzee nest groups at various sites, arranged in descending order of mean nest group size. The Bulindi data are emboldened. A dash indicates that the value was not reported.

Study site	Country	Habitat	No. nests	No. nest groups	Mean nest group size	Range	Reference
Gashaka	Nigeria	Forest woodland	–	38	5.7	1–23	Sommer et al. (2004)
Ugalla	Tanzania	Savanna–woodland	563	104	5.4	1–23	Ogawa et al. (2007)
Semliki	Uganda	Riverine forest–savanna	348	–	5.0	1–12	Hunt and McGrew (2002)
Kahuzi-Biega	DRC	Montane forest	310	72	4.3	1–15	Basabose and Yamagiwa (2002)
Kalinzu	Uganda	Medium altitude forest	1159	315	3.7	–	Furuichi et al. (2001b)
Rubondo	Tanzania	Medium altitude forest	–	138	3.4	1–19	Moscovice et al. (2007)
Bulindi	**Uganda**	**Riverine forest–farmland**	**930 ***	**296**	**3.1**	**1–15**	**This study**
Goualougo	Rep. Congo	Lowland rainforest	972	375	2.8	1–12	Morgan et al. (2006)
Motaba River	Rep. Congo	Lowland rainforest	150	55	2.7	–	Kano and Asato (1994)
Mbaéré-Bodingué	CAR	Lowland rainforest	155	58	2.7	1–8	Brugiere et al. (2005)
Lac Télé	Rep. Congo	Lowland swamp forest	486	197	2.5	1–11	Poulsen and Clark (2004)
Ntakata	Tanzania	Savanna–woodland	154	61	2.5	1–15	Ogawa et al. (2006)
Petit Loango	Gabon	Coastal forest	323	154	2.1	–	Furuichi et al. (1997)
Various sites	Gabon	Lowland rainforest	1606	896	1.8	1–10	Tutin and Fernandez (1984)
Campo–Ma'an	Cameroon	Lowland rainforest	196	124	1.6	1–7	Matthews and Matthews (2004)

* No. nests at Bulindi is a subset of the total nests recorded during the study ($N = 1247$) because nest groups could not always be distinguished.

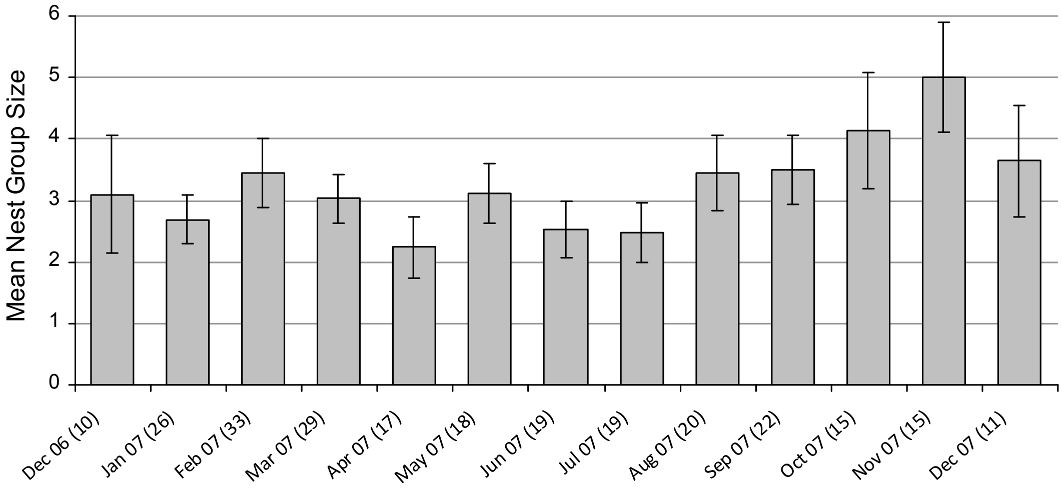

Figure 7.3. Monthly variation in mean (± SE) nest group size (Dec 06–Dec 07). Monthly sample sizes (no. nest groups) are shown in parenthesis below bars. The low value for April 07 may be spurious because in that month nest group size was frequently undetermined due to repeated nesting by chimpanzees at the same site. Months with lowest forest fruit availability were September–November.

Dietary analysis showed that the overall representation of non-seasonal fruit cultivars in dung increased when availability of forest fruits was low and chimpanzees ate less fruit (Chapter 5). In fact, the significance of the negative correlation is strengthened considerably when the monthly FAI comprises known chimpanzee foods only (R^2 = 0.689, $F_{1,10}$ = 22.12, p = 0.001). A multiple regression of the effects of the FAI and cultivar consumption on nest group size was overall significant (R^2 = 0.685, $F_{2,8}$ = 8.68, p = 0.01). However, the second model to emerge was not significantly strengthened by the inclusion of the FAI and only 'mean % fruit cultivars in dung' was retained (R^2 = 0.637, $F_{1,9}$ = 15.77, p = 0.003). Therefore monthly changes in the representation of non-seasonal cultivars in dung seemed to have more influence on nest group size: larger nest groups were recorded when chimpanzees fed most heavily on these cultivated fruits (Figure 7.4).

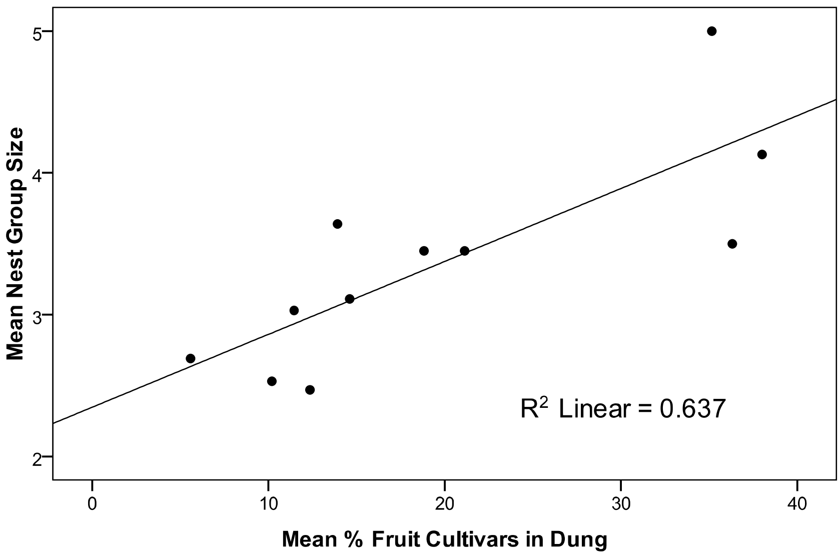

Figure 7.4. Relationship between the monthly mean % fruit species in dungs that were non-seasonal cultivars and nest group size (Dec 06–Dec 07). Data for April 2007 are excluded because the sizes of many nest groups in that month were undetermined.

7.3.3. Nest Distribution

Between October 06 and January 08 nests were recorded in all main riverine forests as well as in smaller ecotone patches, principally in Katigiro but also within Kandanda (Plate 13). Chimpanzees occasionally nested outside of forest in small thickets or in gardens, most commonly within a large banana plantation by Mparangasi forest. Figure 7.5 shows the proportion of the total sample of fresh and recent nests recorded in each main forest patch and also within Kandanda. Overall, the largest number of nests was recorded in Mparangasi–Nyakakonge (27%). Even so, the apes' use of this forest for nesting was under-estimated overall because the swampy Nyakakonge sector, which was not covered by the phenology trail, was visited infrequently by the research team although it was regularly utilised by chimpanzees; consequently, most nests were recorded in the drier Mparangasi gallery forest sector. Similar numbers of nests (19–20% of the sample total) occurred in three other riverine patches (Kyamalera, Kiseeta, Kyamusoga), but chimpanzees rarely nested in Kaawango forest (2%). In fact, more nests were recorded in small ecotone patches at Katigiro (8.5%). Nests were also occasionally found in ecotone habitat inside Kandanda FR (Figure 7.5).

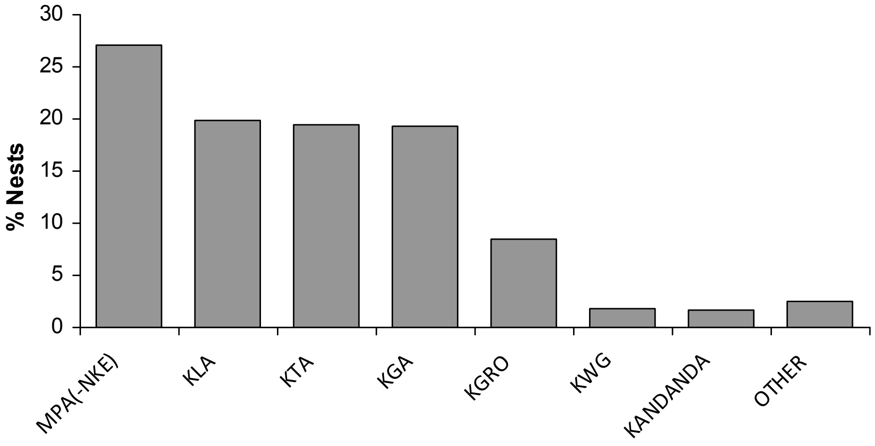

Figure 7.5. The percentage of fresh and recent nests recorded in main forest fragments at Bulindi (Oct 06–Jan 08; $N = 1247$): MPA(–NKE) = Mparangasi(–Nyakakonge); KLA = Kyamalera; KTA = Kiseeta; KGA = Kyamusoga; KGRO = Katigiro; KWG = Kaawango. ‘Kandanda’ is the Kandanda–Ngobya Forest Reserve. ‘Other’ refers to nests recorded in other locations such as gardens or small thickets outside main forests.

The Relationship Between Nesting and Fruit Availability in Patches

Multiple regression analysis indicated a predictive relationship between measures of food availability or cultivar consumption and monthly changes in the relative proportion of nests recorded within three of the five riverine patches. In each case a single IV was retained in the final model (Table 7.3). For both Kyamalera and Kyamusoga, food availability within the patch was a significant predictor of changes in the proportion of monthly nests recorded (Kyamalera: $R^2 = 0.517$, $F_{1,10} = 10.68$, $p = 0.008$; Kyamusoga: $R^2 = 0.520$, $F_{1,10} = 10.82$, $p = 0.008$). In contrast, only % fruit cultivars in dung was a significant (positive) predictor for Kiseeta ($R^2 = 0.623$, $F_{1,10} = 16.55$, $p = 0.002$). None of the IVs predicted changes in the proportion of nests found in Mparangasi–Nyakakonge or Kaawango each month.

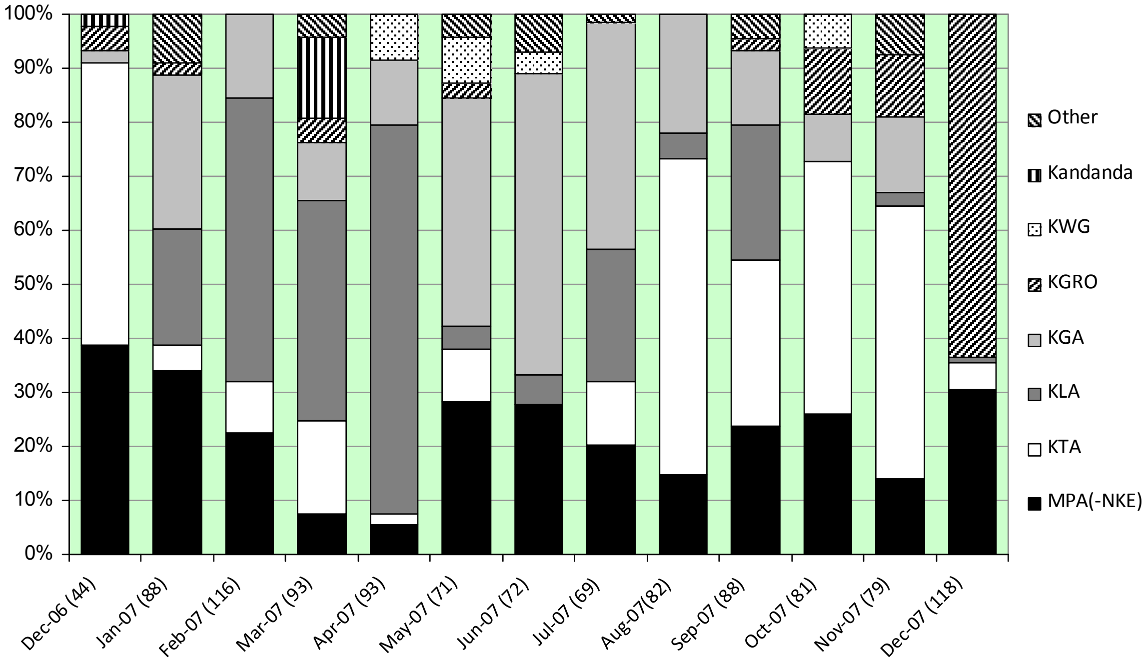

Figure 7.6. Bars show the relative % fresh and recent nests recorded monthly in each forest patch (Dec 06–Dec 07; *n* = 1094): MPA(–NKE) = Mparangasi(–Nyakakonge); KLA = Kyamalera; KTA = Kiseeta; KGA = Kyamusoga; KGRO = Katigiro; KWG = Kaawango. ‘Kandanda’ is the Kandanda–Ngobya FR. ‘Other’ refers to nests recorded in other locations, e.g. gardens or small thickets outside main forests. Nest sample sizes for each month are shown in parenthesis below bars.

The proportion of nests recorded in each forest patch as a percentage of the total monthly sample of nests varied markedly (Figure 7.6). In some months the majority of nests were found in a single forest (e.g. Kyamalera in April, Kiseeta in August and Katigiro in December 07); in others, nests were distributed more evenly among several patches (January and September 07). When the number of nests in each patch was considered as a proportion of the total number of nests encountered within the chimpanzees’ range per month, significant models again emerged only for Kyamalera, Kyamusoga and Kiseeta forests (Table 7.3). The only significant predictor of the overall proportion of monthly nests that occurred in Kyamalera was its individual forest FAI ($R^2 = 0.470$, $F_{1,10} = 8.89$, $p = 0.014$). For Kiseeta, the representation of fruit cultivars in dung remained the only significant predictor ($R^2 = 0.584$, $F_{1,10} = 14.02$, $p = 0.004$). In the case of Kyamusoga, two IVs contributed significantly to the final model ($R^2 = 0.662$, $F_{2,9} = 8.80$, $p = 0.008$): the individual forest FAI and the habitat-wide FAI, though the former had a stronger individual effect (Table 7.3). As with the within-forest analysis, the IVs failed to predict changes in the overall proportion of monthly nests that occurred in Mparangasi–Nyakakonge and Kaawango.

Table 7.3. Multiple regression model parameters. The number of nests recorded in individual forest patches was regressed against food availability and cultivar consumption, when: (A) the monthly number of nests was considered as a proportion of all nests recorded in the patch, and (B) number of nests was considered as a proportion of all nests encountered within the chimpanzees' range per month. Independent variables (IV) are the habitat-wide fruit availability index (FAI) of chimpanzee foods, the FAI of chimpanzee foods in the associated forest patch, and mean % fruits in dungs that were non-seasonal cultivars. A backward stepwise method was used. For each analysis only the final model retaining IVs that contribute significantly to the model is shown. Values are the standardised Beta coefficients (*ß*), which give a measure of the contribution of the IV to the model, together with the values of *t*-tests and their significance. Forest patches: KLA = Kyamalera, KGA = Kyamusoga, KTA = Kiseeta; models for two other forests (Mparangasi–Nyakakonge and Kaawango) were non-significant.

	Forest (significant predictor)	***ß***	***t***	***p***
(A)				
	KLA			
	FAI Chimp Foods (KLA)	0.719	3.269	0.008
	KGA			
	FAI Chimp Foods (KGA)	0.721	3.289	0.008
	KTA			
	% Fruit Cultivars in Dungs	0.790	4.068	0.002
(B)				
	KLA			
	FAI Chimp Foods (KLA)	0.686	2.981	0.014
	KGA			
	FAI Chimp Foods (habitat-wide)	-0.964	-2.359	0.043
	FAI Chimp Foods (KGA)	1.521	3.722	0.005
	KTA			
	% Fruit Cultivars in Dungs	0.764	3.744	0.004

7.3.4. Seasonal Patterns of Range Use

In Figure 7.7 the distribution of fresh/recent nests and dungs, and the locations of encounters, are plotted on maps of the study site for each month between November 06 and January 08. (November and December 06 are combined because data sets are small for those months). The patterns of range use depicted are readily interpretable with reference to the foods dominating the monthly diet (see Table 5.4) and the distribution of these foods in the habitat. Six main seasonal patterns of range use can be distinguished, associated with the fruiting events of several ‘important’ species or, during one season, a shortage of forest fruits. As noted above, the swampy Nyakakonge sector of Mparangasi–Nyakakonge, in the southwest of the chimpanzees’ range, was often utilised by chimpanzees but infrequently visited by the research team; consequently its use is under-represented on the monthly maps.

1. November–December 06: 1st *Pseudospondias* season

Throughout November 06 and December 06 chimpanzees fed heavily on *Pseudospondias microcarpa* fruits, mainly in Mparangasi gallery forest where many large *Pseudspondias* trees had full ripe fruit crops. In late November local people reported seeing chimpanzees high up in the hills in Kandanda. In the same period chimpanzees reportedly fed on mangos at a homestead by the reserve boundary, one km south of Katigiro. A single nest was found nearby in a steep hillside thicket (Figure 7.7a).

2. January–April 07: main *Phoenix* season (high fruiting season)

By January *Pseudospondias* and mango season was over and the chimpanzees fed mainly on *Phoenix reclinata* fruits which had ripened the previous month, as well as figs. During January and February they ranged within swamp forest in Kyamalera, Kyamusoga and Nyakakonge, where *Phoenix* palms occur at high densities (Figure 7.7b,c). In early-January a small party nested on ≥3 consecutive nights in forest–woodland to the west of Kyamalera, and raided sugarcane in an adjacent garden each morning and evening. No further evidence of their use of this forest–woodland was found during the study, though residents reported that the sugarcane was again raided in November.

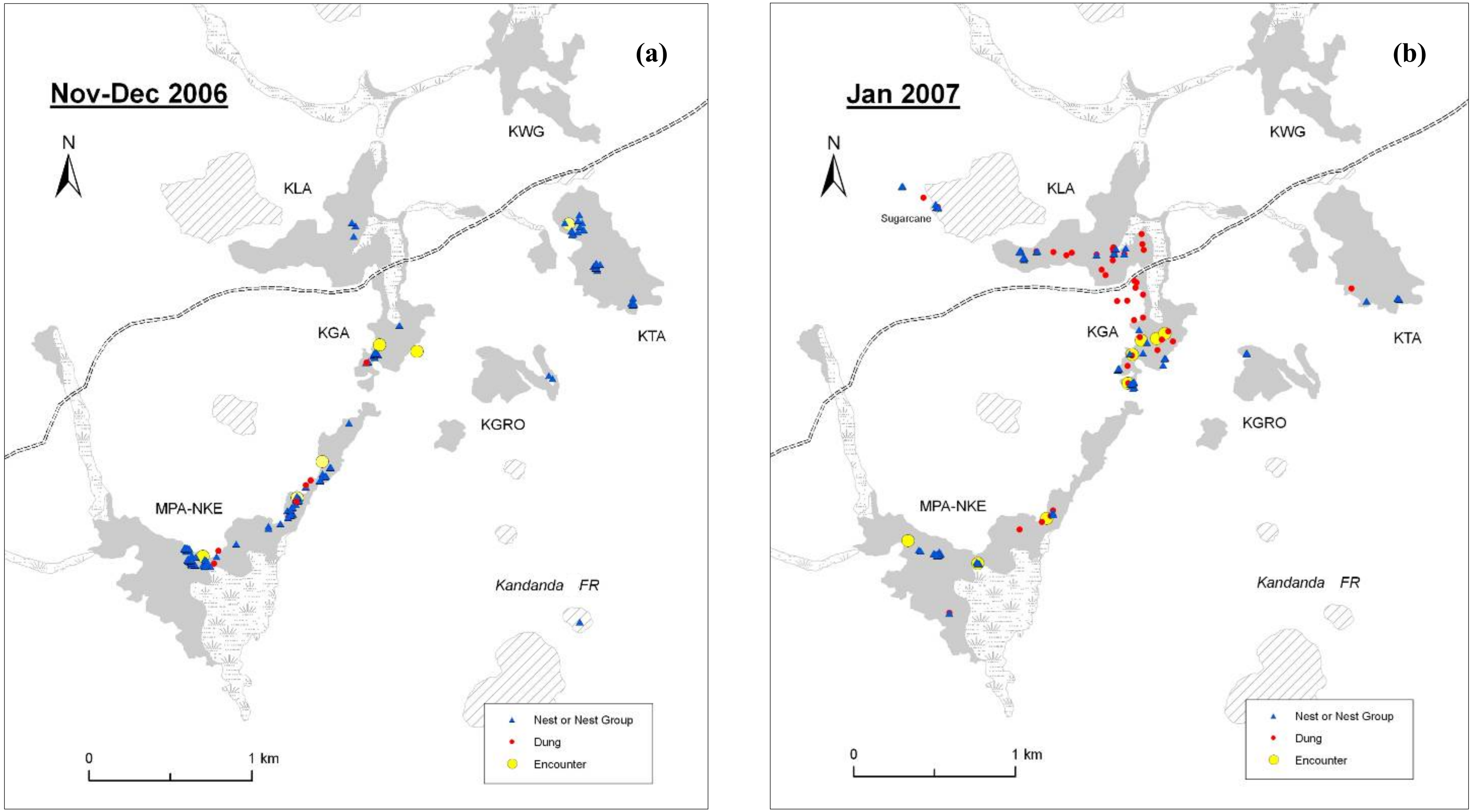

Figure 7.7. Patterns of range use by Bulindi chimpanzees, Nov 2006–Jan 2008 (cont. overleaf). Maps show monthly locations of nests or nest groups encountered, dung specimens collected and encounter sites. Only fresh or recent nests are mapped. Main forest patches (grey fill): KLA = Kyamalera, KGA = Kyamusoga, KTA = Kiseeta, KWG = Kaawango, MPA–NKE = Mparangasi–Nyakakonge (riverine forests), KGRO = Katigiro (ecotone forest). Hatched areas represent additional patches of ecotone forest in peripheral parts of the range. Where ranging was influenced by particular food sources outside of main forest patches (e.g. cultivars), the associated food is indicated on the map.

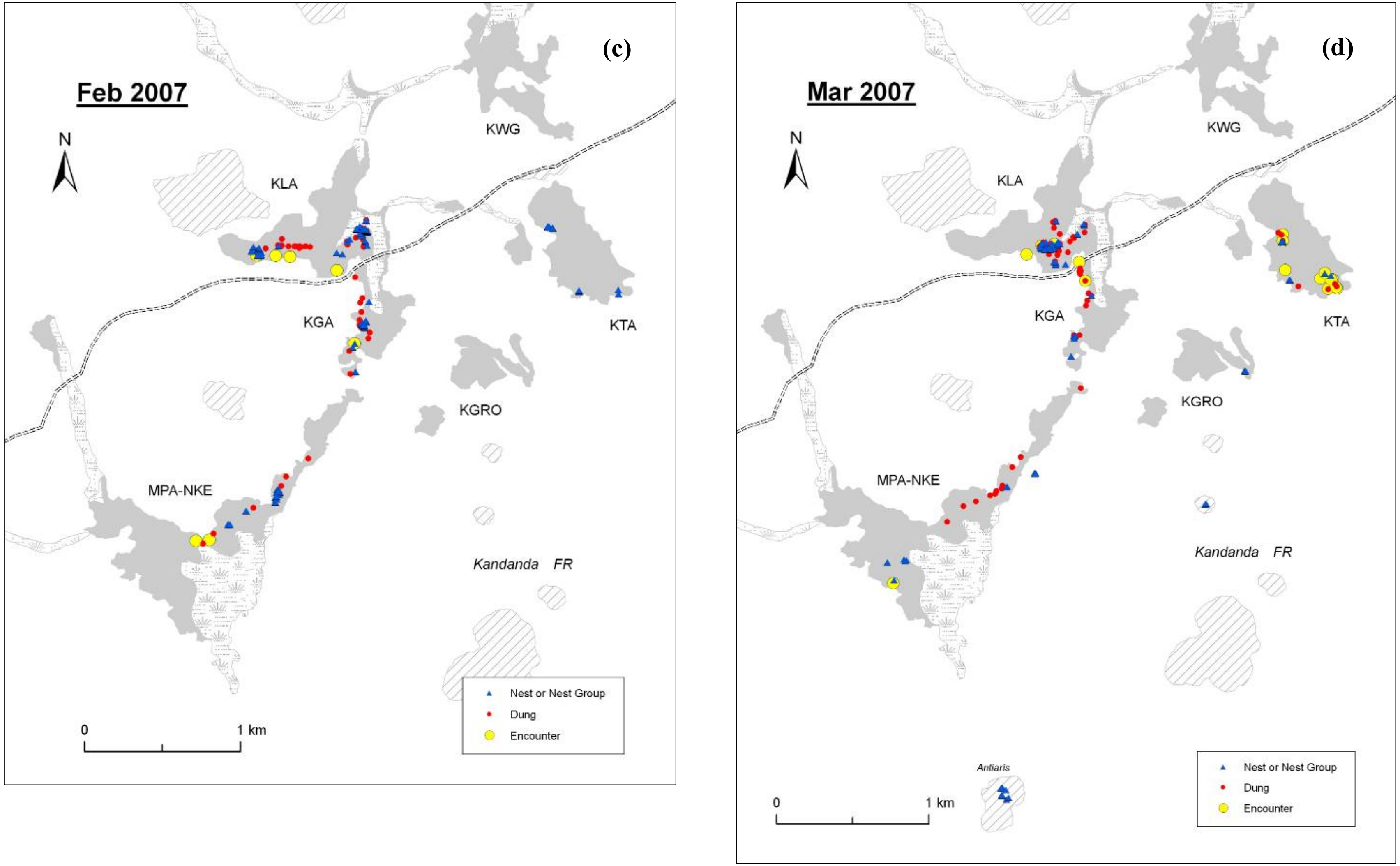

Figure 7.7. *cont*.

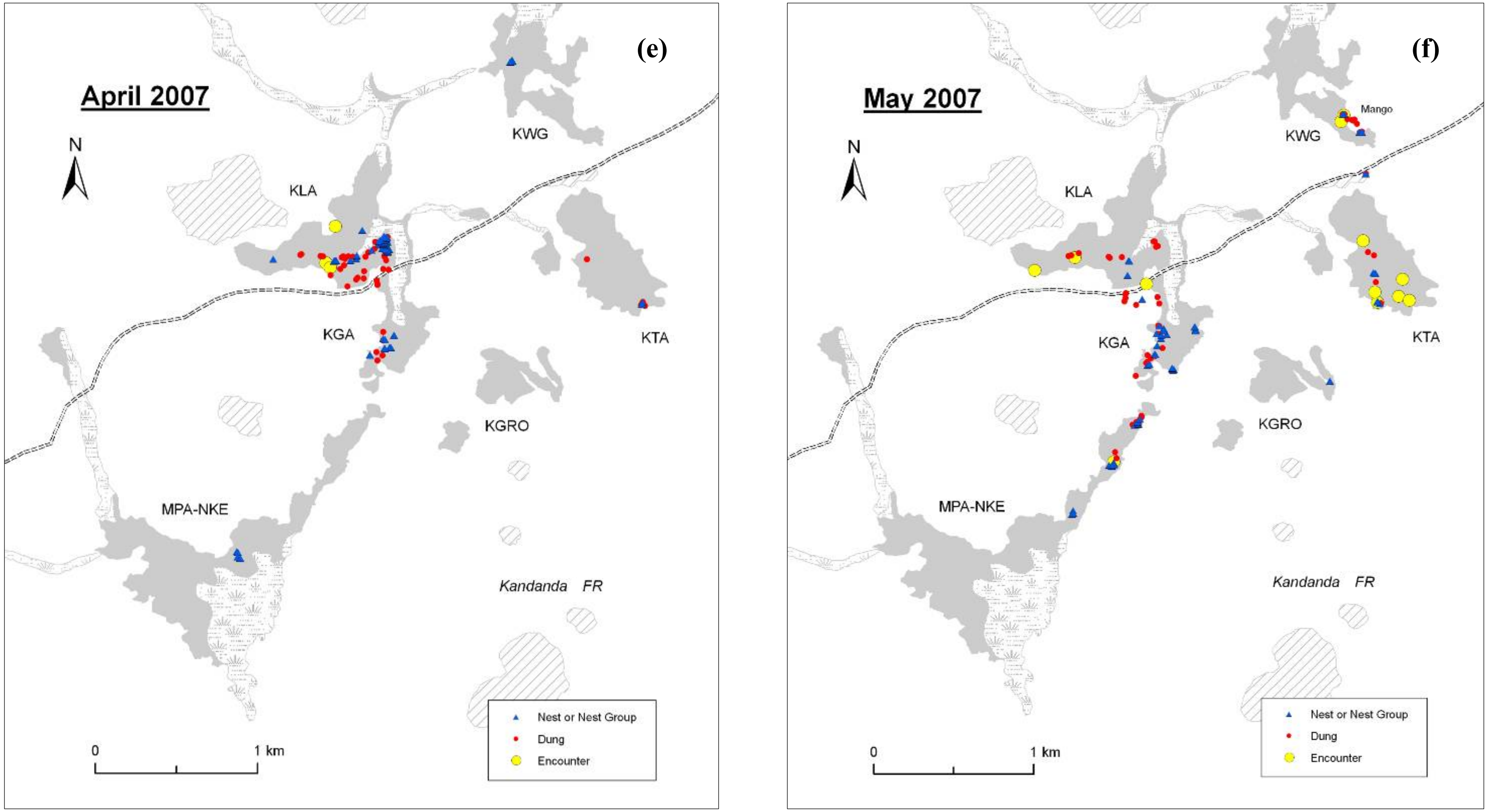

Figure 7.7. *cont*.

Note. Many dung specimens collected in April–May were not georeferenced and thus not shown on the above maps. In April and early May these were mainly in Kyamalera around the swamp, while later in May these were in Kyamusoga and Mparangasi gallery forest.

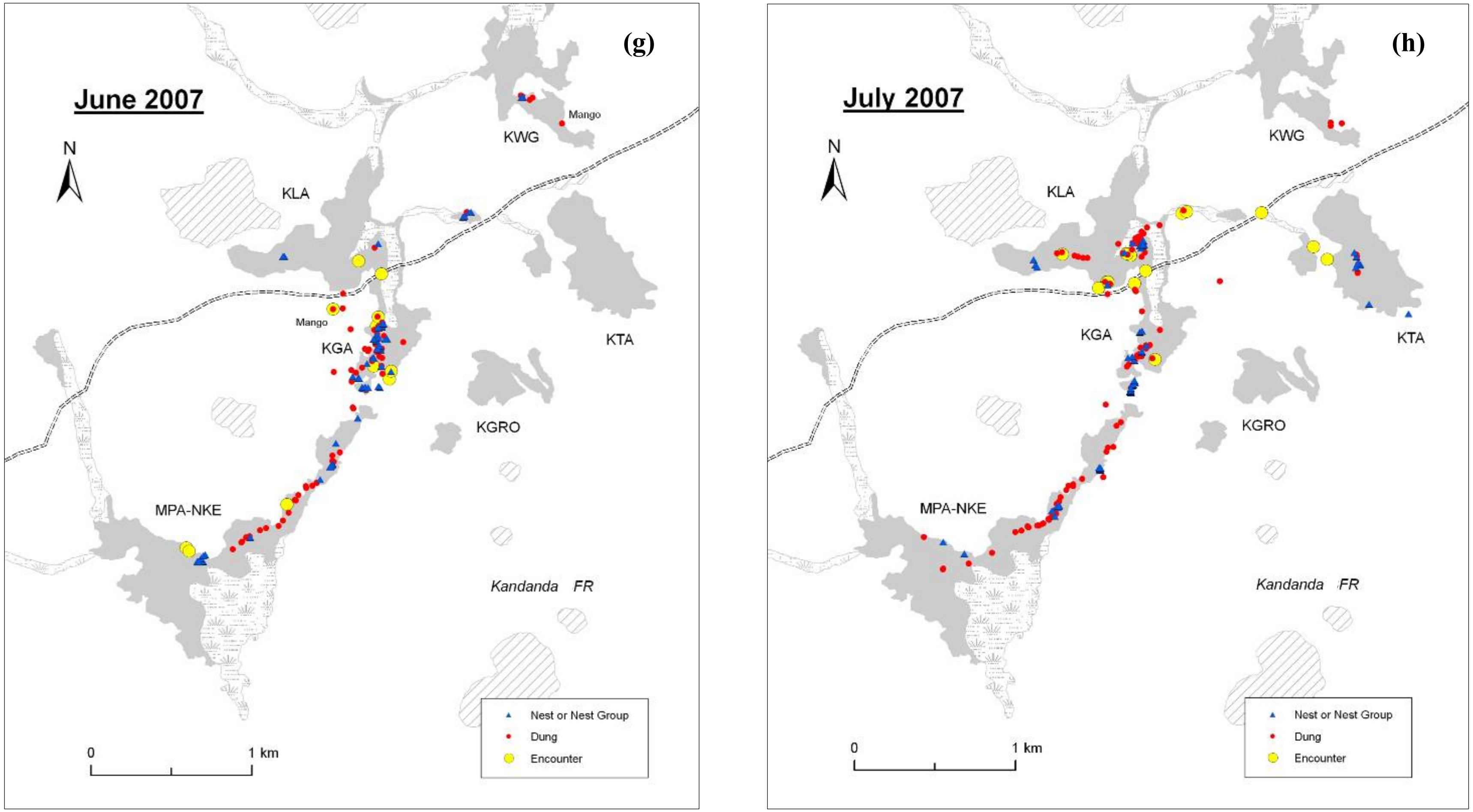

Figure 7.7. *cont*.

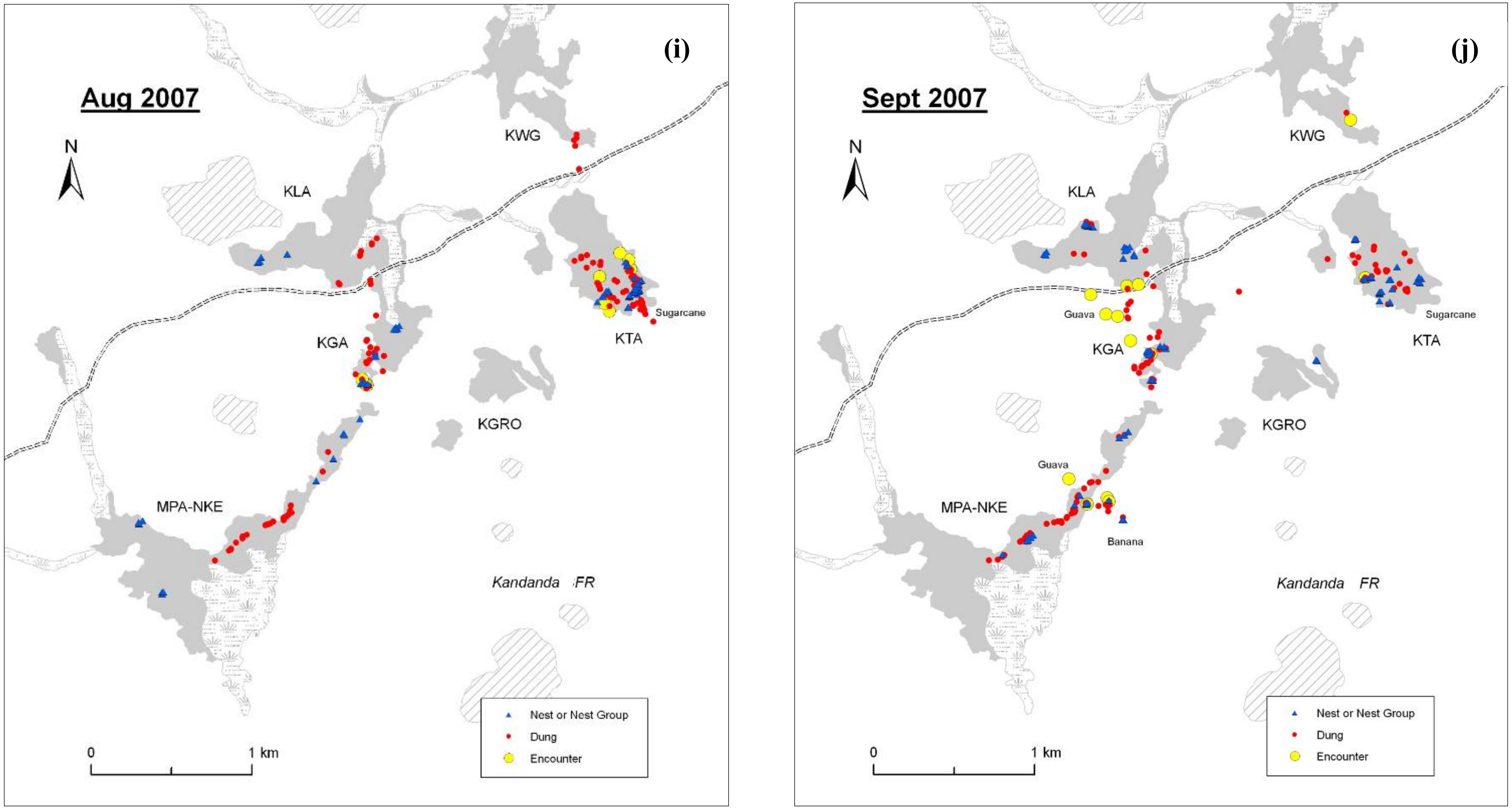

Figure 7.7. *cont.*

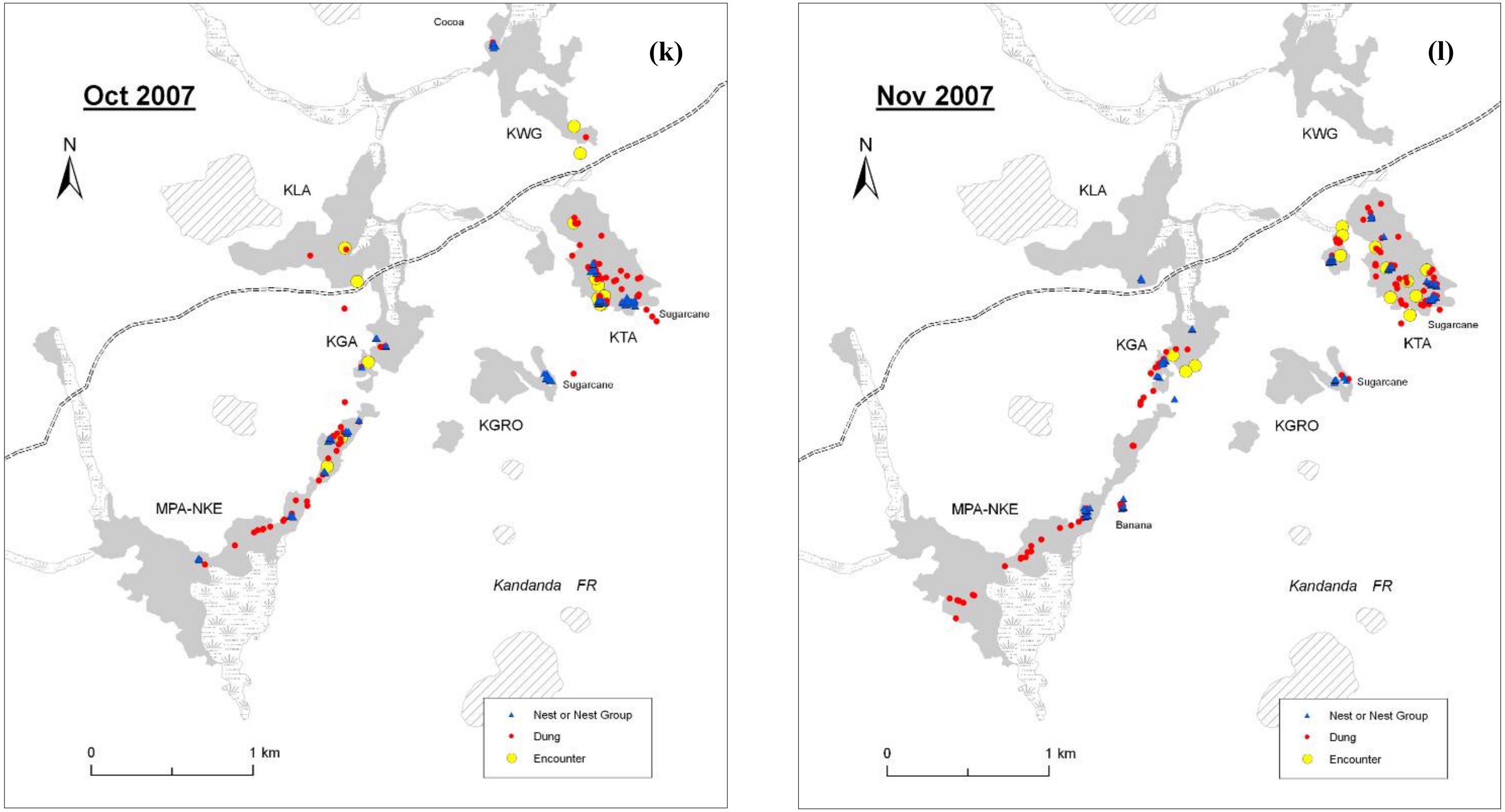

Figure 7.7. *cont*.

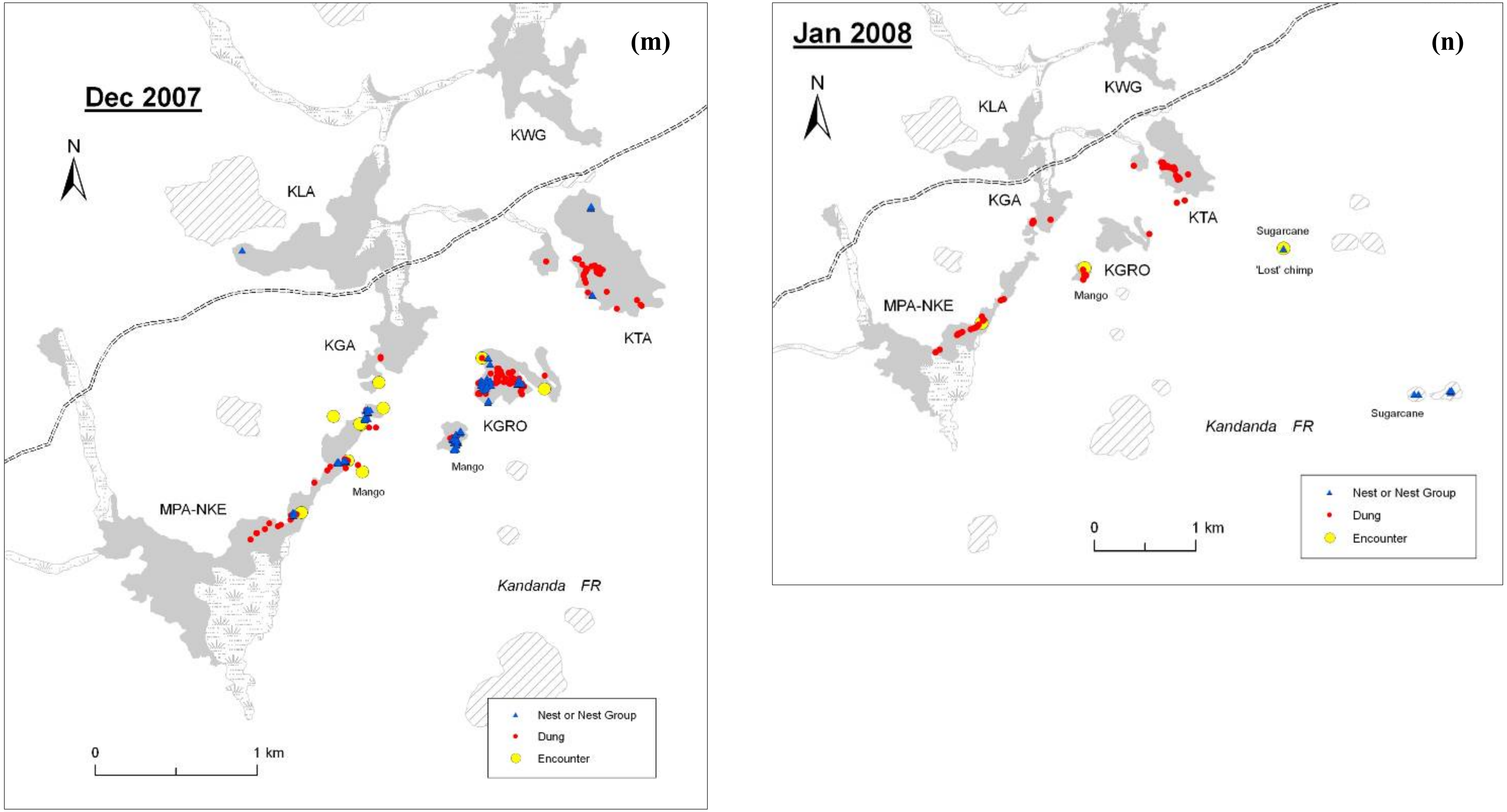

Figure 7.7. *cont*.

During March chimpanzee parties were usually located in swamp forest in Kyamalera. While they continued to feed heavily on *Phoenix* fruits, they also ate ripe fruits of *Antiaris toxicaria*; a number of large fruiting *Antiaris* occurred near the swamp where the forest was unlogged. In mid-March local people reported seeing chimpanzees in the hills of Kandanda and nests were found in two patches within the reserve, separated by 2.5 km. It appeared the chimpanzees were searching for fruiting *Antiaris* trees: in one patch ten recent nests were in the vicinity of several *Antiaris* with ripe fruit crops. This patch is located south of Nyakakonge and represents the southernmost limit of the chimpanzees' confirmed range (Figure 7.7d). In late March or early April chimpanzees were reported in a different part of the reserve, 1.5 km east of Kiseeta forest, but a subsequent exploration of the area yielded no nests. Several times in March chimpanzees were encountered in Kiseeta feeding on ripe fruits of *Morus mesozygia*, which was not seen with fruit in other forest patches.

In April the chimpanzees continued to forage predominantly within a small area of swamp forest in Kyamalera where large *Parkia filicoidea* trees had come into fruit. *Phoenix* palms were still fruiting heavily, as was the understorey shrub *Dovyalis macrocalyx*, and chimpanzees ate all three species in large quantities. While habitat-wide fruit availability was estimated to be at equally high or higher levels in December 06–February 07 (during the peak fruiting phase of *Phoenix*), the simultaneous local abundance of several 'important' fruit foods in this part of Kyamalera during April was probably at the highest point in the study. Throughout April chimpanzees nested in a narrow band of *Phoenix–Macaranga* forest extending into the papyrus swamp. Aside from adjacent Kyamusoga, little evidence suggested they used other forests at this time (Figure 7.7e). At the end of April a small party nested on two consecutive nights in Kaawango – the first evidence of chimpanzees in that forest since the start of the main study in October.

3. May–June 07: 1st mango and 2nd *Pseudospondias* season

Estimated forest fruit availability dropped dramatically in May: *Parkia* and *Dovyalis* seasons were over and few *Phoenix* palms remained with fruit. The chimpanzees ranged more evenly among forest patches, feeding on fruits of the invasive shrub *Lantana camara*. The frequency of guava seeds in dungs increased at this time though the source of the fruits was unknown. From mid-May to early June, small parties made frequent journeys to Kaawango to feed on an ornamental variety of mango at a homestead bordering the forest (Figure 7.7f); these trees fruited earlier than other mango trees in the chimpanzees' range. The concentration of activity in Kyamusoga and Mparangasi forests during June is attributable to the second fruiting of *Pseudospondias*, which was most abundant in these forests. Chimpanzees also fed heavily on mango trees growing around these forests (Figure 7.7g).

4. July–mid-August 07: lesser *Phoenix* season

The end of *Pseudospondias* and mango season in July coincided with a second, shorter ripening of *Phoenix* fruits, and chimpanzees returned to foraging predominantly around swamps in Kyamalera, Kyamusoga and Nyakakonge (Figure 7.7h). In mid-August chimpanzees reportedly raided sugarcane in Kyam-Paka village, to the east of Kiseeta, and spent several days in the hills in Kandanda. Recent feeding remains of *Uvaria angolensis* were found in a valley thicket (not shown on map), but no other sign was observed.

5. Late August–November 07: Low fruiting season

By late August *Phoenix* season had ended. This marked the start of the >3-month low fruiting season in Bulindi forests and a major shift in the chimpanzees' ranging and diet. From late August through November large parties were most frequently present in Kiseeta forest and less often in swamp forest elsewhere in their range. In Kiseeta the apes fed heavily on cocoa (as indicated by the abundance of half-eaten pods observed on the forest floor most days), figs, *Caloncoba crepiniana* fruits and young leaves of *Trichilia dregeana*, which occurs at the highest density in Kiseeta. Nest sites were concentrated in the southern half of the forest in proximity to a sugarcane plantation (Figure 7.7i), which the apes raided on mornings and evenings.

Throughout August–November the sharp rise in reports of chimpanzees entering village areas for food was supported by direct observations as well as feeding trace evidence and dung analysis (Chapter 5). Parties comprised mainly of adult males made frequent excursions to Kaawango forest and raided cultivars (including sugarcane, papaya, oranges and ripe cocoa) from villages surrounding the forest before returning to Kiseeta; only once were they known to nest within Kaawango (in October, when they ate ripe cocoa at a *shamba* 300 m from the forest in Kyabawaza village; Figure 7.7k). In September chimpanzees repeatedly raided guavas from homesteads bordering Kyamusoga and Mparangasi forests, and were several times located in and around the banana plantation alongside Mparangasi in Nyaituma village, attracted by bananas ripening in an underground store (Figure 7.7j; Appendix 4). Occasionally, parties nested within this plantation. Chimpanzees continued to nest most frequently in Kiseeta during October–November, often in large groups (Figure 7.7k,l). From October, the apes began travelling between Kiseeta and Kyamusoga forests via Katigiro to feed on sugarcane at a garden situated between Katigiro and Kiseeta. This route necessitated travel across >500 m of farmland and directly past homes, causing anxiety and consternation among residents. Frequent aggressive confrontations occurred between people and chimpanzees, particularly around Kaawango, including ≥2 incidents in which chimpanzees were chased and attacked by hunting dogs and one instance in which a man repeatedly fired a rifle to scare them off (McLennan 2010; Appendix 6).

Although quantitative data on daily travel length are lacking, qualitative observations suggested adult males ranged over considerable distances during the low fruiting season, for example travelling from Mparangasi or Nyakakonge in the morning to Kyamusoga and Kiseeta, and passing in a loop through Kaawango and Kyamalera forests before returning to nest in Kyamusoga or Mparangasi – an estimated travel distance of >7 km. Twice during September–October the whereabouts of chimpanzees could not be ascertained; local people had not seen or heard them and we found no recent sign (nests, dung, knuckle-marks, feeding traces) in any of the main forests. Although the chimpanzees may have been separated into small quiet groups, the complete absence of sign suggests at least some apes were in the hills or in a peripheral part of their range unknown to the research team. In mid–October a large *Ficus mucuso* fruited in Kiseeta and ≥5 adult females and their young spent several days feeding on the figs. During this important fruiting event, none of the adult males were located for >1 week. In November local people saw ≥2 large chimpanzees crossing the main road west of Nyakakonge where they ate papaya in a village >1 km to the west of their confirmed range (not shown on map). Thus, it appeared the chimpanzees were ranging widely in search of food.

6. December 07–January 08: Monanthotaxis and 2nd mango season

Late November brought another change in diet and range use by the chimpanzees. The vine *Monanthotaxis ferruginea* fruited and the apes shifted their foraging activity to forest–woodland in Katigiro, where the fruit was abundant. Throughout December dungs and nests were recorded in this small ecotone patch (Figure 7.7m). Mangos also ripened in December and the chimpanzees sought fruiting trees around Katigiro and Mparangasi. Nests were not recorded in January 08, except where they occurred outside of the chimpanzees' usual range. In the first two weeks of January a small party were reported ranging deep in the Kandanda hills beyond Kyam-Paka village, possibly searching for mangos. Recent nests in association with sugarcane damage were found in two hillside thickets 3 km southeast of Kiseeta – the furthest east the chimpanzees were confirmed to range (Figure 7.7n). Also in early January a juvenile male was observed in trees at a homestead in Kyam-Paka where he had remained for about one week, apparently having become separated from his mother or other group members. Chimpanzees sometimes visited this homestead for sugarcane when travelling between Kiseeta forest and Kandanda; possibly, this individual's mother had been killed, since at least one ape was caught in a trap placed near this sugarcane in April 07.[2]

By the study's end in late-January *Monanthotaxis* and mango seasons were drawing to an end. *Phoenix* palm fruits had ripened again, after an interval of almost four months, and chimpanzees resumed foraging in swamp forest in Mparangasi–Nyakakonge, but had yet to return to Kyamalera or Kyamusoga forests.

7.4. Discussion

Home Range Size

A variety of methods are available for estimating home range size, and each has advantages and disadvantages (Boyle et al. 2009). Since different methods produce differing estimates, it is useful to report estimates derived from multiple methods (e.g. Newton-Fisher 2003; Boyle et al. 2009; Ren et al. 2009; Wartmann et al. 2010). However, data used in the present analysis were derived not from follows of habituated individuals, but from opportunistic sightings and indirect indicators, and thus the MCP method was appropriate for estimating chimpanzee range size at Bulindi. Given the study's limitations, this analysis should be considered preliminary.

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[2] Local residents were rumoured to be planning to sell this juvenile. A man from outside Bulindi visited the homestead on 4th January and allegedly offered a considerable sum of money for it. The following day field assistants reported the chimpanzee gone; one resident apparently tried to hide when they approached the homestead. Nevertheless, if an attempt was made to catch the animal it seemingly failed because on 7th January a juvenile male was observed alone in Katigiro. This was almost certainly the same individual.

Table 7.4. Comparison of home range size of chimpanzee communities at 16 sites, arranged in ascending order of estimated home range (HR) size. Estimates are only roughly comparable due to methodological differences: MCP = minimum convex polygon (where % MCP was not reported, it is most likely 100%); GC = grid cell method (cell width shown in parenthesis). For studies that report >1 estimate using different methods, only the MCP is shown as this is the most commonly used method. *Study sites followed by an asterisk indicate sites where chimpanzees were only partially habituated; at these sites range size was estimated from the location of encounters and/or indirect indicators (e.g. nests), and not from systematic follows. Data from Bulindi are emboldened. A dash indicates data were unreported.

Site (community)	**Country**	**Habitat**	**HR Size (km^2)**	**Observ. Period**	**Method**	**Community Size**	**Reference**
Budongo	Uganda	Mid-altitude forest	6.8	15 mo	MCP (100%)	38–46	Newton-Fisher (2003)
Taï (Middle)	Côte d'Ivoire	Lowland rainforest	12.1	10 mo	MCP (100%)	11	Herbinger et al. (2001)
Kahuzi-Biega	DRC	Montane forest	12.8	60 mo	GC (250 m)	23	Basabose (2005)
Bossou	Rep. Guinea	Forest–farmland	15.0[1]	–	–	12–14	Hockings et al. (2009)
Taï (North)	Côte d'Ivoire	Lowland rainforest	16.8	10 mo	MCP (100%)	35	Herbinger et al. (2001)
Bwindi *	Uganda	Montane forest	17.0[1]	12 mo	–	≥25	Nkurunungi and Stanford (2006)
Goualougo	Rep. Congo	Lowland rainforest	19.2	–	MCP	54	Morgan et al. (2006)
Mahale (M group)	Tanzania	Forest–woodland	19.4	20 mo	GC (400 m)	~100	Hasegawa (1990)
Bulindi *	**Uganda**	**Riverine forest–farmland**	**21.0**	**15 mo**	**MCP (100%)**	**≥25**	**This study**
Gashaka *	Nigeria	Forest–woodland	26.2	24 mo	GC (934 m)	≥35	Sommer et al. (2004)
Taï (South)	Côte d'Ivoire	Lowland rainforest	26.5	10 mo	MCP (100%)	63	Herbinger et al. (2001)
Kibale (Ngogo)	Uganda	Mid-altitude forest	27.7	19 mo	MCP (100%)	137–148	Amsler (2009)
Kibale (Kanyawara)	Uganda	Mid-altitude forest	37.8	36 mo	MCP	49–51	Wilson et al. (2007)
Semliki *	Uganda	Riverine forest–savanna	38.3	–	MCP	≥29	Hunt and McGrew (2002)
Fongoli	Senegal	Savanna–woodland	65.0[1]	17 mo	–	35	Pruetz and Bertolani (2009)
Assirik *	Senegal	Savanna–woodland	72.1	48 mo	MCP	≥24	Baldwin et al. (1982)

[1] Methodology not reported; estimated range size likely to be an approximation.

During the study period the chimpanzees' confirmed range was 21 km^2; however, the inclusion of reliable local information suggests their home range was in fact 25 km^2 or more. Within this range chimpanzees preferentially used a much smaller core area of <5 km^2, consisting of four of the five riverine forests and adjoining farmland. In a previous analysis I estimated the *probable* home range of the Bulindi chimpanzees at ~38 km^2 (McLennan 2008). Included in this earlier calculation were several unconfirmed peripheral locations, where local people reported seeing chimpanzees apparently travelling from Bulindi. These locations include a swamp north of Kibugenya hill and northeast of Kaawango within Kyabatumbya forest (see Figure 7.2). A third location was south of the chimpanzees' known limit in Kandanda–Ngobya, but this sighting occurred in early 2006, prior to the main study. While other chimpanzee communities occur >5 km north of Bulindi along the Waki River and around Kasongoire FR, the southern limits of their ranges are unknown, and it is unclear if the Bulindi chimpanzees have contact with these neighbours at all. But since the sightings to the north could potentially have been of other chimpanzees, the locations were not included in the present analysis. However, it seems likely that the Bulindi apes did visit these areas. The extent of the chimpanzees' ranging within the 26 km^2 Kandanda–Ngobya FR was undoubtedly underestimated; attempts to track the apes in this hilly terrain were always unsuccessful. These observations suggest the larger range estimate of 38 km^2 may in fact be more accurate. Nevertheless, some evidence indicated the chimpanzees are currently expanding their range: several of the outer limits of the polygon shown in Figure 7.2 are locations where chimpanzees have recently been sighted for the first time by local people. Habitat disturbance in the riverine forests – the apes' core area – may be causing them to travel greater distances in search of food. This study found no evidence that chimpanzee ranging was limited by features of the human landscape such as roads and agricultural land. For example, when crossing between Kiseeta and Katigiro forests the apes traversed >500 m of open farmland.

The size of chimpanzee home ranges are likely to be most strongly influenced by variation in food density and access to water, with the most productive habitats supporting the largest communities (e.g. Ngogo; Amsler 2009) and/or those where local population density is high (e.g. Budongo; Newton-Fisher 2003). Comparative data on home range size are shown in Table 7.4. Although estimates are not strictly comparable owing to methodological differences, several observations can be made. The confirmed (minimum) range at Bulindi falls roughly in the centre of the range of estimates (mean for all sites = 27 km^2; median = 20 km^2). The largest estimates are for dry savanna-dominated sites. While a positive association between community size and range size has been reported (Amsler 2009), no such relationship is apparent for the studies listed in Table 7.4 ($r_s = 0.300$, $p = 0.26$).[3] It can be seen that minimum home range size at Bulindi is larger than that calculated for several forest-living communities containing roughly twice (Budongo, Goualougo) to four times (Mahale) as many members. While community size is imprecisely known at Bulindi, it is unlikely to number more than about 30 (Chapter 8). The relatively large home range for the community size may be related to the fact that, while the riverine forests are rich in chimpanzee foods (e.g. figs, *Phoenix* palms, *Pseudospondias microcarpa*, and cocoa), they are small: the combined area of the main patches is about 1.7 km^2 (see Table 3.1), which corresponds to 8% of the confirmed range size. In the arid savanna sites of Fongoli and Assirik in Senegal, and Ugalla in Tanzania, gallery forest covers just 2–3% of the land area (Baldwin et al. 1982; Ogawa et al. 2007; Pruetz and Bertolani 2009). While chimpanzees at Bulindi do not inhabit a similarly dry and open environment, their range evidently includes considerably less forest cover than is the case for ‘true’ forest-living populations.

Nest Group Size and Food Availability

The size of nest groups at Bulindi was similar to other sites. But in contrast to previous studies (Furuichi et al. 2001b; Hohmann et al. 2006), nest group size *increased* when availability of chimpanzee forest foods was low. Multiple regression analysis showed that the proportion of fruit species in dungs comprised of non-seasonal fruit cultivars had an even greater effect on nest group size. (Feeding trace evidence strongly indicated that this period was also when sugarcane was most frequently raided). While this may suggest that party size at Bulindi was not limited by forest food abundance due to the year-round availability of cultivars in gardens outside of forest (see also Hockings 2007), the result should be interpreted with caution. In this study, nest group size was used as a proxy for the size of foraging parties (cf. Furuichi et al. 2001b). However, the relationship between chimpanzee nest group size and daytime party size seems to vary among sites. For example, while mean daytime party size was larger than mean nest group size at Kahuzi-Biega (Yamagiwa et al. 1996), daytime parties were smaller than the size of nesting parties at Ugalla (Ogawa et al. 2007) and Gashaka (Sommer et al. 2004), but similarly-sized on Rubondo Island (Moscovice et al. 2007). Average nest

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[3] If community size was presented as a range, the mean value was calculated for the correlation.

group size at Bulindi (3.1) was somewhat smaller than the mean number of individuals *visible* per encounter (4.0; see Chapter 8). However, as discussed in the next chapter, dense vegetation in forest patches meant that all chimpanzees in a party were seldom visible; thus average daytime party size may be considerably larger. This suggests that Bulindi chimpanzees split into smaller parties in the evening, as occurs at Budongo (Reynolds 2005). Nevertheless, seasonal changes in nest group size presumably reflect differences in the chimpanzees' tendency to aggregate, at least during evenings and mornings.

In a study of the relationship between fruit abundance and party size at four sites, Hashimoto et al. (2003) concluded that party size is only affected by fruit availability when it falls to sufficiently low levels as to be limiting. Where fruit availability does not fall to such low levels, due to the presence of abundant and reliable fallback foods (e.g. figs and *Musanga* fruit at Kalinzu; Hashimoto et al. 2001), party size will be predominantly influenced by social factors, particularly the presence of estrous females. The finding that sleeping group size at Bulindi did not decrease during the low forest fruiting season might be related to the presence of similar high-quality fallback foods, for example figs and cocoa. Indeed, during the low fruiting season the chimpanzees were most often located in large parties in Kiseeta forest where cocoa was abundant. The apparent relationship between crop-raiding and nest group size could therefore be incidental. However, during this period chimpanzees made regular forays into village areas for cultivated fruits such as papaya, guava and banana, and nested at forest edges near gardens. Greater cohesiveness implied by larger nest groups during the low fruiting season might be related to habitat use and foraging strategies that increased chimpanzees' proximity to humans. For example, the risk of disturbance from people was undoubtedly higher when chimpanzees nested in a busy and open forest like Kiseeta, compared to dense swamp forest in Kyamalera or Nyakakonge where the apes were less exposed and levels of human activity were lower. Unfortunately, the influence of estrous females on nest group size could not be assessed in this study. At least three different parous females with full estrous swellings were observed in large noisy parties between late August and mid-December, when chimpanzees fed most heavily on cultivars. This suggests that the presence of females with sexual swellings may interact with other ecological and human factors in determining grouping patterns at Bulindi.

Seasonal Ranging and Use of Individual Forest Patches

Chimpanzees did not use forest patches evenly throughout the year; instead distinct seasonal patterns of use were evident. In Kalinzu forest, Uganda, chimpanzees slept in sections of forest where fruit was most abundant (Furuichi and Hashimoto 2004). At Bulindi, however, fruit availability within individual forest patches predicted the monthly proportion of nests encountered in only two of five riverine forests (Kyamalera and Kyamusoga). For both forests the positive relationship held when the monthly number of nests was considered as a proportion of all nests recorded in the patch during the study, and as a proportion of the total number of nests encountered within the chimpanzees' range per month. While nests were found in Kyamalera during most months, the majority were recorded during the high fruiting season in January–April when ripe *Phoenix* fruits and other seasonal fruits such as *Parkia* and *Antiaris* were abundant; after *Phoenix* season ended in August, Kyamalera was seldom used. Chimpanzees also nested and foraged in adjacent Kyamusoga throughout *Phoenix* season, but their use of this patch was particularly intense during June–July when *Pseudospondias* trees fruited. Their more regular use of Kyamusoga relative to Kyamalera during the low fruiting season probably relates to the large cocoa *shambas* in Kyamusoga, as well as its location in the heart of the apes' core range (Figure 7.2).

Levels of fruit availability in the remaining three riverine forests (Kiseeta, Kaawango and Mparangasi–Nyakakonge) were not connected with changes in the monthly proportion of nests encountered within them. It is possible that significant effects were not detected due to low statistical power associated with a low number of cases in the multiple regressions (n = 12 months). Also, measures of food availability in patches did not take into account certain foods eaten frequently by the apes in some seasons (e.g. *Trichilia* leaves in Kiseeta). Mparangasi–Nyakakonge was the most consistently utilised forest throughout the study; only during March–April when chimpanzees fed on *Parkia* and *Phoenix* in Kyamalera were few nests recorded in the gallery forest. The finding that seasonal nesting in Kiseeta was related to cultivar consumption and not fruit abundance may indicate that the distribution of agricultural foods outside forest also influenced seasonal range use by chimpanzees. The apes ranged within Kiseeta during the low fruiting season, feeding on cocoa and other forest foods such as *Trichilia* leaves. However, they were also attracted by the large sugarcane garden on its southern edge. Furthermore, the apes appeared to use Kiseeta as a base from where parties travelled to other parts of their range and raided crops, often returning to Kiseeta the same day.

Qualitative data indicated the adult males ranged widely during this period, sometimes covering considerable distances in a day. Consumption of high-energy crops may have compensated for the increased energetic demands of travel. At Budongo, chimpanzees also travelled further, and in large groups, when fruit was scarce and the apes raided crops along the forest edge (Tweheyo and Lye 2005).

Ranging patterns indicate that Kaawango forest – alone among riverine forests at Bulindi – was not part of the chimpanzees' core area. Visits by chimpanzees were highly seasonal, being restricted to mango season and the low fruiting season. In most instances, visits were made by parties comprised of adult males only, which spent little time within the forest but raided crops from surrounding villages. During these excursions the males also visited a homestead where they interacted aggressively with their reflections in the glass windows of a door (McLennan 2010; Appendix 6). Nests were rarely encountered, and adult females were never seen in or around Kaawango unless accompanied by adult males. A likely explanation for the limited use of Kaawango is the relatively low density of food tree species identified as particularly important in the chimpanzee diet (Table 7.5). For example, higher densities of figs, cocoa, *Phoenix* and *Pseudospondias* are found in other forests within the core area.

Table 7.5. Adult densities (stems ha^{-1}) of some 'important' forest tree fruits in five riverine forests. Important fruits are those that appeared in ≥50% of dungs in at least one month or >10% all dungs. Values in bold indicate highest densities of each species. Figs (*Ficus* spp.) are lumped. A dash indicates adult individuals of the species did not occur. Forest fragments: KLA = Kyamalera, KGA = Kyamusoga, KTA = Kiseeta, MPA–NKE = Mparangasi–Nyakakonge, KWG = Kaawango.

Fruit Species	KLA	KGA	KTA	MPA–NKE	KWG
Antiaris toxicaria	11.7	11.9	**12.5**	6.4	5.4
Ficus spp.	9.0	11.3	11.7	**14.4**	11.9
Morus mesozygia	–	2.4	**3.1**	–	1.8
Parkia filicoidea	**5.3**	–	3.1	0.5	–
Phoenix reclinata	126.6	**161.9**	9.4	160.6	85.7
Pseudospondias microcarpa	2.1	**19.0**	6.3	12.8	3.6
Theobroma cacao [cocoa]	4.3	95.2	**106.3**	0.5	5.4

Chimpanzees nested and foraged most frequently in swamp and cocoa forest, and spent less time in mixed forest. Their use of ecotone forest was seasonal. Although Katigiro fell within the core area polygon (Figure 7.2), this part of the range was used by large parties only during *Monanthotaxis* vine season in December 07–January 08. As noted above, use of the hilly Kandanda–Ngobya FR was poorly documented; available evidence indicated chimpanzees ranged into the reserve mainly during *Antiaris* and mango seasons, apparently searching for fruiting trees. Finally, the effect of human disturbance (e.g. logging) on range use patterns is unclear. Pitsawyers were frequently present in all riverine forests, but chimpanzees appeared to avoid only the immediate area around pitsawing activity. Although qualitative observations suggested chimpanzees temporarily avoided forest patches subject to mechanical logging, on more than one occasion apes were heard vocalising and drumming near logging teams, apparently in response to the chainsaws.

Summary

1. Chimpanzees at Bulindi had a minimum home range of 21 km^2 during the study, which is similar to or somewhat larger than range size in most forest-living populations, including several with a much larger community size, but smaller than estimated ranges in savanna habitat. Ranging did not appear to be restricted within this fragmented forest–farm landscape.
2. Nest group size was negatively correlated with forest fruit availability but positively related to increased consumption of fruit cultivars. The presence of high density fallback foods (e.g. forest cocoa *shambas*) may buffer the impact of reduced food availability during the low fruiting season, but larger nest groups may have been a response to increased proximity to people when the apes regularly fed on cultivars.
3. The chimpanzees utilised forest patches within their range on a seasonal basis. Patterns of range use suggested the apes' ranging was influenced by the distribution of foods both within forest patches and outside of forest (i.e. cultivars).

Plate 1. Landscape views of Bulindi.

Top: View from Mparangasi hill looking north towards Kibugenya hill (on the left). Kyamalera forest is at the centre.
Bottom: View from same hill looking east towards wooded grassland in Kandanda–Ngobya Forest Reserve (hill in background); in the foreground a narrow strip of gallery forest forms a border between Mparangasi and Nyaiyuma villages. Scattered trees among the matrix of settlements and farmland include mango trees. A banana plantation is visible at the right-centre in Nyaituma.

Plate 1. *cont*.

Top: View facing west from Katigiro towards Kyamusoga forest; forest land in the foreground was cleared several years prior to this study.
Bottom: Garden on recently cleared land at the edge of Kyamusoga forest. Immediately behind the *Phoenix reclinata* palms is a papyrus swamp.

Plate 2. Streamside distillery, Mparangasi–Nyakakonge forest.

Plate 3. Pitsaw structure, Mparangasi–Nyakakonge forest.
The log is *Trilepisium madagascariensis*. Note the stacked timber on the right.

Plate 4. Forest types.

Top: Permanently wet *Macaranga* swamp forest, Nyakakonge.
Bottom: Degraded mixed forest, Kyamusoga. Trees include *Albizia* sp., *Trilepisium madagascariensis* and *Funtumia africana*. The logged tree in the garden is *Antiaris toxicaria*.

Plate 4. *cont*.

Top: Cocoa forest, Kyamusoga; two old chimpanzee nests are in the cocoa tree (the lower nest is <1 m from the ground).
Bottom: Ecotone forest–woodland, Katigiro.

Plate 5. Forest disturbance from logging.

Top: Forest logged in preparation for a pine plantation, Kiseeta forest.
Bottom: Felled *Antiaris toxicaria* tree (chain-sawn) in open, heavily-logged forest in Kyamusoga; note lack of large trees.

Plate 6. *Phoenix reclinata* palm with clusters of ripe fruit.

Plate 7. Freshly discarded 'wadge' of *Monanthotaxis ferruginea* fruit seeds and skins.

Ripe figs (*Ficus sur*)

Antiaris toxicaria

Dovyalis macrocalyx

Monanthotaxis ferruginea

Parkia filicoidea
(The remains of a chimpanzee meal)

Unripe cocoa pods
(*Theobroma cacao*)

Plate 8. Some ‘important’ fruit foods for Bulindi chimpanzees.

Plate 9. Diversity of fruits in chimpanzee dung.

Top: Freshly washed dung containing mixture of fruit species. Large seeds are *Antiaris toxicaria* and *Phoenix reclinata*; smaller seeds are guava (*Psidium guajava*), *Morus mesozygia* and *Aframomum* sp. The pink fruit pulp in the centre is guava. Unidentified fibrous pith is also present (March 2007).
Bottom: Dung dominated by *Monanthotaxis ferruginea* seeds; other seeds present in small quantities include *Aframomum* and *Ficus* sp. (December 2007).


Mango [*Mangifera indica*]


Papaya [*Carica papaya*]


Cocoa [*Theobroma cacao*] (unripe pod from abandoned forest *shamba*)


Cocoa (ripe pod from village *shamba*; note large seeds discarded)


Jackfruit [*Artocarpus heterophyllus*] (note large seeds discarded)


Damage to a young banana plant [*Musa* sp.]. The chimpanzee has fed on the pith.

Plate 10. Feeding traces of chimpanzee cultivar feeding.

Plate 10. *cont*.

Chimpanzee damage to sugarcane [*Saccharum officinarum*] (Kyabawaza village).

Plate 11. Tool-use to access honey from a subterranean bee nest (*Meliponula lendliana*).

Top: Hole dug by a chimpanzee; note stick tool protruding from centre. Traces of beeswax were alongside the hole suggesting the chimpanzee was successful in obtaining honey (October 2007).
Bottom: A selection of chimpanzee digging sticks (August–December 2007).

Plate 12. Circumstantial evidence of chimpanzee tool-use in predation on a carpenter bee (*Xylocopa* sp.) nest.

Top: Modified sticks immediately below an occupied *Xylocopa* nest in the branch of a small *Oxyanthus speciosus* tree (January 2008).
Centre: Cross-section view of a *Xylocopa* nest showing chambers that house adults, larvae and honey. The entrance hole is visible on the upper section.
Bottom: Adult *Xylocopa* bees (with pen for scale).

Plate 13. Chimpanzee nests.

Top: Fresh nest using *Phoenix reclinata* palm fronds, Mparangasi gallery forest.
Centre: Adult male (KT) still in his night nest in a *Pseudospondias microcarpa* tree, Mparangasi (video still).
Bottom: Fresh nest in cocoa tree, Kiseeta forest.

Julius [JL] (prime; alpha or beta male)

Keeta [KT] (prime; alpha or beta male)

Sylvester [SL] (prime; third-ranking male)

Murray [MR] (young; fourth-ranking male)

Jackson [JK] (young; low-ranking male)

Old Larry [LR] (elderly; low-ranking male)

Plate 14. Adult male chimpanzees at Bulindi (photos are video stills).

Adult males KT and SL in an isolated *Ficus varrifolia* tree overlooking gardens. They are monitoring the research team who are standing 40 m from the tree.

The males pant-hoot at the arrival of local people, who have joined researchers in gardens beneath the tree (July 2007).

KT calmly watches researchers who are standing in a clearing made by charcoal burning in Kyamalera forest (July 2007).

Adult female and a juvenile feeding in a fig tree (*Ficus sur*) overlooking a distillery, Kiseeta forest (November 2007).

SL leads the way across a busy path to a village well, Kiseeta forest. Before crossing, chimpanzees vocalised and drummed for 10 min in undergrowth next to the path (November 2007).

Adult males JL and KT performing handclasp grooming; on the right MR is monitoring researchers (May 2007).

Plate 15. Chimpanzee encounters (photos are video stills).

Plate 16. Brewing bananas placed in an underground store to hasten the ripening process, Nyaituma village.

Top: Logs and vegetation are piled on top of the store to seal it. Unless guarded, chimpanzees will remove the logs to get at the bananas.
Bottom: Banana store with the fruits removed.

Plate 17. Tobacco farming.

Top: Forest land burnt and cleared for planting tobacco, Mparangasi gallery forest.
Bottom: A tobacco garden stretching to the riverbank, Nyaituma village. The land was cleared 2–3 years previously; forest remains only on the Mparangasi side of the river.

Plate 18. Land-use changes at Bulindi.

Top: A pine plantation (*Pinus* spp.) established on forest land, Kiseeta. The hill in the background is part of Kandanda–Ngobya Forest Reserve, a wooded-grassland classified as a ‘production’ reserve for development of industrial tree planting.
Bottom: Maize (*Zea mays*) growing on recently cleared land, Kyamalera forest.

Plate 19. Adult males JL and KT handclasp grooming in a *Parkia filicoidea* tree, Kyamalera forest.

CHAPTER 8 – CHIMPANZEE BEHAVIOUR DURING ENCOUNTERS WITH HUMANS

8.1. Introduction

Expanding human populations and forest clearance for agriculture across equatorial Africa has meant that humans and great apes increasingly occupy the same habitat and compete for the same resources (Reynolds 2005; Madden 2006; McLennan 2008; Hockings and Humle 2009). Examination of the animals' behaviour towards people in shared landscapes provides an opportunity to explore the nature of interactions between great apes and their human neighbours, as well as the wider conservation implications of human–great ape sympatry. Available data indicate that competition is a prominent feature of human–ape interactions where great apes live in close proximity to people (Hockings and Humle 2009). However, more information is needed about chimpanzee behaviour in human-dominated landscapes, and the nature of their interactions with their human neighbours, in order to devise appropriate strategies for successful coexistence.

The response of chimpanzees to the arrival of researchers varies according to the population's prior experience with humans as well as features of the habitat. For example, flight is the predominant response in populations that experience hunting pressure (Bertolani and Boesch 2008). However, in low-visibility rainforest at Lopé, Gabon, where apes were not hunted, chimpanzees also responded to observers most often with rapid flight (Tutin and Fernandez 1991). In contrast, in the remote forests of the Goualougo Triangle, Republic of Congo, chimpanzees showed intense curiosity rather than fear during encounters with researchers, suggesting they had no prior experience with humans (Morgan and Sanz 2003). At Kibale, Uganda, where human population density surrounding the national park is high, chimpanzees being habituated for tourism ignored or fled from observers in equal measure but also exhibited occasional aggression by charging at humans (Grieser Johns 1996). Other threatening behaviours sometimes directed at researchers include aggressive vocalisations, and branch slapping or breaking (Reynolds and Reynolds 1965; Izawa and Itani 1966; Sugiyama 1969). The responses of unhabituated chimpanzees to contact with researchers in a human-dominated, agricultural landscape have not previously been documented.

In African great apes, habituation – defined as the acceptance by wild animals of a human observer as a neutral element in their environment (Tutin and Fernandez 1991) – may take several years to accomplish without provisioning (Doran-Sheehy et al. 2007; Bertolani and Boesch 2008), but is a requisite first phase before detailed behavioral research can be conducted (Tutin and Fernandez 1991; Morgan and Sanz 2003; Sommer et al. 2004; Doran-Sheehy et al. 2007; Ando et al. 2008; Bertolani and Boesch 2008) or successful viewing-based tourism implemented (Grieser Johns 1996; Blom et al. 2004; Goldsmith et al. 2006). With increasing human penetration into ape habitats, the conservation implications of habituating populations in human-dominated landscapes for research or tourism warrant careful consideration.

While habituation was not an aim of this research, encounters with chimpanzees at Bulindi were sought opportunistically to gain demographic information and to supplement ecological data. In addition, chimpanzees were encountered inadvertently in the course of other research activities (e.g. phenology surveys or nest and faecal data collection). Quantitative data on chimpanzee behaviour during encounters, as well as anecdotal data concerning their interactions with local villagers, are presented to increase understanding of human–ape interactions in human-dominated environments. Additionally, the data permit evaluation of the suitability of habituating great apes in this situation for tourism, as a means of increasing local tolerance for them through income generation.

The aims of this chapter are to:

1. Examine the behavioural responses of chimpanzees at Bulindi to encounters with a research team; and determine factors influencing responses and assess whether responses changed over time;
2. Determine the size and composition of the Bulindi chimpanzee community;
3. Describe the nature of interactions between apes and local people;
4. Consider the implications of the findings for management and conservation of great apes in unprotected human-dominated landscapes.

8.2. Methods

8.2.1. Encounter Protocol

Encounter data were collected over 18 months during May–June 2006 and October 2006–January 2008. Chimpanzees were located by following vocalisations and local reports, and by visiting fruiting trees. Efforts were made to establish visual contact from locations that afforded the animals a clear view of researchers, for example from gardens at the forest edge, or from clearings within the forest such as logging gaps, community wells and streamside distilleries. Researchers (myself and field assistants) avoided approaching chimpanzees in forest areas where visibility was low, because initial encounters indicated that this provoked considerable alarm and agitation. Nevertheless, at times the apes were unexpectedly met at close range in dense vegetation. We also tried to avoid surprising chimpanzees in the forest by talking quietly and/or by gently tapping a *panga* (machete) against a tree trunk when entering areas where chimpanzees might be present. The use of *pangas* to aid passage through dense vegetation was curtailed entirely when chimpanzees were nearby.

A median of three researchers were present during encounters with chimpanzees (range: 1–5). We stood during most contacts because ground vegetation in the forest, or standing crops at the forest edge, meant that sitting would have partially concealed us. During initial minutes of an encounter, which were often tense, we avoided prolonged staring at the chimpanzees (i.e. through binoculars). *Pangas* – sometimes used by local people to threaten the apes – were held low or placed on the ground. Ordinarily, the animals were not followed once they departed the encounter site.[1] However, chimpanzee parties were occasionally encountered twice in one day in separate localities. Same-day encounters were separated by ≥2 hours. We frequently terminated contacts by moving away from the chimpanzees if they remained inactive or out of view for long periods, or responded to our presence with prolonged alarm and/or aggression indicative of stress.

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[1] An exception was twice made when adult males travelled from Kiseeta to Kaawango, where on previous occasions they had interacted with their reflections in the glass door of a house at the forest edge (McLennan 2010); on both occasions researchers waited 10–20 min before following in an effort to observe the behaviour.

The human-dominated landscape at Bulindi meant that local people were sometimes visible (and frequently audible) during encounters, most commonly when observations were conducted from gardens or areas of regular human activity such as forest wells. Rarely, local people joined us during an encounter. The chimpanzees occasionally responded to the nearby activities or approach of local people (e.g. by vocalising or descending the tree), and visual observations were at times terminated as a result, but only responses to the research team are considered here.

8.2.2. Data Collection

Encounters involved direct observation of one or more chimpanzees as well as non-visual contacts with animals obscured by dense ground vegetation. Chimpanzees were frequently out of view but within audible distance (i.e. 20–100 m) of researchers engaged in other data collection activities. At such times, chimpanzees often vocalised and drummed, which may have been related to our presence, though it was rarely possible to confirm this unequivocally. Similarly, chimpanzee parties sometimes fell silent upon our arrival in the vicinity and were thought to be hiding or monitoring us, but this was not verifiable in the absence of direct observation. Therefore only cases where non-visible chimpanzees responded unambiguously to our presence or approach (typically at close range) were considered encounters. Field assistants occasionally met chimpanzees while searching for nest sites or dung but chimpanzee behaviour was not recorded on such occasions.

In each encounter the following data were recorded: location method (vocalisations, local report, fruiting tree, none); location type (dense forest, forest clearing, forest edge, garden, roadside); number and age-sex class (Goodall 1986) of individuals seen; whether individuals were terrestrial or arboreal; distance between researchers and chimpanzees (measured with a range-finder); whether or not additional chimpanzees were present but not visible; whether or not local people were in visual proximity; and encounter duration, defined as the time from when the first chimpanzee was visible until the last chimpanzee disappeared from view or the researchers left the encounter site. For non-visual encounters, encounter duration is the time between the first and last unambiguous reaction to researchers prior to the departure of humans or chimpanzees from the encounter site.

Table 8.1. Individual chimpanzee responses to researchers (adapted from Tutin and Fernandez 1991).[1]

Response	Definition
Ignore	No discernible response shown; after noticing researchers the individual continues with previous activity (but may continue to show casual interest in them).
Monitor	Active surveillance of researchers; includes ≥2 of the following elements: staring, head swaying, moving to obtain a clearer view of the researchers, peering at researchers from behind tree trunk. The individual may appear 'curious' (*sensu* Morgan and Sanz 2003) or exhibit signs of nervousness such as pilo-erection and self-scratching.
Stealthy Retreat	Slow, cautious, and almost silent descent from tree or avoidance on the ground. The individual may depart the encounter site or remain hidden from view nearby.
Threaten	Researcher-directed aggression; includes ≥1 of the following elements frequently accompanied by loud vocalisations (waa-barks, roar pant-hoots; Goodall 1986) and/or buttress drumming: rapid, noisy charging display, either direct or oblique, towards researchers; vegetation shaking or thrashing; slapping the ground; pursuit of departing researchers; slow, purposeful approach with pilo-erection and fixed stare.
Flight	Rapid jumping or sliding out of a tree, or running along the ground causing much noise.
Hide	Pulling vegetation in front of face or body to form a screen from behind which the individual continues with previous activity or peers at researchers.

[1] In agreement with Morgan and Sanz (2003), the 'loud' and 'soft' vocalisation categories defined by Tutin and Fernandez were considered elements of other categories and not independent responses, as was the 'approach / wait for another' category.

Individual Responses

Responses were recorded for each individual whose reaction was clearly observed during the first minute following mutual visual detection. Other studies have recorded the response of the first animal to detect observers (Grieser Johns 1996; Van Krunkelsven et al. 1999), or that of each individual that detected observers independently of other group members (Tutin and Fernandez 1991; Werdenich et al. 2003). However, at Bulindi it was often not possible to verify the 'first detector' or be sure of the independence of responses. Chimpanzee parties frequently contained both terrestrial and arboreal animals, and could be widely spread. The individuals present were seldom visible simultaneously. In many instances we were evidently detected by individuals that were obscured by the dense understory or foliage within the crowns of trees, so their initial reactions could not be recorded. Response categories were adapted from Tutin and Fernandez (1991) but tailored to better reflect behaviors exhibited towards humans by chimpanzees at Bulindi. Six categories were distinguished: Ignore, Monitor, Stealthy retreat, Threaten, Flight, and Hide (Table 8.1). Data were not collected for immature chimpanzees (below 8 years) unless their response was judged to be independent of associated adult females. Adolescents (8–15 years) of both sexes were lumped in the analysis due to the low number of cases.

Encounter Types

Initial responses of visible chimpanzees did not always aptly reflect the predominant group reaction to researchers that characterised the entire encounter. Thus, following Morgan and Sanz (2003) entire encounters were categorised based on the overall response of the chimpanzee party to us during the majority of the encounter. The behavior of non- or barely-visible animals was taken into account when it could be reasonably determined. Four 'encounter types' were distinguished: Ignore, Monitor, Intimidation, and Stealthy retreat (Table 8.2). It was not possible to control for the effect of interactions that chimpanzees might have had with local people prior to an encounter with researchers.

Table 8.2. Chimpanzee encounter types. Encounters were categorised based on the overall response of the chimpanzee party to researchers during the majority of the encounter.

Encounter type	**Definition**
Ignore	After initial response the chimpanzees resume previous activities (but may continue to show casual interest in researchers).
Monitor	The majority of chimpanzees display continued monitoring behaviour (or, rarely, curiosity) throughout the encounter.
Intimidation	Encounter characterised by continuous or repeated outbursts of threatening behaviour by visible and/or non-visible animals (see individual response category; Table 8.1), usually accompanied by loud group vocalisations (waa-barks, screams, pant-hoots) and/or buttress drumming, continuing until researchers or chimpanzees depart the encounter site. Includes the following sub-categories: (i) *Mobbing*: when ≥2 chimpanzees in a party reduce the distance to researchers to display and/or thrash the vegetation. (In animals, 'mobbing' refers to conspicuous group displays and/or vocalisations in response to a predator or intruder and need not involve physical aggression; e.g. Lord et al. 2009). (ii) Silent, aggressive *pursuit* of retreating researchers by ≥2 chimpanzees.
Stealthy Retreat	Same as individual response category (Table 8.1).

Chimpanzee Interactions with Villagers

Information concerning interactions between chimpanzees and local people was obtained via informal discussions with residents and from *ad libitum* observations. Reports of human–chimpanzee disturbances were investigated by visiting the incident site and talking with people that were present.

8.2.3. Data Analysis

Nonparametric tests were used to assess the relationship between individual response and encounter type categories and other variables. As a measure of habituation, Spearman's rank correlations were used to evaluate changes in encounter duration and the proportion of each encounter type across five time periods over the study. The analysis was performed using SPSS version 17. All probabilities were two-tailed and significance was set at $p < 0.05$.

8.3. Results

8.3.1. Chimpanzee–Researcher Encounters

Data were collected during 115 encounters with chimpanzees on 97 days (33% of 297 days in the forest). Chimpanzees were most frequently located by following vocalisations and buttress drumming (56%), but local reports (12%) and visits to fruiting trees (7%) provided additional means of encountering the apes. In 25% of encounters chimpanzees were met unexpectedly. Mutual visual contact with ≥1 animal was made in 95% of encounters whereas 5% were entirely non-visual. For visual encounters, the mean number of individual chimpanzees clearly seen was 4.0 ± 2.9 SD (range: 1–13). However, vocalisations, drumming and/or movement in the vegetation indicated additional animals were present but not visible in the majority of encounters (63%). In most instances (74%), non-visible chimpanzees were terrestrial and obscured by dense ground vegetation. Mean encounter duration was 50 min ± 62 SD (range: 10 s – 300 min). Local people were in visual proximity or joined researchers during 23.5% of encounters. Encounter duration was unrelated to presence or absence of local people (Mann–Whitney: $U = 1010.5$, $p = 0.24$).

Individual Responses

The most frequent first response was 'ignore' (49%) followed by 'monitor' (33%) (Table 8.3). Less common responses were 'stealthy retreat' and 'threaten' (9% and 7%, respectively). 'Flight' and 'hide' were seldom observed and were dropped from the subsequent analysis.

Chimpanzee parties frequently included terrestrial individuals hidden by dense ground vegetation, and the majority of observed first responses were for arboreal animals (74%) (Table 8.4). The distance between researchers and apes was significantly shorter when visible chimpanzees were on the ground (median: 30 m) compared to when they were in trees (75 m) (Mann–Whitney: $U = 2255.0$, $p < 0.001$). There was a significant difference between the responses of arboreal and terrestrial animals ($\chi^2 = 106.4$, $df = 3$, $p < 0.001$) (Figure 8.1). 'Ignore' was the most common response of arboreal chimpanzees (65%) but was rarely recorded for terrestrial individuals (8%). Instead, 'monitor' was the most frequent first response of terrestrial chimpanzees (54%). Ninety-one percent of visible threats were from individuals encountered on the ground. In addition, the proportion of 'stealthy retreat' responses was twice as high in terrestrial versus arboreal animals.

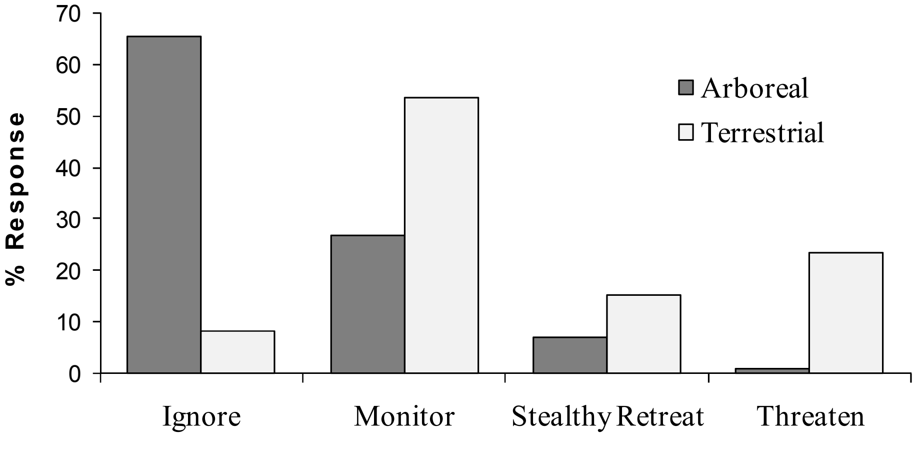

Figure 8.1. First observed response of arboreal and terrestrial chimpanzees to researchers.

Adult males were seen more often than other age–sex classes and accounted for >50% of observed responses. The mean (± SD) number of adult males seen per encounter was 1.8 (± 1.7), compared to 0.7 (± 0.9) for adult females, 0.3 (± 0.5) for adolescents, and 1.1 (± 1.4) for immatures. Adult males accounted for 90% of terrestrial first responses.

Table 8.3. First observed individual chimpanzee response to researchers. Only cases in which age-class (and sex for adults) was identified are included (*n* = 334).

Response	**All**		**Adult male**		**Adult female**		**Adolescent**		**Immature**	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%
Ignore	164	49.1	65	36.1	41	63.1	17	65.4	41	65.1
Monitor	110	32.9	75	41.7	12	18.5	8	30.8	15	23.8
Stealthy Retreat	30	9.0	16	8.9	10	15.4	0	0	4	6.3
Threaten	22	6.6	22	12.2	0	0	0	0	0	0
Flight	4	1.2	1	0.6	2	3.1	1	3.8	0	0
Hide	4	1.2	1	0.6	0	0	0	0	3	4.8
Total:	334	100	180	100	65	100	26	100	63	100

Table 8.4. The proportion of first responses recorded (i) when chimpanzees were arboreal or terrestrial, and (ii) at short (<50 m) or long distances (≥50 m). Values are shown for each age–sex class. Also shown is the mean difference at which first response was recorded.

	All	**Adult male**	**Adult female**	**Adolescent**	**Immature**
% arboreal responses	73.7	56.1	89.2	96.2	98.4
% terrestrial responses	26.3	43.9	10.8	3.8	1.6
% short-distance responses	37.7	45.6	24.6	19.2	36.5
% long-distance responses	62.3	54.4	75.4	80.8	63.5
Mean (± SD) distance (in metres)	60.4 (± 31.6)	53.4 (± 30.9)	70.7 (± 32.0)	69.8 (± 24.3)	66.2 (± 31.3)

The proportion of first responses for adult males that occurred on the ground (44%) was significantly higher than for adult females (11%), adolescents (4%) and immatures (2%) (χ^2 = 63.4, *df* = 3, *p* <0.001). Accordingly, the initial distance at which adult males were seen was shorter on average compared to other age–sex classes (Table 8.4). Responses were categorised as either short-distance (<50 m) or long-distance (≥50 m). The proportion of first responses that were short- or long-distance differed significantly among age–sex classes (χ^2 = 13.3, *df* = 3, *p* = 0.004). Adult male first responses were recorded at shorter distances more often than expected, whereas the opposite was true for adult females and adolescents.

Adult males and females differed significantly in their first response to researchers (χ^2 = 25.3, *df* = 3, *p* <0.001) (Figure 8.2). Compared to females, males were more likely to monitor and less likely to ignore and retreat from us. Threatening behaviour was only performed by adult males. Although ‘threaten’ was the first response of adult males in only 12% of cases (Table 8.3), instances of researcher-directed aggression were recorded during 34% of all encounters and often involved charging displays by terrestrial individuals obscured by thick vegetation. Chimpanzees reduced the distance to researchers in 23% of encounters, typically when adult males charged at or displayed towards us. On eleven occasions the distance was reduced to 10 m or less. The profile of responses for immatures was similar to that of adult females, while adolescents were observed too infrequently to draw conclusions.

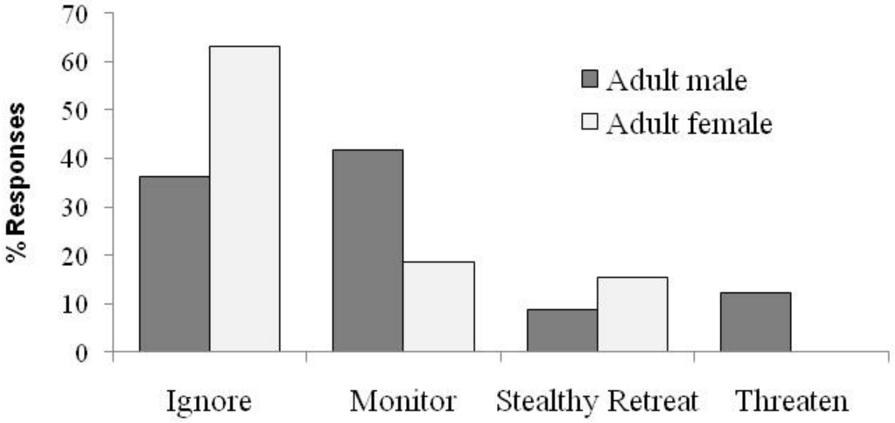

Figure 8.2. First observed response of individual adult male and adult female chimpanzees to researchers.

Community Size and Composition

By September 07 six adult males were individually recognised by researchers. These individuals were seen regularly and comprised two young adults (~18–20 years), three prime adults (21–about 30 years), and an elderly individual, whose grey coat, crooked back and bald head suggested he was ≥40 years (Plate 14). Individual adult females were seen less frequently than males, and at typically greater distances, but a minimum of seven parous females were present during the study. Only one young adult female was seen without dependent offspring. All others were accompanied by 1–3 infants/juveniles.[2] A young adolescent male and at least two adolescent females were occasionally seen. Thus the chimpanzee community at Bulindi comprised a minimum of 25 individuals during 2006–8, but probably numbered 30 or more. None of the chimpanzees exhibited obvious snare-related injuries, though an adult male (JL) had scarring on one wrist that could have resulted from a snare. Despite the fact chimpanzees at Bulindi are occasionally caught in steel man-traps (see below), no individuals were seen with missing hands or feet.

Encounter Types

The most common encounter type was 'Ignore' (36%), followed by 'monitor' (21%), 'intimidation' (18%) and 'stealthy retreat' (18%). Eight encounters were not categorised due to the range of behaviours recorded. Location tended to have an influence on encounter type, although this pattern could not be tested statistically due to insufficient data across all conditions (Table 8.5). In dense forest 'intimidation' was the most common encounter type (40%) whilst 'ignore' was rarely recorded (6.7%). In contrast, when chimpanzees were observed from gardens at the forest edge the majority of encounters were categorised as 'ignore' (67%). Encounters in forest clearings showed an intermediate pattern. The most common encounter types in gardens outside of forest were 'monitor' and 'stealthy retreat'. Roadside encounters were few, but were most often characterised by monitoring behaviour. 'Intimidation' encounters rarely occurred outside of dense forest or forest clearings. Visual proximity to local people did not influence encounter type ($\chi^2 = 0.718$, $df = 3$, $p = 0.87$). Encounter type was related to the distance between chimpanzees and researchers during the majority of the encounter (Kruskal–Wallis: $H = 40.28$, $df = 3$, $p < 0.001$). Distances were shortest during

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[2] One female had two infants, initially assumed to be twins. In fact, one infant was almost certainly older than the other by approximately one year, suggesting one of these infants had been adopted.

‘intimidation’ encounters (median: 30 m) and greatest in ‘ignore’ encounters (75 m); corresponding distances for ‘monitor’ and ‘stealthy retreat’ types were 35.5 and 36 m, respectively.

Chimpanzees demonstrated a notable reluctance to depart contact sites after encountering researchers. In only one case of ‘intimidation’ (5%) did chimpanzees terminate the encounter by moving away. Chimpanzees remained present but out of view in ≥38% of ‘stealthy retreat’ encounters. In ≥63% of ‘monitor’ encounters chimpanzees were still at the encounter site when we left the area. (In some instances it was not possible to confirm if parties that were silent and no longer visible remained present or had moved away).

Table 8.5. The proportion of chimpanzee encounter types recorded in different locations.

Location Type	***n***	**Encounter Type [1]**									
		Ignore		Monitor		Intimidation		Stealthy Retreat		Undetermined	
		%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
Dense Forest	30	6.7	2	20.0	6	40.0	12	26.7	8	6.7	2
Forest Clearing	22	36.4	8	22.7	5	27.3	6	9.1	2	4.5	1
Forest Edge	43	67.4	29	9.3	4	4.7	2	11.6	5	7.0	3
Garden	15	6.7	1	40.0	6	6.7	1	40.0	6	6.7	1
Roadside	5	20.0	1	60.0	3	0.0	0	0.0	0	20.0	1
All	115	35.7	41	20.9	24	18.3	21	18.3	21	7.0	8

[1] Values show the percentage of encounters in each location type that were categorised as ‘ignore’, ‘monitor’, ‘intimidation’ or ‘stealthy retreat’, or were undetermined.

Mobbing and Pursuit of Researchers

‘Intimidation’ encounters were characterised by prolonged or repeated outbursts of display behavior and alarm vocalisations in response to researcher proximity or approach. Further, in 12 of 21 cases (57%) a concerted effort was made to drive us away through aggressive mobbing (n = 10) or pursuit (n = 2). In at least five instances of mobbing ≥2 chimpanzees approached simultaneously from different directions so we felt partially surrounded. On five occasions the mobbing was brief (≤3 min), occurring when we inadvertently encountered chimpanzees at close range (5–30 m) apparently resting, or perhaps hiding, on the ground. In each case the apes quieted once we retreated a short distance (e.g. 50 m). In four of the remaining cases adult males continued mobbing us until we exited the forest. On these occasions mobbing was sustained for between 8 and 35 min; as we retreated chimpanzees maintained the distance separating us by displaying closer. In the final case we did not retreat in spite of the mobbing and the chimpanzees departed the encounter site after 30 min. Instances of mobbing were restricted to encounters in dense forest (*n* = 8) or forest clearings (*n* = 2); in all but one case mobbing was performed by terrestrial individuals. Only on three occasions were mobbing individuals visible (though other chimpanzees present were sometimes observed in trees); in all other instances dense ground vegetation precluded visual observation despite the short distances between researchers and apes.

The two cases of 'pursuit' were particularly alarming for the researchers and warrant description. On 26 January 07 two researchers were advancing along a narrow chimpanzee trail in a strip of gallery forest. At 1302 movement in the undergrowth ahead indicated the presence of chimpanzees apparently travelling from the opposite direction. We began walking back along the trail for ~50 m seeking a clearing so we could move to the side and observe the animals as they passed. However, visibility on either side of the trail was less than 5 m. At 1306 a large male chimpanzee (SL) came into view behind us (10 m distant), staring threateningly. Anticipating that the apes would wait for us to depart before following, we resumed walking back along the trail towards gardens. Immediately, however, chimpanzees began to follow, remaining at a distance of 5–10 m. Four adults were seen, presumed to be males, moving in single-file and in a tight pack. As we quickened our pace, so did the apes. All four animals then charged together, causing us to panic and run along the trail. The apes did not vocalise but the sound of their running was audible. When we reached the garden at 1310 the chimpanzees cut short their pursuit. For the first time the animals vocalised, pant-hooting and drumming from approximately 20 m inside the forest edge. At 1324 calls and drumming indicated they had moved back into the forest from the direction they had come. The length of the pursuit was 230 m.

The second incident occurred on 22 June 07. Three researchers were collecting nest data and no vocalisations had been heard during the preceding three hours in the forest. Abruptly at 1329, following a brief drum, vegetation began to be thrashed about 5 m behind us. It was not clear if chimpanzees had silently approached to 'ambush' us or had been present all along, potentially resting on the ground. The ground vegetation was chest-high and the apes were not visible. After a moment at least one chimpanzee charged, very rapidly, from a different direction straight towards us. At 5 m the animal showed no sign of stopping, prompting us to retreat hurriedly for 80 m to a patch of elephant grass at the forest edge. On this occasion the pursuing chimpanzees were not seen. However, as in the previous case, the apes vocalised and drummed inside the forest edge at 1331, demonstrating they had indeed followed us. The two instances of pursuit were distinct from mobbing in that the chimpanzees remained silent until we left the forest patch, after which they appeared to return to the location where they were initially encountered (as indicated by calls).

Changes in Encounters Over Time

In order to assess whether the relative proportion of each encounter type changed as the study progressed, data were divided into five time periods: period 1 = May–June and October–December 06 (*n* = 10 encounters); period 2 = January–March 07 (*n* = 25); period 3 = April–June 07 (*n* = 21); period 4 = July–September 07 (*n* = 27); period 5 = October 07–January 08 (*n* = 32). Whereas ‘monitor’ and ‘stealthy retreat’ encounters showed no significant change throughout the study, ‘ignore’ encounters increased significantly whilst the incidence of ‘intimidation’ encounters decreased significantly across time periods (Table 8.6). Notably, no encounters during the final four months of the study were categorised as ‘intimidation’. To illustrate this shift towards tolerance, on 31 December 07 three adult males approached two researchers to 7 m and calmly watched us from the shade of a *Lantana camara* thicket for 24 min before moving away. On 14 January 08 we encountered a party of chimpanzees including ≥4 adult males in the same stretch of gallery forest where males had aggressively pursued us 12 months earlier. On this occasion they silently bypassed us on the ground at a distance of 8 m before resting out of view nearby.

Table 8.6. The proportion of encounters categorised as ‘ignore’, ‘monitor’, ‘intimidation’ or ‘stealthy retreat’ over five time periods.

Encounter type	***n***	**Time Period (%)** [1]					r_s
		1	**2**	**3**	**4**	**5**	
Ignore	41	10.0	32.0	38.1	33.3	46.9	0.900*
Monitor	24	10.0	8.0	23.8	33.3	21.9	0.600
Intimidation	21	50.0	28.0	23.8	14.8	0.0	-1.000**
Stealthy Retreat	21	30.0	24.0	14.3	11.1	18.8	-0.700

[1] Values show the percentage of each encounter type in each time period: period 1 = May–Jun and Oct–Dec 06 (*n* = 10 encounters); period 2 = Jan–Mar 07 (*n* = 25); period 3 = Apr–Jun 07 (*n* = 21); period 4 = Jul–Sept 07 (*n* = 27); period 5 = Oct 07–Jan 08 (*n* = 32). In some columns values do not total 100% because eight encounters that could not be categorised are omitted.

* $p < 0.05$; * * $p < 0.01$

Although median encounter duration did not significantly change across time periods (Kruskal–Wallis: $H = 7.59$, $df = 4$, $p = 0.11$), the average length of encounters increased from 21–38 min in periods 1–3 to >1 hr in periods 4 and 5 (Figure 8.3). This was due to an increase in the incidence of encounters lasting ≥2 hrs in the latter periods. These results suggest that during the final months of the study some habituation had occurred.

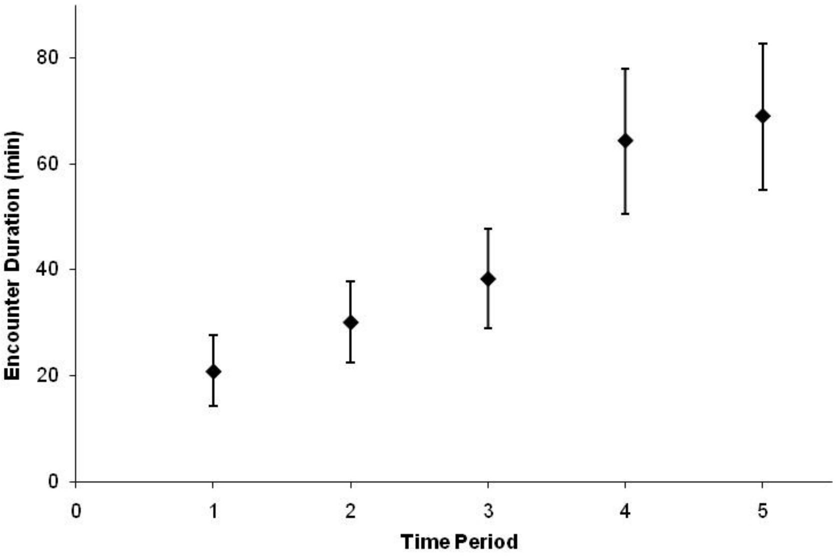

Figure 8.3. Changes in the average (mean ± SE) duration of encounters over five time periods: period 1 = May–Jun and Oct–Dec 06; period 2 = Jan–Mar 07; period 3 = Apr–Jun 07; period 4 = Jul–Sept 07; period 5 = Oct 07–Jan 08 ($N = 115$). Spearman Rank Correlation: $r_s = 1.000$, $p < 0.01$.

8.3.2. Interactions Between Chimpanzees and Local People

Harassment of Chimpanzees

Chimpanzees at Bulindi encounter local people daily, both in and outside the forest. During this study, interactions between people and apes varied from passive indifference, as when chimpanzees fed in trees overlooking gardens, to aggressive confrontation. Although some villagers were tolerant of chimpanzees, harassment by people, including shouting, stone-throwing and chasing with dogs, occurred regularly – most often in the context of crop-raiding or when a threat of crop-raiding was perceived. The motivation for the harassment was not always clear, however. For example, when travelling between Kiseeta and Kaawango forests chimpanzees crossed the main Hoima–Masindi road at Bulindi trading centre. If the apes were seen or heard, people at the trading centre would sometimes attempt to prevent them crossing (e.g. by shouting and throwing stones). Migrant workers at a small-scale distillery bordering Kiseeta forest routinely threw stones and sticks at chimpanzees travelling to and from the forest, apparently for entertainment. Harassment also came from hunters. For example, in December 07 hunters entered a small ecotone forest patch at Katigiro and began driving the chimpanzees away by ringing bells, shouting and whistling loudly (by blowing through their hands). Hunters also used dogs to harass crop-raiding apes. On 31 August 07 chimpanzees raided papaya and ripe cocoa in Kyabateke and Kyabawaza villages around Kaawango forest and were pursued by two teams of trained hunting dogs. A male chimpanzee was attacked by the dogs, but apparently escaped. The following day, the largest adult male (SL) was observed with fresh wounds on his back, possibly caused by dog bites.

Perhaps the most frequent harassment was by children who habitually mimicked the pant-hoot vocalisations of nearby chimpanzees, and for whom provoking the apes was evidently a game. Several times boys were discovered attempting to disturb or chase apes with dogs. In one instance, boys chased two chimpanzees with dogs from a community well directly into the path of researchers who were in adjacent forest. Twice, following reports of ‘fights’ between groups of children and chimpanzees at forest wells in Kiseeta and Mparangasi, we found broken branches on footpaths in association with disturbed vegetation, apparently resulting from chimpanzee displays. The branches were reportedly used by the apes to threaten people. In the Kiseeta case, boys apparently went at dusk specifically to disturb chimpanzees that had nested in forest behind the well. Harassment may have been a causal factor in a chimpanzee attack on a child in January 07 (see below).

Killing of Chimpanzees

The Banyoro do not eat nonhuman primates but no evidence suggested that local people at Bulindi hold totemic beliefs about chimpanzees. However, killing them is traditionally believed to bring bad luck or death, and carries a perceived risk of prosecution. Even so, according to several villagers, about one year prior to the study ≥1 chimpanzee was killed raiding sugarcane in Nyakakonge village. During April–May 07 two apes were locally reported to have been caught in steel ‘man-traps’ set to protect sugarcane. The first incident occurred in Kyam-Paka village; Alur hunters subsequently reported seeing the chimpanzee in nearby hills in Kandanda–Ngobya FR, the trap still attached to its arm or leg. The second ape was caught in a trap placed on a chimpanzee path leading to a sugarcane garden adjoining Kiseeta forest. The garden's owner had previously complained angrily about crop-raiding by chimpanzees; since baboons were absent from Kiseeta, the trap was probably intentionally set for chimpanzees. According to local reports, the ape freed itself after several days (apparently leaving its foot in the trap), during which time other chimpanzees had remained at the trap-site, which prevented the approach of people. In each case, news of the trappings reached field assistants after an interval of ≥1 week, apparently because local villagers feared prosecution and were reluctant to inform the research team. Our attempts to locate the trapped individuals were unsuccessful, and since no injured chimpanzees were subsequently seen, these individuals may have died.

On two occasions we found apparent evidence of an attempt to poison chimpanzees. In June 07 bananas were placed on a chimpanzee trail in gallery forest adjacent to a large banana plantation in Nyaituma village. Farmers in this area complained of losing money because chimpanzees frequently raided brewing bananas ripening in an underground store (Appendix 4). In November 07 bananas were put out in a sugarcane garden that, at that time, was being visited daily by chimpanzees travelling between Katigiro and Kiseeta forests; many large stones were also present among the sugar, apparently having been thrown at raiding apes. In both instances, an unknown substance was detectable in small piercings made in the fruits.[3] There was no indication that chimpanzees ate the bananas in either case.

Aggression towards Local people by Chimpanzees

Human-directed aggression by chimpanzees was not limited to encounters with researchers. Across Bulindi local people complained of being threatened and chased by chimpanzees, not only in forest, but also in gardens and on village paths (Chapter 9). Pitsawyers described being "surrounded" by apes while working in the forest. The following interactions between pitsawyers and chimpanzees were recorded: On 31 October 06 chimpanzees were heard displaying and drumming for approximately 2 hours close to men cutting timber with a chainsaw in Kyamusoga; the men were

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[3] Field assistants speculated that the substance was Furadan®, an insect pesticide that has been used to poison 'problem' wildlife in various parts of the world, including in Uganda where cattle herders in Queen Elizabeth National Park allegedly used it to kill lions (Okeowo 2007). Paterson (2005) mentions use of Furadan to poison bait by farmers in neighbouring Masindi District.

occasionally heard shouting, apparently to dissuade the apes from approaching. On 16 March 07 we were recording phenology in Kiseeta near a busy pitsaw camp. Chimpanzees were thought not to be in the forest at the time. We were therefore surprised at the sudden approach into the logged area by an adult male which displayed and drummed 20 m behind the pitsawyers. On 11 October 07 chimpanzees in Kyamusoga were heard screaming and drumming intensely for 14 min. When we approached to investigate we found pitsawyers had entered the area where chimpanzees were and had begun cutting a tree.

Chimpanzees occasionally demonstrated a willingness to engage in prolonged aggressive confrontation with humans. For example, on 25 October 07 local hunters set dogs on a small party of chimpanzees feeding in a banana plantation in Kyabateke village near Kaawango forest. During the ensuing melee (which was audible >1 km away at the trading centre) two dogs were made lame and, according to local accounts, the chimpanzees did not flee despite the dogs and the many people gathered to watch. One man commented that the apes “wanted to fight”. In the most striking case, chimpanzees remained at a conflict site to confront a man who was trying to scare them away from his home by shooting in the air. An account of this unusual incident is given in McLennan (2010) (Appendix 6).

Physical attacks. Physical aggression towards humans by chimpanzees was very rare during the study and confirmed cases were limited to two attacks on children. In the first case (January 07), children encountered chimpanzees at a well in a small pocket of riverine vegetation between Kyamalera and Kiseeta forests. A four-year old boy was grabbed and bitten on the head, foot and abdomen. This was apparently the first time a young child had been attacked at Bulindi. In the second case (October 07), a four-year old boy collecting firewood in Katigiro disturbed a chimpanzee, possibly hiding in undergrowth by the path, and was grabbed and dragged but not bitten. Further details of these incidents are given in Appendix 5.

There were no confirmed reports of the apes making physical contact with adult humans. However, the following incident was reported by a middle-aged woman in Mparangasi on 20 June 07. The woman was alone in her rice garden in an area of recently cleared gallery forest when she heard chimpanzees vocalising nearby. Presently the animals were heard moving through thick vegetation in order to pass her; however, one “very large” chimpanzee (presumably an adult male) approached the woman directly in the garden. She began running with the ape chasing immediately behind her. She reached a felled *Albizia* tree at the garden’s edge, climbed onto it, but slipped and fell over the other side. The chimpanzee also climbed over the log and reached out to touch or grab the woman’s leg as she lay on the ground, but appeared hesitant. She kicked out and shouted, and the ape retreated. When she stood up, it approached her a second time, but moved away after she shouted again. The woman declared surprise at the chimpanzee’s behaviour since one had never before chased her.

8.4. Discussion

Chimpanzee Behaviour During Encounters

The behaviour of chimpanzees at Bulindi during encounters with humans shows some differences with reports involving unhabituated forest-living chimpanzees at other sites. Unlike chimpanzees at Lopé (Tutin and Fernandez 1991) and Kibale (Grieser Johns 1996), those at Bulindi seldom responded with ‘flight’. Instead the most common first response to visual contact with researchers was ‘ignore’ followed by ‘monitor’. Although the apes occasionally appeared interested in us, the surveillance behaviour typical of monitoring chimpanzees is distinct from the intense curiosity in observers exhibited by ‘naïve’ chimpanzees at Goualougo (Morgan and Sanz 2003). Threat behaviour was an uncommon first response of chimpanzees at Bulindi, but researcher-directed threats were subsequently recorded in one-third of encounters. Eighteen percent of encounters were characterised by intense agitation and/or alarm in response to our proximity. Adult male chimpanzees at times acted together to repel researchers through highly effective intimidation displays (mobbing) or, on two occasions, by pursuing us. It is difficult to compare the frequency of threat responses across sites as it is unclear if the response category ‘charge’ used in previous studies (defined as ‘rapid, noisy running approach, either direct or oblique, towards the observer’; Tutin and Fernandez 1991: 190) encompasses the range of threat behaviours observed at Bulindi (Table 8.1). Regardless, ‘charge’ was a very rare response at Lopé and was absent at Goualougo. At Kibale, where chimpanzees were undergoing habituation for tourism, ‘charge’ was the initial response in 13% of cases. Three times chimpanzee parties at Lopé ‘mobbed’ researchers discovered at close-range, as they might a potential predator, but a full description of the behaviour was not given. The silent, aggressive pursuit of retreating humans at Bulindi appears to be unique among populations studied to date. Although the animals' motivational state during these incidents is unknown, the behaviour shows interesting parallels with the silent stalking and pursuit of extra-group strangers by male chimpanzees during intergroup territorial encounters (e.g. Boesch and Boesch-Achermann 2000).

Though previously unstudied, the Bulindi chimpanzees were not 'unhabituated' in the classic sense of the word. Beginning several years prior to the study, the riverine forests were being logged of most marketable timber and large sections were being cleared as farmers sought fertile soil to plant tobacco and rice, or to establish pine or eucalyptus plantations. Local reports suggest that a change in the frequency and quality of interactions between people and apes had occurred concurrently (Chapter 9). In particular, chimpanzees had begun ranging outside of forest into village areas and the incidence of crop-raiding had reportedly risen dramatically. Intensifying human activities in and around forests, coupled with a shift in the foraging and ranging patterns of the apes, meant that encounters between people and chimpanzees were increasingly commonplace and were frequently agonistic. The mixture of responses shown by chimpanzees during encounters with the research team reflected this familiar yet competitive relationship with humans.

Pitsawyers were an enduring presence in forests throughout this study. In addition, local households relied heavily on forest produce and people regularly entered forests to collect firewood, cut poles, burn charcoal and hunt small mammals. Therefore chimpanzees could expect sudden encounters with humans, including researchers, at any time. The risk of close, unexpected encounters between people and apes was increased by dense undergrowth that hampered visibility on the ground. Noisy parties of chimpanzees were frequently present in forest in proximity (<100 m) to areas of busy human activity (e.g. wells and distilleries inside the forest, or near pitsaw camps). In some instances, the chimpanzees' loud vocalisations and drumming may have functioned to communicate their presence to people and dissuade them from approaching; certainly, chimpanzees at times made no attempt to conceal their whereabouts from local people or researchers. This is in apparent contrast to chimpanzee behaviour in similar forest–farm habitat at Kasokwa, 25 km northeast of Bulindi, where the apes "do not engage in loud pant-hoot choruses", perhaps to avoid detection by humans (Reynolds 2005: 214). At Bulindi some local people would not enter the forest if chimpanzees were heard vocalising. Frequent encounters with people in the forest are likely to have costs for chimpanzees in terms of disruptions to their activity budget (e.g. time spent feeding). Consequently, the animals' marked reluctance to depart an encounter site following contact with researchers inside the forest might reflect a strategy to minimise such costs. Indeed, mobbing and pursuit of intruding humans in forest is an effective strategy if it enables the chimpanzees to remain at a feeding site.

Sex Differences in Behaviour

Adult males and females exhibited contrasting behaviours during encounters. Compared to females, adult males were more likely to be seen on the ground and at shorter distances, and most commonly exhibited surveillance behaviour during the first minute of an encounter. The paucity of response data for terrestrial females is related to the fact that females were mostly seen feeding in trees, and parties encountered outside of the forest in gardens were mainly comprised of adult males on crop-raiding forays. At Bossou, all-male parties were also more likely to enter village areas to raid crops than other party compositions (Hockings 2009). Although the most frequently observed response of adult females at Bulindi was 'ignore', females tended to feed towards the far side of tree crowns where they were less visible to researchers. In contrast, males positioned themselves on exposed branches where they could monitor humans (Plate 15). As at Bossou (Hockings et al. 2006), individual males showed 'guarding' behaviour when mixed parties crossed roads or footpaths by staring at, and occasionally threatening, human observers for up to 3 min before and/or after other chimpanzees had crossed.[4] The fact that infant and juvenile chimpanzees were frequently seen when adult females were not further suggests females tended to remain out of view when in proximity to humans. Whereas adult males risked confrontations with humans in the open, and were disproportionately represented in direct observations, female chimpanzees adopted a more furtive strategy, apparently avoiding visual contact with people unless arboreal and accompanied by adult males. 'Stealthy retreat' was seen

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[4] During one roadside encounter, an adult male (JL) sat glaring at observers across the main Hoima–Masindi road, seemingly oblivious to passing vehicles, which were ordinarily avoided by the apes.

more often in females than males. Only adult males displayed a willingness to confront humans encountered in dense forest or forest clearings by approaching to monitor and/or intimidate them.

Interactions with Local People

Despite exhibiting frequent aggressive behaviour during encounters, the chimpanzees never physically attacked researchers. While western lowland gorillas (*Gorilla gorilla*) occasionally direct physical aggression towards researchers during habituation (Ando et al. 2008), similar behaviour has not been reported for chimpanzees.[5] On rare occasions both gorillas and chimpanzees have been reported to attack local adult humans if wounded or threatened (Sabater Pi 1966; Madden 2006; McLennan 2008). At Bulindi, the two cases of physical aggression against humans involved young children. Following the study, a third attack occurred in August 2008 in which an infant received serious injuries to the face and head (M. Ssemahunge, pers. comm., 2008). Chimpanzee attacks on children, including instances of predation, are recorded at a growing number of sites where encroachment on chimpanzee habitat has increased contact between apes and local humans (Goodall 1986; Wrangham et al. 2000; Kamenya 2002; Reynolds 2005; McLennan 2008; Hockings et al. 2010). The incidents at Bulindi do not appear to represent predatory attempts since in neither of the documented cases did the attacking chimpanzee eat from the victim. However, insufficient details are available for the third case. Given the frequency with which these chimpanzees encounter children, perhaps the most striking aspect of these incidents is their rarity. Regardless, attacks understandably generate fear and hostility towards the apes locally and may trigger retaliatory killings (Wrangham 2001; Reynolds 2005). Indeed, following the second attack, the question of whether or not the chimpanzees should be killed was discussed by residents at Bulindi trading centre.

Chimpanzees at Bulindi experience high levels of harassment from local people. The most severe harassment occurred when chimpanzees travelled to Kaawango and raided crops in Kyabateke and Kyabawaza villages, home to three hunting households who

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[5] The only published report of an unhabituated chimpanzee attacking researchers occurred at Mahale when members of the habituated study group attacked an infant from a neighbouring community. During the incident the victim's presumed mother seriously wounded two researchers (Kutsukake and Matsusaka 2002).

occasionally fiercely pursued the apes with dogs to drive them away from their village. Kaawango was outside of the apes' core range (Chapter 7) and, perhaps as a consequence, residents were especially outraged when chimpanzees' appeared at their homesteads. Adult male chimpanzees seem to have responded to increasing competitive encounters with people with frequent non-physical threatening behaviour that often causes humans to retreat. Local reports suggest the habit of charging and pursuing fleeing humans, especially women and children, was adopted only recently (Chapter 9). Such behaviour is not equivalent to the displays occasionally directed at research personnel at some sites by over-habituated apes; at Bulindi encounters with people carry a real risk of danger for the chimpanzees, as when people throw stones and sticks or chase them with dogs. While boldness in encounters with humans and during forays into village areas may enhance the social status of adult males (cf. Hockings et al. 2007), human-directed aggression by chimpanzees at Bulindi is best viewed as a strategy adopted by the animals under difficult and deteriorating circumstances. Ultimately, such confrontational behaviour jeopardises their future survival, for in the long-term local people are unlikely to tolerate it. Relevant to these observations, Goldberg et al. (2008) describe unusual human-directed aggression by red colobus monkeys (*Procolobus rufomitratus*) in degraded forest fragments around Kibale NP, which they attribute to the frequent hostile interactions that primates have with local people and dogs.

The Bulindi Chimpanzee Community

During the study the chimpanzee community at Bulindi comprised a minimum of 25 individuals, including six adult males. While small relative to most rainforest-living communities (which average ~50 individuals; see Table 7.4), community size is larger than might be expected in such heavily disturbed and fragmented habitat. Elsewhere at Kasokwa and Bossou where chimpanzees also occupy small forest patches surrounded by farmland community size has numbered 12–20 individuals, including just 1–3 adult males (Reynolds et al. 2003; Sugiyama 2004). One possibility is that prior to extensive deforestation the riverine forests at Bulindi and elsewhere in Hoima were rich in chimpanzee foods (Chapters 3 and 4), supporting a higher population density than expected (McLennan 2008). Apparent differences in loud vocal behaviour between Bulindi and nearby Kasokwa (discussed above) may reflect the larger community size and/or greater number of adult males at Bulindi. Similarly, the frequent aggression directed towards humans at Bulindi could be related to the number of males, although temperaments of individual apes might also be a factor. For example, the largest (but not highest-ranking) male (SL) was disproportionately responsible for visible charging displays at researchers.

The absence of snare- or trap-related injuries in the chimpanzees was unexpected. Incidental snaring of chimpanzees is common in Uganda's main forest blocks. As many as 25% of individuals in study communities at Budongo (Reynolds 2005) and Kibale (Muller 2000) exhibit injuries attributable to snares; the figure exceeds 50% for adult males at Kalinzu (Hashimoto 1999). Local hunters at Bulindi catch small mammals with nets and dogs and no snares were encountered in the forest. Even so, some farmers do place steel 'man traps' (or 'leg-hold' traps) around cultivated fields to deter crop raiding animals, and two apes were reportedly trapped during this study. A chimpanzee caught in a trap, whether intended or accidental, may have great difficulty removing the device. For example, an adult male at Kasokwa – already missing a foot from a previous trap encounter – died from septicaemia some 10 days after getting his hand caught in a trap (Munn and Kalema 2000). The lack of observations of injured chimpanzees at Bulindi implies that the trapped individuals may have died from their wounds.[6]

Habituation Issues

The decision to habituate wild great apes for research or tourism must be carefully evaluated (Goldsmith 2005). The habituation process itself is evidently stressful for the animals, especially during initial stages, frequently provoking fear and/or aggression and disrupting foraging and ranging patterns (e.g. Blom et al. 2004). Compounding the potential negative effects of physiological stress on the animals' immuno-response system, increased contact with humans carries the considerable risk of disease transmission, which may cause high mortality and result in local population declines (Wallis and Lee 1999; Woodford et al. 2002; Kaur and Singh 2008; Köndgen et al. 2008). Other major concerns are that loss of fear of humans leaves apes more susceptible to poaching (Kasereka et al. 2006), exacerbates crop-raiding behaviour

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[6] A third case occurred in January 2009 when an adolescent female was caught in a man-trap in Kyabawaza village by Kaawango forest. The device was successfully removed by veterinarians from the Budongo Conservation Field Station and the Jane Goodall Institute (Kidega 2009).

(Goldsmith et al. 2006; Madden 2006), and increases the risk of physical attacks on humans (Madden 2006; Hockings et al. 2010).

Habituating chimpanzees without the aid of artificial provisioning may take years of repeated contacts (Bertolani and Boesch 2008). In this study, chimpanzees were encountered both opportunistically and inadvertently and no systematic attempt was made to habituate them. In spite of this, and despite the low visibility in the forest and the frequent negative interactions between apes and local people, certain chimpanzees at Bulindi showed signs of habituating relatively quickly to researchers. The apes' familiarity with villagers meant that the flight response characteristic of unhabituated chimpanzees during initial contacts with people was seldom seen, and from the start they often ignored humans in gardens when feeding in trees overlooking farmland. As the study progressed, the proportion of encounters categorised as 'ignore' increased, as did the average duration of encounters. During the final three months large mixed parties could be observed in trees from distances of 30–50 m without inciting more than mild interest, and observation of social behaviour was possible. While chimpanzees continued to exhibit monitoring or avoidance behaviour when encountered on the ground, and occasionally threatened us, they no longer reacted with intense alarm and aggression even when approached in dense forest.

This change in behaviour was mainly due to the growing tolerance of adult males, since individual adult females were seen infrequently. Following a succession of close-range charges and displays in July–August 07, which aroused no reaction from the research team, adult males became noticeably more relaxed around us (Plate 15). Importantly, this increased tolerance was not extended to local people. August–December was a time of relative fruit scarcity in Bulindi forests and chimpanzees regularly sought agricultural foods in village areas (Chapter 7). During this period, disturbances between people and apes occurred on a near-daily basis and included incidents of chimpanzees chasing and threatening people. Apparently, the chimpanzees distinguished members of the research team from other humans in their habitat.

It is widely recognised that both real and perceived costs associated with living alongside wildlife decrease local people's tolerance for wildlife (e.g. Newmark et al. 1993; Hill 2002, 2005; Naughton-Treves and Treves 2005; Madden 2008). Tourism is a significant growth industry (Brockington et al. 2008), and wildlife tourism is commonly proposed as a non-consumptive method of directing income to local stakeholders as a way to promote more positive, and therefore more tolerant, attitudes towards wildlife (Archabald and Naughton-Treves 2001; Walpole and Thouless 2005; Mugisha 2008). One strategy for the management and conservation of chimpanzees occupying human-dominated landscapes outside of protected areas is to establish ecotourism based on chimpanzee-viewing. However, data from Bulindi, together with reports from elsewhere in Uganda of negative interactions between humans and chimpanzees at forest–farm sites around Kibale and Budongo (Wrangham 2001; Reynolds 2005), and between people and mountain gorillas at Bwindi Impenetrable Forest (Madden 2006), strongly caution against habituating great apes for tourism where they live amongst rural human communities. Aside from exacerbating the stress that ape populations may experience from habitat degradation and aggressive competition with humans, a general loss of fear of humans resulting from repeated encounters with tourist groups could lead to increased crop-raiding and aggression towards local people by emboldened or stressed apes. Chimpanzee attacks on humans, especially children, have already occurred at Bulindi and at similar forest–farm sites in the region (Wrangham 2001; Reynolds 2005; McLennan 2008). Here, local people perceive chimpanzees as neither ancestors nor food, but as wild animals that pose a threat to their livelihoods and physical safety. What is needed is effective law enforcement, combined with education programmes and long-term rural development initiatives to provide alternative income sources that reduce pressure on unprotected forests. These issues are discussed further in Chapter 10.

Summary

1. This chapter describes the behaviour of unhabituated chimpanzees at Bulindi during opportunistic encounters with the research team. The most common first responses were ‘ignore’ for arboreal apes and ‘monitor’ for terrestrial individuals; chimpanzees rarely responded with flight;
2. Community size was at least 25 individuals including six adult males. The males were seen disproportionately often relative to adult females; only adult males were frequently observed on the ground;

3. Encounters characterised by intense researcher-directed intimidation occurred when chimpanzees were encountered in dense forest where visibility was low. Adult males sometimes acted together to repel researchers through aggressive ‘mobbing’ and pursuit;
4. Average encounter duration and the proportion of encounters in which the predominant response was ‘ignore’ increased over time, whereas ‘intimidation’ encounters decreased, indicating some habituation occurred during the study;
5. Male chimpanzees at Bulindi display frequent aggressive behaviour during encounters with local people, apparently in response to harassment and increased competition with humans;
6. Habituation of the chimpanzees for viewing-based ecotourism is an inappropriate management strategy since it may lead to increased negative interactions between residents and apes.

CHAPTER 9 – LOCAL ATTITUDES TOWARDS CHIMPANZEES & FORESTS

9.1. Introduction

As humans continue to encroach upon and modify natural habitats, particularly outside of formally protected areas, the importance of human-dominated landscapes for the survival of many primate populations is increasingly recognised (Marsh 2003; Paterson and Wallis 2005; Anderson et al. 2007; Riley 2007a; Isabirye-Basuta and Lwanga 2008; Nasi et al. 2008; Lee 2010). In some circumstances certain primate taxa, notably baboons (*Papio* spp.) and vervet or tantalus monkeys (*Chlorocebus* spp.) in Africa, and macaques (*Macaca* spp.) in Asia, thrive in agricultural and even urban landscapes. However, the propensity for members of these genera to incorporate cultivated foods into their diets may bring them into conflict with their human neighbours (Hill 2000; Saj et al. 2001; Chalise and Johnson 2005; Riley 2007b; Warren et al. 2007; Marchal and Hill 2009; Strum 2010). Unless hunted, African great apes also seem able to adapt to anthropogenically-modified landscapes including forest–farm ecotones, at least in the short-term (Dunnett et al. 1970; Leciak et al. 2005; Goldsmith et al. 2006; Duvall 2008a; Hockings et al. 2009). Aside from availability of resources, however, the activities and attitudes of local people, with respect to both wildlife and land use, are critical to the survival of ape populations inhabiting human-dominated landscapes. The continuing existence of apes in such habitat is dependent on local communities using forests and forest resources sustainably. Studies have shown that local tolerance of primates declines where natural forests are over-exploited or converted to farmland or soft-wood plantations (e.g. Paterson 2005; Goldberg et al. 2008; Nijman and Nekaris 2010). In view of these issues, there is growing interest in the implications of people–ape interactions in shared landscapes for long-term coexistence of humans and great apes (Hockings and Humle 2009; Campbell-Smith et al. 2010; Hockings et al. 2010; McLennan and Hill 2010).

In Africa, attitudes towards great apes are culturally constructed (Richards 1995; Sicotte and Uwengeli 2002; Watkins 2006). While in some regions people's totemic beliefs promote tolerance of the animals (Yamakoshi 2005), human cultural beliefs are subject to modification in response to changing socioeconomic circumstances and other external influences (Lingomo and Kimura 2009). For example, farmers around Budongo Forest formerly held generally positive views of chimpanzees, which caused little damage to food crops. However, tolerance of the apes declined from the mid-1990s when farmers began growing sugarcane – a highly attractive food to chimpanzees – for Kinyara Sugar Works outgrower scheme (Hill 2004; Reynolds 2005). As discussed in the previous chapter, when great apes and people share a landscape and resources and encounter one another frequently, conflicts are likely to emerge (Reynolds 2005; Madden 2006; Hockings and Humle 2009; Laudati 2010; McLennan and Hill 2010). Accordingly, strategies are needed to facilitate human–ape coexistence in shared landscapes.

Successful conservation requires the support and participation of local human communities (Ancrenaz et al. 2007; Browne-Nuñez and Jonker 2008; Kasenene and Ross 2008). Yet conflicts with wild animals resulting from crop losses and/or threats to human physical safety promote negative attitudes towards wildlife, particularly when animals involved are protected by legislation, reducing people's support for conservation (Newmark et al. 1993; Hill et al. 2002; Hill 2004, 2005; Gadd 2005; Naughton-Treves and Treves 2005; Madden 2008). Taking into account local attitudes and concerns regarding wildlife is therefore essential for informing management and policy decisions that reduce conflict (Browne-Nuñez and Jonker 2008). However, little attention has been devoted to understanding the experiences and opinions of local people who live alongside great apes (but see Watkins 2006; Campbell-Smith et al. 2010). The Bulindi situation provides an opportunity to examine factors influencing tolerance of a great ape species in a dynamic and unprotected human-dominated habitat. Consideration of residents' perspectives is essential for developing and implementing locally-appropriate conservation and conflict mitigation strategies at this site and in similar forest–farm mosaics regionally. Accordingly, this aspect of the study aimed to:

1. Explore residents' experiences of living alongside chimpanzees; and examine perceptions of the history of human–chimpanzee interactions at this site;
2. Gauge local opinion about (i) the need for intervention to address residents' concerns about the apes, and (ii) the form that such intervention might take;
3. Assess the importance of local forests to households at Bulindi; and examine residents' perspectives about forest utilisation and management.

9.2. Methods

9.2.1. Interviews

Data were collected by means of structured interviews. Information and opinions communicated during informal discussions with residents outside of interviews are used to supplement the data where appropriate. A total of 134 interviews were conducted between May and August 2007 with residents of 12 villages at Bulindi. Figure 9.1 shows the location of each interview, recorded with a GPS receiver. Most people interviewed (89%) were from seven villages surrounding the chimpanzees' core area (Kihambya, Kihoro, Kiseeta, Kyabateke, Mparangasi, Nyaituma and Nyakakonge), but interviews were also conducted in four villages towards the periphery of the chimpanzees' range (Katikara, Kyabawaza, Kyabigambire, and Kyam-Paka). In addition, two interviews were conducted at Kyarubanga, a village 3 km northwest of Bulindi where chimpanzees were reported seasonally. It is unclear if these chimpanzees were from Bulindi or a neighbouring community that ranged along the Waki River, east of Mukihani FR (see Figure 2 in McLennan 2008).

Interview Protocol

The interview team consisted primarily of two field assistants: a female European with previous experience of conducting social science interviews, and a locally-employed male who acted as facilitator and interpreter when required. During some interviews a second local male assistant was also present. Prior to data collection, local assistants were trained in interview practice. All members of the interview team also participated in forest research activities and were thus locally associated with 'the chimpanzee project'. Interviewers followed a random route through villages, stopping at homesteads if adults were at home. Some interviews were conducted at the Bulindi trading centre, where some residents had shops. With few exceptions a single interview was carried out per homestead, and an effort was made to balance participants according to sex. Although most interviewees were selected opportunistically, some key forest owners were purposely included. In addition, several individuals approached the local assistants requesting an interview; in most cases the interview was duly carried out.

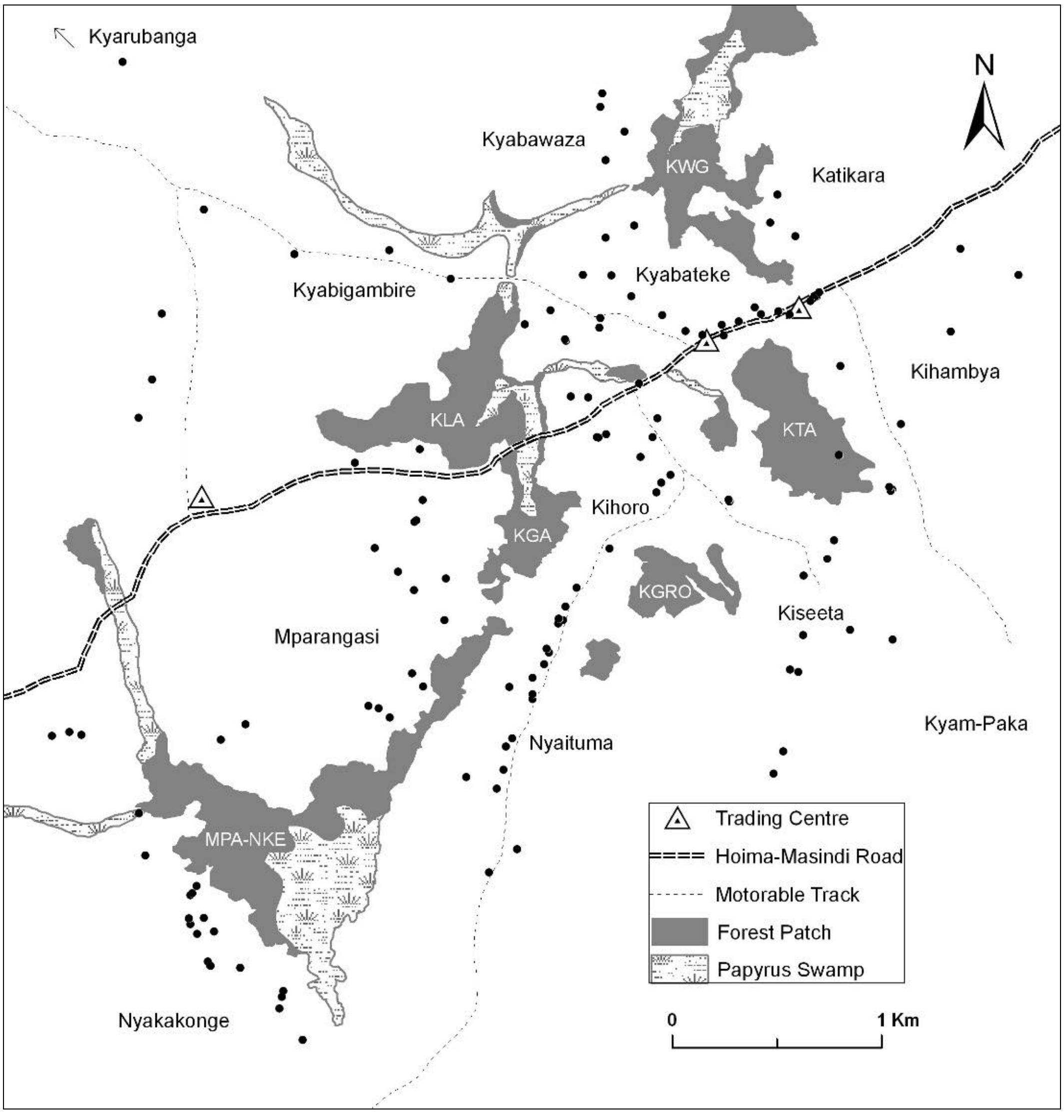

Figure 9.1. Map of study area showing interview locations (black dots) in 12 villages. Two interviews conducted in Kyarubanga village were located 1 km northwest of the area shown. Forest patches: KLA = Kyamalera, KGA = Kyamusoga, KTA = Kiseeta, KWG = Kaawango, MPA–NKE = Mparangasi–Nyakakonge, KGRO = Katigiro.

Prior to interviews the aims of the survey and future use of the data were first explained to would-be interviewees, and they were asked if they wished to take part; only five individuals declined to participate. The majority of interviews (58.2%) were conducted in the local Lunyoro language, 25.4% were conducted in English and 16.4% were carried out using both Lunyoro and English. Participants were asked a predetermined set of questions in a fixed order (Table 9.1). Nevertheless, interviews were carried out in an informal manner and participants were not dissuaded from discussing topics at length if they wished to do so. Interviews lasted 20–60 min. Following the interview participants were given the opportunity to ask questions about the research. Given the interest generated by the interviews a limited amount of interference from passers-by was at times unavoidable.

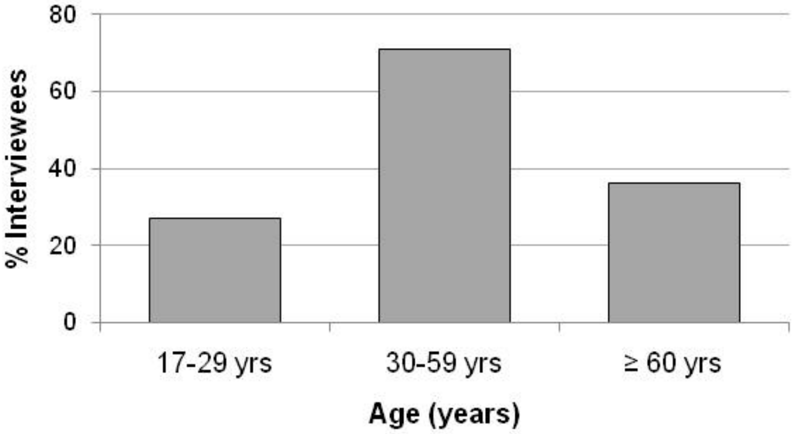

Figure 9.2. Percentage of interviewees in three age classes (*N* = 134).

Men accounted for 53.7% of interviewees and women for 46.3%. Participants ranged in age from 17 to approximately 90 years old. Twenty percent were below 30 years, 53% were aged 30–59, and 27% were aged 60 years or above (Figure 9.2). The majority of interviewees (93%) were native Banyoro. Most had lived locally all their lives; only three individuals had lived in Bulindi for less than five years whereas 41% were resident for >40 years (Figure 9.3). Farming was the stated occupation of the majority of interviewees (69%). Other stated occupations included teaching, shop-keeping, tailoring, carpentry, cattle-herding and pit-sawing. However, such individuals also engaged in agriculture to varying extents.

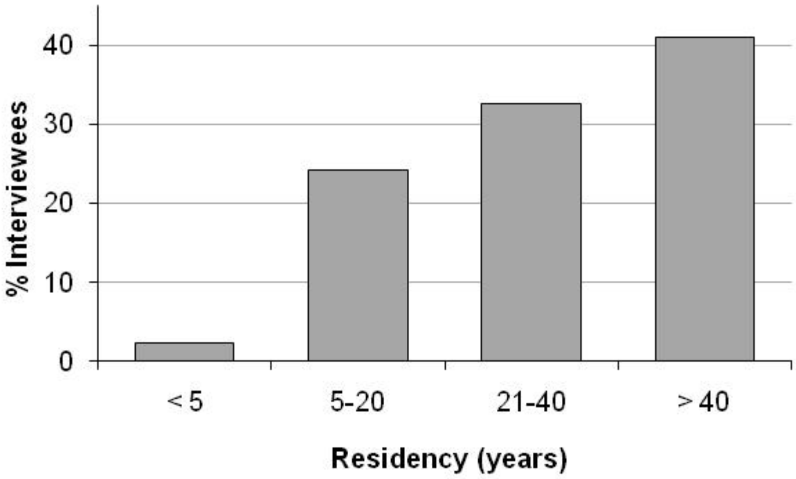

Figure 9.3. Interviewee length of residency at Bulindi (*N* = 134).

Table 9.1. Structured interview questions. For each question, cells show (i) sample size (the number of unambiguous/relevant responses; N = 134), and (ii) the % of responses categorised as 'yes', 'no' or 'unsure'; alternative responses are indicated in parenthesis where applicable.

Question	***n***	**% Interviewee Response**				
		Yes	**No**	**(other)**	**Unsure**	**Total**
1. Have chimps always been in the forests here? ▪ Interviewees who answered 'no' were asked when, and from where, the apes came, and why.	120	87.5	11.7	–	0.8	100
2. In the time you have lived here have chimps become more, less or stayed the same in number? ▪ Interviewees who perceived a change in number were asked why this was so.	132	86.4 ('more')	2.3 ('less')	4.5 ('same')	6.8	100
3. Do you see chimps more often, less often, or about the same, in recent years compared to in the past?	125	83.2 ('more')	6.4 ('less')	5.6 ('same')	4.8	100
4. Do you hear chimps more often, less often, or about the same, in recent years compared to in the past?	125	91.2 ('more')	4.0 ('less')	4.8 ('same')	0.0	100
5. Are chimps dangerous animals? ▪ Interviewees who answered 'yes' were asked to provide a reason(s).	125	73.6	22.4	–	4.0	100
6. Do you fear them?	118	72.9	27.1	–	0.0	100
7. Have the behaviours or habits of chimps changed over time? ▪ Interviewees who answered 'yes' were asked to provide a reason(s).	122	58.2	28.7	–	13.1	100
8. Have the attitudes or behaviours of people towards chimps changed over time? ▪ Interviewees who answered 'yes' were asked to provide a reason(s).	111	48.6	39.6	–	11.7	100
9. Do chimps eat any crops from your own garden? ▪ Interviewees who answered 'yes' were asked which crops.	134	53.0	45.5	1.5 (no garden)	0.0	100
10. How much damage do chimps cause to crops compared to other animals? (Answers were categorised as none, little [or 'not much'], or a lot)	128	25.8 ('none')	64.1 ('not much')	7.8 ('a lot')	2.3	100
11. Which animal(s) cause the most damage?	116	–	–	–	–	–

Cont. overleaf

Table 9.1. *cont.*

Question	***n***	**% Interviewee Response**				
		Yes	**No**	**(other)**	**Unsure**	**Total**
12. Are there any good things about chimps? ▪ Interviewees who answered ‘yes’ were asked to provide a reason(s).	128	70.3	25.8	–	3.9	100
13. In your view, should anything be done about the chimps? ▪ Interviewees who answered ‘yes’ were asked to provide a reason(s).	116	65.5	31.0	–	3.4	100
14. Have the forests at Bulindi changed over time? ▪ Interviewees who answered ‘yes’ were asked to provide a reason(s).	128	68.8	29.7	–	1.6	100
15. Do you or your household own any forest used by chimps? ▪ Interviewees who answered ‘yes’ were asked where the forest was located.	129	48.1	47.3	–	4.7	100
16. Which of the following resources do you or your household obtain from local forests: firewood, craft materials, building materials, wild plant foods, medicines, honey, meat, and resins. ▪ Interviewees were then asked where they would get these resources from if forests are cut down. ▪ Interviewees were also asked if they benefited from the forest in other way(s).	123	–	–	–	–	–

9.2.2. Data Analysis

Interview data are presented as the percentage of participants that gave a particular response to each survey question. Sample size of responses to individual questions varied because interviewees sometimes gave responses that were vague or ambivalent, or else not applicable to the question (Table 9.1). Only responses that could be unambiguously categorised as ‘yes’, ‘no’ or ‘unsure’, or readily grouped into common themes, were included in the analysis. The mean percentage of responses to each question that could be used in analysis was 93.1% (range: 82.8–100%). Chi-square tests were performed to examine relationships between responses and interviewee age, sex and length of residency. In some instances, the number or proportion of interviewees that raised a particular issue at any point during their interviews is given, but these data were not analysed statistically. Likewise, qualitative data obtained outside of interviews are included for supplementary purposes only. Data were analysed in SPSS version 17 and significance was set at $p < 0.05$.

9.3. Results

9.3.1. Chimpanzees at Bulindi – Local Historical Perspectives

The majority of interviewees (87.5%) said that chimpanzees had always been present at Bulindi, particularly in Kyamalera forest (Table 9.1). However, 14 interviewees claimed chimpanzees had arrived from outside the area within their lifetime. Of these, 12 were aged above 60 years and all were older than 50. These individuals variously estimated that chimpanzees came to Bulindi between approximately 55 and 20 years previously. Ten interviewees were able to state where the apes had come from and in all cases said they arrived from Budongo Forest and surrounding areas north of the Hoima–Masindi District border. According to five interviewees, chimpanzees were displaced from this region following widespread forest clearance for the Kinyara sugar estate in Masindi, or else were ‘chased’ away from the sugar. One man opined that chimpanzees came to Hoima after cocoa was planted in the District’s forests during the 1960s. The 73-year old chairman of Kiseeta village commented that when chimpanzees were first seen locally villagers did not know what they were, and one ape was hunted and killed with dogs.

Chimpanzees were widely perceived to have traditionally lived in Kyamalera forest (and adjoining Kyamusoga). In contrast, many residents around Kiseeta, Kaawango and Nyakakonge forests stated that the apes began using these forests only relatively recently (5–10 yrs in Kiseeta and Kaawango forests; 10–20 yrs in Nyakakonge). Recent forest clearance in Kyamalera and the apes' searching for food (e.g. cocoa) were the reasons offered for this perceived range expansion.

Most interviewees (86.4%) claimed chimpanzees had increased in number over time. Asked why they thought this, 75.4% said the apes are "producing" (i.e. breeding) or seen with "babies". Other reasons offered were that the apes are not hunted or harassed; they are "feeding well'; and that nowadays they are seen in places where previously they were not. Several people commented that chimpanzees are now seen in big groups whereas in the past only small numbers were seen (e.g. "1 or 2 animals"), and only rarely. Only three individuals (2.3%) believed chimpanzees had decreased in number. For instance, one woman claimed apes were killed and eaten in Kyamalera by Milton Obote's soldiers during the 'bush war' in 1981–86. (Several other residents also spoke of the presence of soldiers in Kyamalera forest during that period).[1] A large majority of interviewees said they both saw and heard chimpanzees more often in recent years relative to past years (83.2 and 91.2%, respectively; Table 9.1).

9.3.2. Chimpanzees as Dangerous Animals

> *Chimps are coming to people's homes looking for food. In the past they stayed in the forest and were not dangerous. Now chimps threaten children, they want to eat children. So they bring fear* (75-yr old man, Kihambya).
>
> *They are not dangerous because I have been with them [in the forest] for many years and they have never attacked me. If you're humble with them, they're ok* (74-yr old man, former cocoa guard, Kiseeta).

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[1] Curiously, several interviewees also maintained that a number of chimpanzees were taken from Kyamalera forest by a European man in mid-2006, between my field trips. This claim was made by additional residents outside of interviews.

Most interviewees (73.6%) considered chimpanzees dangerous animals (Table 9.1). Of these, 26.1% said that chimpanzees are dangerous, but only if disturbed or attacked by people (Table 9.2). A commonly expressed sentiment was: "If you don't disturb them, they don't disturb you". However, 23.9% cited the recent attack on a child in Kyabateke village as confirmation of the apes' dangerousness. Another reason commonly offered was that chimpanzees 'chase' or 'disturb' people (20.7%). A further 9.8% said the apes can carry away, attack or eat human children, particularly infants, but did not refer to a specific incident, while 6.5% cited chimpanzee attacks on humans which had occurred elsewhere in the Bunyoro region. At various points during interviews, five participants said they had heard that chimpanzees can rape women. Likewise, 11 individuals claimed the apes transmit an unknown skin disease ('*ekisararu*') to people, or else asked if it was true.

Table 9.2. Reasons why chimpanzees are dangerous. Cells show the number and % of interviewees that said chimpanzees are dangerous (n = 92) who gave each reason.

Reason	***n***	**%** [1]
Chimps are dangerous if people disturb (i.e. harass) them	24	26.1
Chimp attack on local child in Jan 2007 cited	22	23.9
Chimps chase / disturb people	19	20.7
General risk to children cited	9	9.8
Other chimp attack on a person cited	6	6.5
Chimps are wild animals	4	4.4
Chimps don't fear people or dogs	2	2.2
Chimps are dangerous if carrying babies	2	2.2
Other individual reason	8	8.7

[1] Percentage values add up to >100% because several interviewees gave > 1 reason.

Women were significantly more likely to say chimpanzees are dangerous compared to men (χ^2 = 5.44, df = 1, p = 0.02). Neither sex was more likely to offer a particular reason to support the claim than the other. Most interviewees (84.5%) who said chimpanzees are dangerous also said they fear them. The overall proportion of interviewees that claimed to fear chimpanzees was 72.9% (Table 9.1). Again, women were significantly more likely to say they fear chimpanzees compared to men (χ^2 = 17.84, df = 1, p <0.001).

9.3.3. Changing Behaviour of Chimpanzees and People

> *In past years I just heard them in the forest, but now they are moving out of the forest everywhere ... At first when chimps saw a person they ran away, now they just come to you. They are becoming serious* (70-yr old woman, Kihoro).
>
> *If you go into the forest and start chasing them it will say to you "where will I go? – this is my house!" If you chase it in the forest it will chase you at the well, and you won't get your water* (59-yr old man, Kyabawaza).

Asked if the habits or behaviour of the apes has changed over time, most interviewees (58.2%) said it has (Table 9.1). However, it was also common for individuals who answered 'no', or were unsure, to describe how chimpanzees have recently changed their behaviour in response to other interview questions. Neither age nor length of residency influenced people's tendency to claim chimpanzees have changed (Age: $\chi^2 = 0.815$, $df = 2$, $p = 0.67$; Residency: $\chi^2 = 1.47$, $df = 2$, $p = 0.48$).[2] Of those who answered 'yes', the most common reason offered was that nowadays the apes are coming out of the forest to people's homes and gardens and damaging crops (53.5%) (Table 9.3). A further 36.6% said chimpanzees are now chasing, threatening or attacking people, while 19.7% claimed the apes no longer fear or run away from people. One woman simply said "These days they look so dangerous". Others noted that chimpanzees have become 'stubborn', 'tough' or 'rude'. An elderly woman in Kihoro village said the apes "are enemies now". One man, referring to the January 07 attack on a child, remarked that "chimps have become tired of people".

Table 9.3. Reasons why chimpanzees have changed over time. Cells show the number and % of interviewees that said chimpanzees have changed (n = 71) who gave each reason.

Reason	***n***	**%** [1]
Chimps are coming out of the forest to homes or gardens	38	53.5
Chimps are chasing, threatening or attacking people	26	36.6
Chimps no longer fear people	14	19.7
Other individual reason	4	5.6

[1] Percentage values add up to >100% because some interviewees gave > 1 reason.

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[2] See Figures 9.2 and 9.3 for age/residency categories. Villagers resident <5 years in Bulindi were not included in analysis of residency.

During their interviews ten women and four men (10.4% of participants) described a recent instance when they were personally pursued, or else actively approached in a threatening manner, by one or more chimpanzees. (Note that interviewees were not specifically asked about this). In addition to such charges or chases, it was common for interviewees to describe chimpanzee display behaviour directed at humans (e.g. slapping the ground, shaking vegetation). Three interviewees related an incident that occurred in Kyabateke village in June 07 in which a chimpanzee threatened a man and apparently grabbed hold of his bicycle. Some interviewees remarked that the apes mainly chase women and children but usually fear men – an observation made by numerous residents outside of interviews. However, several participants expressed scepticism over claims that chimpanzees chase people. For example, one woman commented that, “Some people just see a chimp and say it has chased them”.

Fourteen women and four men (13.4% of participants) specifically mentioned that they or their children fear to enter the forest to collect firewood or water if chimpanzees are nearby, and at times go without. Furthermore, with the apes’ increasingly foraging outside of forest the threat to children in village areas was also cited. One man in Mparangasi complained, “You can’t leave children alone at home in case chimps come to the house, and you can’t tell children to guard gardens from baboons and monkeys as they may find chimps there”. In Nyaituma, an interviewee said she cut her guava trees to stop chimpanzees coming to her home out of concern for her children’s safety.[3] Several interviewees complained that chimpanzees disturb children walking to school. Between September and December 07, when the apes frequently fed on cultivated foods, researchers were occasionally asked to escort local women or children along village paths because chimpanzees were nearby. In September, women in Mparangasi requested that we move chimpanzees on from a homestead where they were feeding on guava, because school children could not return home. Also in September, we were asked to help guard a store of brewing bananas in Nyaituma because chimpanzees were nearby, apparently waiting to raid it (Appendix 4) (Plate 16).

Regarding the start of these perceived changes in behaviour, interviewees variously stated that chimpanzees had been leaving the forest and entering gardens for 2–10 years,

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[3] At least two other residents cut down domestic fruit trees during the study (guavas in one case and a large *Ficus mucuso* fig in the other), following repeated visits by chimpanzees during fruiting events.

and behaving aggressively towards people for ≤5 years. Several villagers suggested this change had occurred because there was insufficient food in the forest to support the growing chimpanzee population. Others, however, related the change to forest clearance, timber cutting or declines in productivity of forest cocoa *shambas*, which have reduced the apes' food supply. Notably, two interviewees said that some persons in their community blame the research project for the chimpanzees' 'bad behaviour'. In fact, this belief may have been widespread. The following accusations were directed to me by senior residents outside of interviews: (i) the red paint used to mark vegetation plots was a drug that makes the apes 'mad'; (ii) chimpanzees are coming to gardens to eat because we are disturbing them in the forest; and (iii) I have brought in "the white chimp" (or "the brown-faced chimp" in another account) from elsewhere, upsetting the resident animals and making them aggressive. According to local field assistants, these explanations enjoyed considerable support locally.

Changes in Human Behaviour and Attitudes

While a recent change in the behaviour of the apes was widely emphasised, a smaller proportion of interviewees (48.6%) stated that people's attitudes or behaviour towards chimpanzees has likewise changed over time, and many (39.6%) said it has not (Table 9.1). In the latter cases, a common explanation was that "people have always lived with chimps" or "people don't mind about chimps". For those who acknowledged a change, however, the most common reason was that nowadays people harass apes or chase them away from gardens (42.6%) (Table 9.4). Some interviewees noted that children in particular disturb the apes more often than they did previously. Others said that people now fear chimpanzees (22.2%), or are angry with them because they damage crops and disturb people (22.2%). While several participants claimed some residents want to kill them, others voiced the belief that if a person kills a chimpanzee they or their clan will have bad luck or die. Four interviewees said that residents nowadays refrain from disturbing the apes, in two instances because they were 'sensitised' during meetings about the research.[4] Outside of interviews, several residents claimed that prior to these meetings they did not realise it was illegal to kill chimpanzees.

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[4] The term 'sensitise', meaning to educate or raise awareness among local communities, is widely used by local people in Uganda as well as by government and NGO personnel.

Table 9.4. Reasons why attitudes or behaviour of people towards chimpanzees have changed over time. Cells show the number and proportion of interviewees that said local attitudes have changed (*n* = 54) who gave each reason.

Reason	***n***	**%** [1]
People are chasing or harassing chimps	23	42.6
People are unhappy or angry with chimps	12	22.2
People now fear chimps or run away from them	12	22.2
People have become used to chimps	5	9.3
People have stopped chasing or harassing chimps	4	7.4
People want to see chimps	1	1.9

[1] Percentage values add up to >100% because several interviewees gave >1 reason.

9.3.4. Crop Damage by Chimpanzees

> *I had planted a sugarcane garden and there is not a single one left. I can't plant sugarcane while chimps are there. I would be selling those canes to get money for salt and paraffin* (69-yr old woman, Nyakakonge).

> *There are differences in chimps, just as some people are good or bad; some people will steal – it's the same with chimps. Chimps can't speak to ask, "Assist me with a mango, some sugarcane"* (52-yr old man, Kyabigambire).

Approximately half the interviewees (53.0%) claimed that chimpanzees consume cultivars from their own gardens (Table 9.1). These interviewees were asked which foods chimpanzees take from their gardens (Table 9.5). Of 12 crops reported eaten, the most common were sugarcane (53.5% of interviewees reporting any crop loss to chimpanzees), papaya (46.5%), mango (33.8%) and banana (25.4%). The overall percentage of interviewees reporting losses of each main cultivar eaten by chimpanzees is shown in Figure 9.4. Damage to cocoa was mostly reported by former cocoa growers whose forest *shambas* are long-abandoned; nevertheless, these farmers still regard the cocoa trees and their produce as their property. Note that figures in Table 9.5 are likely biased against certain fruits that are neither cash-crops nor 'food crops'. For example, guava is considered a 'child's food' and, compared to sugarcane and banana, loss of fruits to wildlife *per se* is of least concern. In fact, guava-feeding by chimpanzees was reported by only four interviewees despite the fact guava was the most frequently eaten fruit cultivar as indicated by faecal analysis (Chapter 5). This distinction between cash crops or food crops and domestic tree fruits is illustrated by one man's comment that, "Chimps don't spoil gardens – they come for fruits".

Table 9.5. Cultivars reported eaten by chimpanzees and the percentage of interviewees claiming losses. Percentage values are shown for (i) interviewees claiming that chimpanzees eat ≥1 cultivar from their garden (*n* = 71); and (ii) all interviewees, excluding two individuals without gardens in Bulindi (*n* = 132).

Crop eaten	**% interviewees reporting losses to chimpanzees**	
	Interviewees who claim chimpanzees eat crops from their gardens	All interviewees
Sugarcane (*Saccharum officinarum*)*	53.5	28.8
Papaya (*Carica papaya*)*	46.5	25.0
Mango (*Mangifera indica*)*	33.8	18.2
Banana (*Musa* spp.)*	25.4	13.6
Jackfruit (*Artocarpus heterophyllus*)*	11.3	6.1
Cocoa (*Theobroma cacao*)*	9.9	5.3
Guava (*Psidium guajava*)*	5.6	3.0
Maize (*Zea mays*)	5.6	3.0
Passion fruit (*Passiflora* spp.)*	4.2	2.3
Pineapple (*Ananas comosus*)	4.2	2.3
Avocado (*Persea americana*)	1.4	0.8
Yam (*Dioscorea* sp.)*	1.4	0.8

* Indicates cultivars for which evidence of consumption by chimpanzees was obtained during the study.

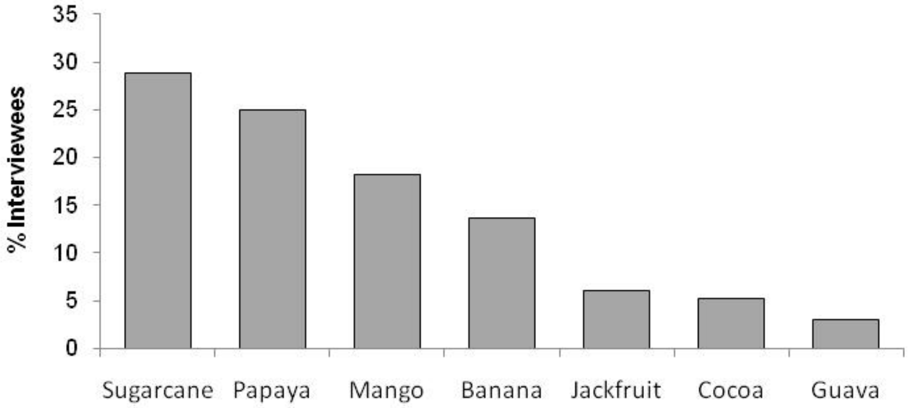

Figure 9.4. The percentage of interviewees with gardens at Bulindi (*n* = 132) reporting crop losses to chimpanzees. Only the main crops reported eaten are shown (see Table 9.5).

Interviewees were asked how much damage chimpanzees cause to crops compared to other animals. The majority (64.1%) replied that the apes cause 'little' or 'not much' damage, while (25.8%) said they caused no damage at all (Table 9.1). Again, these results may be influenced by the perception that fruits such as papaya, guava and mango do not constitute ‘food’ in the same way as do staples including cassava, rice, beans, potato and maize, and have little cash value. Only 7.8% of interviewees claimed chimpanzees cause ‘a lot’ of damage and in all cases this was with regard to specific cash crops (sugarcane in six instances, cocoa in four and banana in two; mango and papaya were additionally cited by one participant). Several interviewees mentioned that chimpanzees cause non-consumptive damage to other food or cash crops, for example by treading on tobacco seedlings or knocking down maize. Indeed, considerable damage to stands of maize by chimpanzees was seen several times during the study, when apes had apparently been chased by people or else had displayed through gardens.

Table 9.6. Animals that cause the most damage to crops. Cells show the number and proportion of interviewees who cited each animal (n = 116); most interviewees cited > 1 animal.

Animal	***n***	**%**
Baboon (*Papio anubis*)	77	66.4
Tantalus monkey (*Chlorocebus tantalus*)	76	65.5
Black and white colobus monkey (*Colobus guereza*)	39	33.6
Porcupine (*Hystrix cristata*)	14	12.1
Wild pig (*Potamochoerus* sp.)	8	6.9
Chimpanzee (*Pan troglodytes*)	5	4.3
Cane rat (*Thryonomys* sp.)	3	2.6
Domestic animal: cow (*Bos taurus*) or goat (*Capra hircus*)	2	1.7
Birds (unknown spp.)	1	0.9
Squirrel (*Xerus erythropus*)	1	0.9

Interviewees were asked which animal(s) cause the most damage to crops (Table 9.6). The most commonly cited species were baboon (cited by 66.4% of interviewees), tantalus monkey (65.5%), and colobus monkey (33.6%). Many participants made the point that, unlike chimpanzees, these primates eat important food crops including cassava, potatoes and maize. For example, a woman in Kihoro remarked, “Chimps only eat our fruits – other animals eat our *food*”. Compared to baboons and monkeys, other wildlife such as porcupines and wild pigs were infrequently cited (12.1% and 6.9%, respectively). Two individuals cited domestic livestock as among the worst causes of crop damage. Only five participants (4.3%) said that chimpanzees are the worst, or among the worst. These individuals had sugarcane or banana plantations, or cocoa *shambas*, and each claimed to have lost their entire crop to chimpanzees. More generally, some villagers claimed to have discontinued growing certain crops (sugarcane, cocoa, banana, or yam) specifically because chimpanzees "finished off" the crop ("I was planting only for chimps!" said one man).

Chimpanzee predation on livestock (chickens and goats and, in one case, piglets) was reported by seven interviewees (5.2%). The apes were also reported to raid domestic beehives. In Kyabateke some villagers claimed a local bee-keeping enterprise was abandoned because chimpanzees took all the honey.

9.3.5. Positive Aspects of Living Alongside Chimpanzees

> *I like them to stay around. Baboons never come to Kyabateke as chimps are there* (60-yr old woman, Kyabateke).
>
> *People are coming from outside to tell us that chimps are useful ... Here in Uganda, people know chimps are not useful* (23-yr old man, Mparangasi).

Most interviewees (70.3%) acknowledged benefits ('good things') in having chimpanzees in the area (Table 9.1). Among these, the prevailing reason (offered by 75.6%) was that chimpanzees actively chase away, or otherwise displace, baboons, tantalus monkeys and/or black and white colobus, all of which are considered major agricultural pests (Table 9.7). Others (13.3%) noted that chimpanzees "plant trees", while 13.3% cited their educational value, especially for children, or otherwise commented that chimpanzees are interesting to watch. Seven individuals (7.8%) mentioned the apes' role as a future tourist attraction, which would bring cash to Bulindi and provide jobs for local residents. (Eight other persons made the same point elsewhere during their interviews). Many interviewees remarked upon the intelligence of chimpanzees and/or noted that they are "like people".

There was a significant difference in the tendency of different aged participants to perceive good things about chimpanzees ($\chi^2 = 8.97$, $df = 2$, $p = 0.01$). Persons aged 60 years or above were less likely to say there were good things about having chimpanzees in the area compared to adults aged 30–59 or <30 yrs. Men were more likely to say there were good things about chimpanzees compared with women, though this trend did not reach significance ($\chi^2 = 3.42$, $df = 1$, $p = 0.064$).

Table 9.7. Benefits of chimpanzees. Cells show the number and proportion of interviewees that said there were ‘good things’ about the apes ($n = 90$) who gave each reason.

Benefits	***n***	**%** [1]
Chimps chase away baboons / monkeys / colobus	68	75.6
Chimps ‘plant trees’	12	13.3
Interesting to watch / education value	12	13.3
Tourist attraction	7	7.8
Chimps have a good voice	1	1.1

[1] Percentage values add up to >100% because some interviewees gave > 1 reason.

9.3.6. What Should Be Done About the Chimpanzees?

> *The chimps have been here for a long time ... we were born and found them here. If the forest is not cut, they will stay and live well* (49-yr old man, Kyabateke).
>
> *Is this really a good place for chimps to stay, in the middle of people?* (69-yr old woman, Nyakakonge)

Interviewees were asked if, in their view, anything should be done about the chimpanzees, and if so, what? Most participants (65.5%) said that something did need doing (Table 9.1). A variety of proposals were offered. The two most common – each given by 27.6% of these interviewees – were (i) chimpanzees should be ‘collected’ and kept in one place, and (ii) food should be planted for the apes (Table 9.8). Five interviewees explicitly said that a ‘zoo’ should be built for the apes to attract tourists. Some participants (19.7%) said the chimpanzees should be taken away to a government reserve or national park such as Budongo. In Kiseeta a 77-yr old man remarked, “You can’t see lions and hyenas here as they’re in the game park ... a chimp is also dangerous, so remove it”. Less common proposals were (i) protect chimpanzees and/or the forest, for example by stopping people harassing the apes or by restricting timber cutting (9.2%); (ii) stop chimpanzees coming out of the forest (7.9%); (iii) prevent them from chasing or ‘disturbing’ people (6.6%); and (iv) ‘sensitise’ people so they can live peacefully with the apes (6.6%).

Table 9.8. Local suggestions regarding what to do about chimpanzees. Cells show the number and proportion of interviewees that said something needed doing (n = 76) who gave each reason.

Suggestion	***n***	**%** [1]
Keep chimps in one place	21	27.6
Plant food for chimps	21	27.6
Take chimps away (e.g. to government reserve)	15	19.7
Protect chimps and/or forests	7	9.2
Stop chimps coming out of the forest	6	7.9
Stop chimps chasing / disturbing people	5	6.6
'Sensitise' residents to live with chimps	5	6.6

[1] Percentage values add up to >100% because several interviewees gave > 1 suggestion.

In contrast, 31% of interviewees said nothing needed doing about the chimpanzees, or else offered no opinion on the matter. Typical remarks were "what is there to do?", "let them stay" or "people have always lived with chimps". For some individuals the issue of chimpanzees was evidently unimportant; as one woman remarked, "Ugandans don't care about chimps, but *muzungus* do" (*muzungu* refers to a white person in current usage). Four interviewees said the apes should be allowed to remain in the forest because they chase baboons and monkeys. Elderly interviewees (≥60 yrs) were less likely to state the need for intervention compared to younger adults ($\chi^2 = 6.17$, $df = 2$, $p = 0.046$), perhaps regarding the chimpanzee issue as undeserving of such attention. Interviewee sex had no effect on stated opinion ($\chi^2 = 0.95$, $df = 1$, $p = 0.33$).

9.3.7. Perceptions of Forest and its Value to People

> *In coming years children will be asking, "What does the forest look like?", and it will be nowhere to be seen* (70-yr old woman, Kihoro)

> *What is the use of the forest to people? Forests are supposed to be big, not small like this – these are just rivers, not forests* (69-yr old woman, Nyakakonge)

Changes to the Forest

Most interviewees (68.8%) said forests in the area have changed over time (Table 9.1). The prevailing reason, given by 93.2% of these individuals, was that forests have been cut for gardens and/or timber and charcoal. People variously remarked that whereas formerly the forest was very large, or very thick and dark, nowadays it is open and the big trees are gone. Opinion regarding the extent of these changes varied, however. For instance, whereas one man said there had been “rampant timber cutting” and that “most trees have fallen down”, his neighbour – a headmaster and timber dealer – said that though people had been “removing a few trees … the tree density reduces but it still remains a forest”. Thirty percent of interviewees did not perceive (or acknowledge) any change to the forest, while three individuals claimed the forest has increased in size.

Women were significantly less likely to claim that forests have changed compared with men ($\chi^2 = 8.55$, $df = 1$, $p = 0.003$), possibly because some women do not consider what happens to forests their ‘business’. In contrast, neither interviewee age ($\chi^2 = 0.75$, $df = 2$, $p = 0.69$) nor length of residency ($\chi^2 = 0.40$, $df = 2$, $p = 0.82$) influenced perceptions of forest change over time.

Forest Ownership

Almost half the interviewees (48.1%) claimed they or their household own forest locally, although the area of land was in some cases very small (i.e. ≤1 ha). Six individuals (4.7%) said that while they used to own forest, they have since cut it down. Shortly before this study, households in Nyaituma clear-felled a >1 km stretch of gallery forest for a banana plantation and, subsequently, for tobacco cash-cropping, so that forest remained only on the Mparangasi side of the river. Nevertheless, some residents referred to this now-cultivated land as their ‘forest’.

During their interviews 14 forest owners said they have replanted, or declared an intention to replant, their forest. These individuals were asked which kind of trees they used or would use for replanting. Exotic pine (*Pinus* sp.) and eucalyptus (*Eucalyptus* sp.) were mentioned by 11 and seven individuals, respectively, while indigenous timber trees including *Maesopsis eminii*, *Milicia excelsa* and mahogany (e.g. *Khaya anthotheca*) were cited by two respondents. Outside of interviews, other forest owners spoke of their intention to clear forest in order to replant with pine or eucalyptus. Some residents claimed that government officials encourage forest owners to cut their forest in order to establish plantations of these exotic species.

Value of forests

In order to gauge the importance of forests to local households, interviewees were asked about their use of the following forest resources: firewood; craft materials (e.g. for baskets, rope, roofing); building materials (poles and timber); wild plant foods such as mushrooms, leafy vegetables and forest fruits; medicine; honey; meat; and resins (Table 9.9). The proportion of interviewees claiming they or their household obtain each of these resources from local forests was high (≥75% in all cases, reaching 98% for firewood). Asked from where these resources will be got if forests are cut down, most participants (76.2%) replied 'nowhere' or else remarked that it would be a problem; 9.0% said the resources can be obtained or bought from elsewhere; and three individuals said they will plant trees. Twelve interviewees (9.8%) replied that forests will not be cut down.[5]

Table 9.9. Selected resources that local households obtain from forests. Cells show the number and proportion of interviewees that said they or their household obtain the resource from local forests (*n* = 123).

Resource	***n***	**%**
Firewood	121	98.4
Arts and crafts materials	119	96.8
Timber / Building poles	117	95.1
Wild plant foods	113	91.9
Medicines	111	90.2
Honey	109	88.6
Meat	93	75.6
Resins	92	74.8

Asked if forests benefit them in other ways, interviewees commonly emphasised how useful forests are to them. In addition to the abovementioned forest products, 68 individuals (50.7%) pointed out environmental services provided by forest. In most instances, interviewees said forest was important for rainfall, though protection against soil erosion and strong winds was also mentioned. Several individuals expressed concern that forest clearance will cause local rivers to dry up and they will be unable to fetch water; a 39-yr old man claimed to have noticed a decrease in river levels during his lifetime. Four interviewees asserted that forest clearance has brought about a change in local climate. For example, a 66-yr old man in Nyaituma commented, "It used to be

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[5] Several interviewees maintained that they had not, or would not, cut their forest despite the fact they were known to have done so, or were in the process of doing so.

very cold, a healthy climate ... now the temperature has increased as the trees have been cut”. Many people said it was ‘bad’ to cut forest.

Reasons for Cutting Forest

Several interviewees argued that they gain nothing from their forest by leaving it standing. More generally, 26 interviewees (19.4%) discussed forest mainly in terms of its value as land for cultivation, noting the fertility of the soil or stating their intention to dig there. Six individuals pointed out that since they own little land outside the forest, they have no alternative but to clear it for agriculture. One man remarked, “Some rich people can leave the forest, but I will cut it to dig to get food for my children”.

During the study, the buying and selling of trees was evidently an important economic activity for some forest owners and other residents involved in timber production. Despite this, few forest owners stated outright that they cut or sold trees to make money. Nevertheless, a 44-yr old timber cutter in Kyabateke commented, “The forest can be cleared in a month, there are so many people wanting to cut. If a person wants to sell, he can easily ... the whole forest has been cut illegally to make money”. One forest owner in Nyakakonge gave the following reason for cutting forest: “The government is very complicated – the time will come when they will come and cut those trees and what will I have gained?” This same man further remarked, “The time will come when you *muzungus* will stop us cutting trees to build our homes”. A number of participants claimed that migrant or local pitsawyers cut trees on their land without permission, whilst others blamed local forestry officials or, simply, ‘the government’ for timber cutting in the area.

Several interviewees perceived a disadvantage to keeping forests since they harbour wild animals such as baboons and monkeys, which destroy crops. With regard to chimpanzees, one man remarked, “If we keep the forest and there are 50 chimps, don’t you think they will be dangerous and come and attack children? I don’t think it is a good thing to keep the forest as chimps will become many”.

9.4. Discussion

This chapter reports the results of a survey of residents' attitudes about chimpanzees and forests at Bulindi. Interviews revealed considerable ambivalence in local attitudes towards living alongside chimpanzees, and also with regards to forest resource use. It should be emphasised that at the start of interviews research at Bulindi had been in progress for eight months and was already a much-talked about subject locally. Indeed, when asked if they had heard about the chimpanzee research, 82.6% of interviewees said they had. (Although 61.5% of these individuals claimed to not know what the purpose of it was). Some interviewees attended earlier village and/or Subcounty meetings about the research where issues pertaining to chimpanzees and forests were raised. Further, informal discussion with residents across Bulindi was a daily aspect of fieldwork. Consequently, the general theme of the interviews – chimpanzee and forest management issues – had acquired a prominence locally beyond that which would be expected in the absence of the research project. Survey findings must therefore be interpreted within this context. Additionally, a well-known limitation to surveys of this kind is that stated attitudes may not reflect real beliefs or correspond with behaviour (e.g. Browne-Nuñez and Jonker 2008). Since interviews were just one aspect of a much broader study, interpretation of results was aided by information gained outside of interviews from qualitative observations, informal discussions and, particularly, the intimate local knowledge of field assistants.

Historical Perspectives on Chimpanzees at Bulindi

Most people interviewed recognised a long history of human–ape coexistence at Bulindi. However, some older residents believe that chimpanzees did not inhabit Bulindi forests in the past, arriving from Budongo and the neighbouring Kinyara sugar estate in the 1950–1980s. The explanation, given by five interviewees, that the apes came following extensive forest clearance for the sugarcane has some merit, because the establishment of Kinyara certainly entailed the loss of some riverine forests that likely supported chimpanzees in that region (Reynolds 2005). An alternative explanation is that many residents were simply unaware of the chimpanzees before this time. The human population at Bulindi was much smaller during the first half of the 20th Century, and villagers' accounts indicate that prior to the establishment of forest cocoa *shambas* in the 1960/70s, human activity in the forests was minor relative to current levels (C. Hill, pers. comm., 2009).

Within Bulindi, Kyamalera forest is widely perceived as the traditional and, for many, the legitimate 'home' of chimpanzees. In contrast, some residents regard the apes' use of Kiseeta, Kaawango and Nyakakonge forests as a more recent occurrence. Although the accuracy of these claims could not be assessed, in the case of Kiseeta, records kept by one resident – a former chairman of a local cocoa growers association – showed that chimpanzees were in fact recorded in Kiseeta forest as long ago as 1963, three years prior to establishment of cocoa. Claims that the apes did not traditionally inhabit certain forests could be related to human settlement patterns in the area, as well as differing levels of human activity in and around local forests. But such claims might also reflect a perception among some residents that large wild animals such as chimpanzees do not rightfully belong in their areas, because it is not government land.

The widespread belief that chimpanzees have recently increased in number can likewise neither be confirmed nor refuted. One possibility is that this opinion merely reflects the growing visibility of chimpanzees in the landscape. Local reports and evidence of recently converted land indicate that extensive forest clearance was limited prior to 2000. In addition, commercial logging was only initiated at about that time (see below). The clear consensus among interviewees was that, until recently, chimpanzees stayed in the forests and were seldom seen. Thus, regular sightings of groups of apes outside the forest and, in particular, adult females with dependent offspring, are a recent phenomenon almost certainly associated with these land-use changes. Increased sightings may thus have given rise to a mistaken belief that the chimpanzee population has grown.[6] Alternatively, forest clearance in surrounding areas (e.g. along the Waki River and in Kasongoire FR) might have led to recent immigration of adult females into Bulindi, leading to an increase in community size. Such a scenario was suggested by three interviewees.

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[6] Compounding this effect, a seemingly common misconception is that all infant and juvenile chimpanzees carried by their mothers are newborns. For example, local field assistants initially expressed surprise that animals estimated to be aged three or more years were not newborn infants.

Perceptions of Chimpanzees

The Bulindi data are in accord with growing evidence that human communities sharing a landscape with great apes may consider them dangerous and consequently fear them (Madden 2006; Campbell-Smith et al. 2010). In particular, the perceived threat to children's safety is a major concern for residents at Bulindi. (At the time of interviews the incident in January 2007, in which a local child was seriously injured by a chimpanzee, was still fresh in people's minds; Appendix 5). Nevertheless, some interviewees recognised that chimpanzee behaviour is influenced by the conduct of people during encounters. Harassment of chimpanzees by children – witnessed on many occasions during the study – was noted as a particular problem by some residents. In spite of this no evidence suggested that children are admonished for disturbing chimpanzees. In fact, children are at times enlisted or sent to chase them away from gardens or wells.

In many cases, an individual's opinion that chimpanzees are dangerous was informed by direct experience of aggressive confrontation with the apes. That women were more likely than men to say they fear chimpanzees is in accord with the common conviction that chimpanzees are unafraid of women and children, and thus more likely to threaten or chase them than men. Alternatively, it could simply be that men are less inclined to admit they fear these animals (cf. Kaltenborn et al. 2006). Some villagers reported that fear of chimpanzees occasionally prevents them from carrying out important daily subsistence activities such as firewood and water collection. Even so, some residents – usually men – demonstrated a notable disregard for potential confrontation, for example by entering an area where chimpanzees were vocalising in order to cut poles (pers. obs.).

Human-like intelligence and behaviours of chimpanzees are widely recognised by residents of Bulindi, as by communities elsewhere in Africa familiar with these apes (Richards 1995; Watkins 2006; Webber 2006; Lingomo and Kimura 2009). Even so, unlike in some West and Central African societies (Caldecott and Miles 2005; Yamakoshi 2005), the Banyoro do not seem to hold totemic beliefs about these apes. All the same, some Bulindi residents voiced the belief that if a person kills a chimpanzee they, or their clan, will die. More generally, there is a perception that it is 'not good' to harm chimpanzees, perhaps because of their resemblance to humans. In spite of their dangerousness, residents do not regard chimpanzees as morally degenerate as was reported for the Mende in Sierre Leone (Richards 1995). Nor are chimpanzees routinely described as greedy or cunning, as are baboons (see also Hill 1997; Watkins 2006; Webber 2006); however, some residents referred to the apes as 'thieves'. Older people generally held the least positive views of chimpanzees, perhaps reflecting inter-generational differences in attitudes towards wildlife.

Explanations for Chimpanzee Behaviour

Troublesome behaviour by chimpanzees, such as foraging in village areas and threatening and chasing people, is by all accounts a recent phenomenon. However, crop damage by chimpanzees *per se* is not new – the apes' consumption of cocoa planted inside the forest created conflict with cocoa growers as far back as the 1960s. Nevertheless, frequent damage to cultivars *outside* of forest is widely perceived as a recent development, affecting many households across Bulindi.

While some villagers attributed these behavioural changes to recent human activities such as forest clearance and harassment of chimpanzees, this viewpoint may have gained local credence following earlier meetings at which I proposed the idea. In fact, during the initial months of research I was struck by residents' seeming failure to associate widespread forest degradation – which was ongoing and plain to see – with changes in the apes' behaviour that they complained about. It is interesting that ostensibly less-plausible explanations blaming the research for chimpanzees' 'bad behaviour' were, according to field assistants, readily accepted by some villagers (although no persons directly blamed researchers in interviews). One interpretation is that residents are disinclined to accept responsibility for the behaviour of chimpanzees, which many consider to belong to the government, or are unwilling to critically evaluate their own land and resource use. But a willingness to apportion blame to the activities of an outsider may also reflect disquiet among some community members regarding the research, if it was viewed as counter to their interests. One interviewee remarked that at the start of the project residents thought I wanted to seize control of the forests and its resources (see below). Furthermore, some individuals were unhappy about the attention brought on their activities in the forest as a result of the research, of which some was illegal (e.g. unlicensed logging and charcoal burning).

Attitudes Towards Crop Damage by Chimpanzees

Crop losses to chimpanzees were widely reported: half the interviewees claimed chimpanzees ate cultivars from their gardens. In the case of so-called children's food such as papaya and guava, consumption by chimpanzees *per se* is tolerated by many households. What people object to is the threatening presence of the apes when they enter village areas to feed on these fruits. Crop damage by chimpanzees is more likely to be considered a serious problem when it involves cash crops such as sugarcane, cocoa and banana; that the apes are difficult to chase away from gardens is an additional source of aggravation. Both during and outside of interviews, farmers growing these crops to sell at market complained they incur a considerable financial loss because of chimpanzees. In some cases, farmers claim to have abandoned a crop owing to persistent chimpanzee raiding. Since this study made no attempt to quantify crop damage by chimpanzees (cf. Naughton-Treves 1997; Webber 2006), such claims should be interpreted with caution. For instance, cocoa farmers around Kiseeta consistently maintained they abandoned their forest *shambas* because chimpanzees ate all the pods. In fact, the breakdown in Uganda's cocoa industry during the late 1970s and 1980s was probably the main reason for abandonment of *shambas* at Bulindi and elsewhere in Hoima (Kayobyo et al. 2001; Olanyo 2008).[7] It was not uncommon for sugarcane, cocoa or banana farmers to explicitly state their wish for compensation for crop losses to chimpanzees. As such, losses may have been exaggerated by some farmers (cf. Siex and Struhsaker 1999). Nevertheless, repeated raids by chimpanzees on sugarcane grown alongside Kiseeta forest plainly caused considerable damage (pers. obs.).

Laws prohibiting the killing of wildlife can increase local intolerance of troublesome species by depriving farmers of traditional coping strategies or else compelling them to engage in illegal hunting or trapping (Hill 2004; Naughton-Treves and Treves 2005; Madden 2008). Although no interviewee explicitly voiced frustration that laws protecting chimpanzees prevented them from protecting their crops, this complaint was raised during earlier village meetings to introduce the research. In the absence of a regular presence of wildlife authorities in the area, some villagers may have perceived the research team as fulfilling a policing role with regard to chimpanzees. Nevertheless,

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[7] At the time of the study cocoa was being promoted within the government's Plan for the Modernisation of Agriculture, and production was once again increasing (Olanyo 2008). The revitalisation of the cocoa industry has led to the restoration of some abandoned *shambas* elsewhere in Hoima such as in Kitoba subcounty (pers. obs.). Although none of the former cocoa farmers at Bulindi expressed an intention to restore their *shambas*, this could change in the future.

several farmers made apparent attempts to kill the apes using man-traps or poisoned bait despite the ‘protection’ afforded by the research and the risk of detection. In the four cases, traps or fruits thought to contain poison were placed near sugarcane or bananas raided regularly by chimpanzees. But aside from the angry protestations of a minority of farmers (perhaps perceiving an opportunity for compensation), residents were overall keen to emphasise how little damage chimpanzees cause to staple crops compared to other wildlife, especially primates such as baboons and tantalus monkeys. The perception of monkeys as particularly problematic crop raiders is widespread among farmers in Africa and Asia (Hill 1997; Naughton-Treves 1997; Siex and Struhsaker 1999; Saj et al. 2001; Chalise and Johnson 2005; Paterson 2005; Marchal and Hill 2009; Campbell-Smith et al. 2010; Nijman and Nekaris 2010).

Benefits to Living Alongside Chimpanzees

Despite problems associated with aggressiveness and crop-raiding, most residents at Bulindi acknowledge beneficial aspects to having chimpanzees in the area. In particular, they are widely believed to chase, or otherwise displace, baboons and monkeys which, unlike chimpanzees, damage important food crops. A similar ‘crop guarding’ service by chimpanzees was reported by residents around Budongo Forest (Watkins 2006; Webber 2006). Although active chasing of baboons by chimpanzees was never observed at Bulindi, several times the apes were heard responding to baboon barks with aggressive vocalisations, and on at least two occasions seemed to move towards them. In any case, baboons and tantalus monkeys were seldom seen in the same forest patch as large, noisy chimpanzee parties, which could indicate avoidance of the apes by these monkeys. The chimpanzees’ role in dispersing the seeds of useful trees was also recognised by some interviewees.

Ecotourism

Several residents spoke enthusiastically of economic benefits to local households from future chimpanzee ecotourism which, at the time of interviews, was subject to renewed discussion locally. Shortly before this study began, a businessman in Kiseeta proposed to develop an ecotourism programme to include chimpanzee tracking at Bulindi. The proposal was fiercely opposed through village councils because residents feared the forests would be gazetted as reserves for chimpanzees, and they would lose land and/or access to resources. The issue had once again come to the fore following the instigation of a community development project involving a national NGO concerned with chimpanzee conservation and welfare. This project provided support for a local woman's handicraft association through training and product marketing. Additionally, at the time of interviews a wildlife education centre was under construction on the Hoima–Masindi road by Kyamalera forest. While development of viewing-based ecotourism was not an aim of this project, there was widespread speculation among residents that tourists would soon come to Bulindi to see the chimpanzees. This belief appears to have been fostered by a local man, on whose land the education centre was being built. This individual visited households across Bulindi to encourage support for the project and to dispel residents' fears about land appropriation. But some local residents claim they were told tourists would pay to see the apes, and the local community would benefit financially.[8] Some residents also claimed they were misled into believing that my research was connected with this community project.

What to Do With Chimpanzees – Local Opinions

In principle, most residents at Bulindi seem content for chimpanzees to remain in local forests and only a minority advocated their relocation elsewhere. However, the need for intervention to control the apes' 'bad behaviour' was widely expressed. The popular suggestion that chimpanzees should be collected and kept in one place (i.e. in Kyamalera) to stop their roaming was in most instances a reference to the abovementioned community project. According to some interviewees, as well as other community members, the local man associated with that project also informed people that food (namely papaya and other cultivars) would be planted for chimpanzees at the forest edge. As a result, the apes would stay in Kyamalera forest (where they could also be viewed by tourists) – a welcome development in most residents' view. Whether or not this man actually made such claims is unknown. The issue underscores the importance of training and advising local partners involved in conservation and development projects to minimise the risk of them generating unrealistic expectations within their community – in this case, in order to encourage local support. Overall, the results of this survey suggest residents will tolerate chimpanzees providing they stay in

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[8] In fact, the possibility of developing chimpanzee tracking at Bulindi was being considered by some agencies concerned with chimpanzee conservation. In 2007 one of my field assistants was approached by representatives of a Hoima-based NGO who asked about the feasibility of habituating the apes for a tourism initiative.

the forest and cease ‘disturbing’ people. However, it is difficult to imagine that the chimpanzees’ behaviour will change, at least in the short-term. Only a minority of interviewees argued that human behaviour must also change if people and chimpanzees are to continue living alongside one another.

Value of Forests

In Uganda, communities living around forests obtain resources from them such as firewood, timber, craft materials and wild foods such as vegetables, game and honey (Banana and Turiho-habwe 1997, 1998; Eilu and Bukenya-Ziraba 2004; Naughton-Treves et al. 2007; Watkins 2009). It is difficult to gain accurate information on local resource use given that some activities (e.g. hunting and timber extraction) may be conducted illegally. Still, many residents at Bulindi spoke candidly about resource utilisation, and the proportion of residents claiming they obtained such products from local forests was high. For example, 98% of interviewees claimed their household used firewood collected from the forests, while 95% said they got timber and 76% obtained meat from local forests. Note that interviewees were not asked about frequency of use, however, or if they harvested such resources themselves. (The proportion of local men who engaged in hunting was probably very low, for example). Surveys of forest utilisation by communities around both government and non-government forests elsewhere in Hoima and Masindi Districts report far lower levels of usage (Banana and Turiho-habwe 1997; Eilu and Bukenya-Ziraba 2004; Watkins 2009). Possibly, Bulindi residents felt comfortable discussing resource use because the forests are not gazetted and the interview team included familiar local men, but cultural attitudes may also play a part. Paterson (2005) notes that while migrants living south of Budongo FR denied hunting or baiting crop-raiding animals, native Banyoro “freely admitted” to such practices.

Residents at Bulindi acknowledge that forests provide them with important resources and many also recognise ecological benefits of forests, for example in climate regulation. This is unsurprising: environmental issues are taught in schools, and villagers across the region are exposed to environmental announcements and programs on local radio. A paradox is apparent because stated attitudes about the value of forests do not correspond with behaviour: across Bulindi residents are rapidly clearing forest for farming and selling trees on their land to timber merchants. In some instances, responses might reflect a desire to give the ‘right answer’. For example, a local timber dealer – involved in much of the logging witnessed at Bulindi during the study – spoke of the importance of conserving forests for chimpanzees. However, the most likely explanation is that though local people understand that deforestation may have unwanted future consequences (e.g. firewood shortages), the immediate incentives for clearing forest outweigh such concerns.

Factors Influencing Forest Clearance

Local people acknowledge that forests are nowadays smaller, more open and with fewer big trees compared to in the past because of clearance and logging. That neither interviewee age nor length of residency affected this view is in line with available evidence suggesting the most important changes are recent. It appears that a combination of socioeconomic and political factors has recently facilitated rapid forest clearance at Bulindi. Of the proximate causes, the impact of commercial logging on degradation of forests within the chimpanzees’ range was most evident during the study.

Commercial Logging

Local reports indicate that commercial logging began at Bulindi approximately five years prior to this study (i.e. from 2000); before this time, timber trees were apparently harvested infrequently and for local use.[9] According to these reports, Bakiga pitsawyers were brought from Kabale District in Southwest Uganda because, at that time, the Banyoro had no tradition of timber-cutting. These migrant pitsawyers spent months in local forests, especially in Kiseeta and Mparangasi, cutting high value timber trees such as the mahoganies *Khaya* and *Entandrophragma* spp. and the largest *Lovoa trichilioides* and *Antiaris toxicaria* specimens, which were purchased very cheaply. During this period some local men learnt how to pitsaw and – crucially – local forest owners realised that money could be made from selling trees. The removal of the most valuable trees during this first wave of logging is perhaps evidenced by an absence of large mahoganies recorded during tree surveys. Furthermore, many trees cut during this study were relatively low-value species (e.g. *Trilepisium madagascariensis*, *Sterculia dawei*) or else small-sized (Chapter 3). Such specimens would previously have been ignored.

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[9] Commercial logging involving migrant pitsawyers appears to have begun earlier in some riverine forests elsewhere in Hoima and Masindi Districts (Banana and Turiho-habwe 1998).

This pattern of small-sized stems being cut after large trees are depleted is occurring in heavily disturbed forest elsewhere in Uganda (Turyahabwe et al. 2008).

Forest owners repeatedly emphasised throughout this study that they do not receive tangible economic benefits from standing forest. People want money, and selling trees for timber or charcoal production enables them to generate income that can be used to pay school fees and buy basic commodities. For many forest owners it is simply the easiest way to raise cash quickly. Thus in recent years forests have come to be viewed as important financial assets for local households. The flourishing timber trade in the region provides opportunities not only for local people to get money for their trees, but also through buying trees from others and acting as middlemen for dealers from outside the area. It came as a surprise to discover that a number of farming households at Bulindi own chainsaws. While clearance of forest on private land by local owners is not illegal *per se*, a permit from local government is required to harvest timber commercially. Furthermore, it is illegal to cut trees in natural forests using a chainsaw. However, residents know they have little to fear since in most cases timber harvesting is carried out after consultation with local officials. Locally, it is commonly alleged that fake permits are obtained in exchange for cash, even for chainsaws. Several interviewees noted that enforcement of forest laws in the area is weak.

Cash Crops and Plantations

For many local households, natural forest represents land to be ultimately converted for other purposes such as agriculture or woodlots. Thus timber harvesting is often a first stage in a more enduring process of land-use change. Part of the explanation for accelerating rates of forest clearance at Bulindi and elsewhere in the region is the increasing dominance of tobacco cash cropping, for sale to multinationals including British American Tobacco. Most farmers abandoned their coffee and banana gardens as the plants were infected with bacterial wilt diseases, which have caused declines in coffee and banana yields across many parts of Uganda since the mid-1990s and 2000, respectively (Tushemereirwe et al. 2006; Serani et al. 2007). It is unclear when these wilt diseases first appeared in Hoima District. What is certain is that during 2006–8 Bulindi farmers were growing tobacco more intensively than in previous years.[10] Most

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[10] Although brewing bananas were harvested in Mparangasi and Nyaituma during the study, by late 2007 farmers had started to clear the plantations in order to plant tobacco. Only a minority of farmers maintained coffee trees around their homesteads.

forest clearance observed during the study was by farmers seeking fertile soil to plant tobacco or to establish tobacco seedling nurseries along riverbanks (Plate 17). Following a successful crop in 2007, farmers intended to plant two tobacco crops in 2008. The same process of forest clearance associated with intensification of tobacco farming was occurring elsewhere in the district (McLennan 2008).

As part of the government's much-publicised campaign to meet future national timber and fuelwood demands, establishment of woodlots on private land is being encouraged across Uganda (MWLE 2002). At Bulindi, some farmers are clearing forest for the purpose of establishing plantations of exotic pine or eucalyptus. For example, during 2007 a five hectare portion of Kiseeta forest – roughly 20% of the total forest area – was logged and cleared in order to extend an existing pine plantation, previously established on forest land (Plate 18). One problem is that despite widespread publicity regarding the negative impact of deforestation, the distinction between plantations and natural forest is rarely made in the national media or in public statements by forestry officials (pers. obs.). Watkins (2009) also notes that eucalyptus woodlots are referred to as 'forests' by the National Forest Authority. Consequently, local people may perceive an exotic plantation as functionally equivalent to natural forest.

The threat from wild animals provides farmers with an additional incentive to cut forest. In 2006 owners of the main portion of Kyamalera forest told me they intended to convert the land for cattle grazing because the forest "attracts wild animals". By 2010 most of Kyamalera had been clear-felled, following removal of the marketable timber (M. Ssemahunge, pers. comm. 2010). Goldman et al. (2008) note that domestication of the landscape outside Kibale National Park, which removed suitable habitat for dangerous or troublesome wildlife, was regarded as a positive change by most farmers.

Insecure Land Tenure

Further to these important economic incentives, the rush to convert forest resources into cash and get forest land under alternative land uses – as witnessed during this research – may also be motivated by insecurity over land tenure and rights to forest land and resources. Studies in Uganda and elsewhere in rural Africa show that where human population pressure is sufficiently high, rule enforcement is weak and land tenure uncertain, local communities utilise forest land and resources unsustainably since the condition is effectively one of open access (Banana and Gombya-Ssembajjwe 2000;

Place and Otsuka 2000; Romano 2007; Turyahabwe et al. 2008). These studies argue that strengthening tenure is critical for responsible forest management. At Bulindi, though forests are not formally registered, forest is not common property because land ownership and access rights to forest resources by individuals, families and clans, are clearly defined based on the traditional system of customary tenure (Chapter 2). Studies elsewhere in Uganda indicate that extraction levels in forest under private ownership, with strong local institutional arrangements governing use, may in fact be lower than in poorly controlled government reserves where illegal harvesting of resources is rife (Banana and Gombya-Ssembajjwe 2000; Turyahabwe et al. 2008). Moreover, Uganda's 1998 Land Act recognised customary ownership, giving local households – such as those at Bulindi – legal rights to forest and forest resources on non-registered land (Government of Uganda 1998). Why, then, are forest owners insecure about land tenure?

The fact is residents at Bulindi are uncertain about who legally 'owns' forest resources, and fear their forest land is liable for appropriation by government or other outside agencies. With regards to the government, such a belief might have been reinforced by locally-stationed staff of the National Forest Authority, who have no jurisdiction over private forests, but who nonetheless were widely alleged to collect money in exchange for permits. During this study these individuals occasionally seized produce harvested locally such as timber and charcoal (pers. obs.). In addition, other powerful figures in local government allegedly have private interests in timber harvesting at Bulindi and forests elsewhere in the region. More generally, local people plainly believe many government officials are inherently corrupt, with the power to do as they please.

Of particular significance for conservation initiatives regionally, some residents evidently fear that conservation of chimpanzees and forests, and the associated expectation of imminent ecotourism development, may result in loss of land and access to resources (cf. Laudati 2010). Local field assistants affirmed that this concern was widespread among residents during this study. Given local insecurity over tenure, it is easy to understand why intensifying outside interest in chimpanzees and forests – from NGOs as well as this research – might lead some residents to consider closely the cash value of forest resources on their land, and their immediate plans for that land. Currently, there is little incentive for a forest owner at Bulindi to maintain his or her forest, when all around others are converting their trees into cash and, at the same time, expanding the area of land they have available for cash cropping. Some forest owners may feel compelled to make money immediately from their trees, believing they will be prevented from doing so in the future. There may also be a perception that once forest is cleared and the land put under cultivation, it cannot be gazetted.

Summary

1. Interviews were conducted with residents of 12 villages at Bulindi to understand local experiences of living alongside chimpanzees. The results reveal considerable ambivalence in local attitudes towards these animals.
2. Residents overwhelmingly believe the chimpanzee population is increasing and most villagers consider chimpanzees dangerous and fear them. Young children are perceived to be at particular risk from attack by chimpanzees.
3. Chimpanzee behaviour is widely perceived to have undergone recent negative changes; in particular, chimpanzees now leave the forest and enter village areas for food (i.e. sugarcane and sugar fruits) and behave aggressively towards people (e.g. chasing and attacking). Despite these problems, chimpanzees reportedly perform a valued service by chasing away baboons and monkeys which, unlike the apes, damage important staple food crops.
4. Local people at Bulindi will tolerate the chimpanzees providing they remain inside the forest. The popular misconception that the apes can be gathered and maintained in one forest – where they can be viewed by tourists – reflects residents' confusion about the aims of conservation projects under development locally.
5. While households at Bulindi depend on local forests for important resources including firewood and building materials, they are clearing the forests to make money from timber and to plant cash crops, principally tobacco. The need for cash, insecurity over land tenure, alleged institutionalised corruption and lack of law enforcement means there is currently little incentive for local people to maintain forest on their land.

CHAPTER 10 – GENERAL CONCLUSIONS

For this study I examined the ecology of chimpanzees and their relationship with people at Bulindi, Hoima District, in western Uganda. At this site a community of chimpanzees inhabit shrinking forest fragments in exceptionally close proximity to a human farming population exerting unsustainable pressure on unprotected forest land and resources. Since this state of affairs is increasingly reported outside of national parks (NP) and other protected areas in Uganda, it is important to understand how chimpanzees respond to this situation and to consider local people's experiences with these apes in order to devise appropriate management plans. Prior to this study, no research projects had been conducted at Bulindi and the chimpanzees and their environment were entirely unstudied.

10.1. Summary of Findings

I conducted an extensive tree survey in order to quantify the diversity and distribution of plant resources available in the chimpanzees' habitat (Chapter 3). In compositional terms forest patches at Bulindi – which are physiognomically similar to other riverine forests in Hoima District (pers. obs.) – are not merely outliers of Budongo, the nearest main forest block. Instead, these small forests support a groundwater-dependent vegetation community composed of *Phoenix reclinata* palm swamps and mixed forest dominated by members of the Moraceae. Cocoa trees (*Theobroma cacao*) dominate the understorey in abandoned forest plantations. There is little overlap in common tree species between Bulindi and Budongo.

Phenological surveys revealed that forests at Bulindi are markedly productive (Chapter 4). In particular, the abundant *Phoenix* palms produced ripe fruit in 11 of 14 months. The 'low fruiting season' corresponded to the period between *Phoenix* ripe fruiting events, but was also a time when few other forest trees produced fleshy drupaceous fruits. The impact of this period on consumers such as chimpanzees is buffered by the continuous availability of figs, which occur at a relatively high density in the riverine habitat. Yet the potential keystone value of figs may have been artificially supplanted at Bulindi and in private forests elsewhere in Hoima by the introduction of cocoa in the

1960s–70s, which created a clumped, consistently available food source, exploited by a variety of animals.[1] The unprotected riverine forests of Hoima District represent a hitherto unrecognised habitat for chimpanzees and other frugivores in Uganda and should be conserved (cf. Gautier-Hion and Brugière 2005).

Chimpanzee diet at Bulindi was examined in detail, principally via faecal analysis. In common with other populations, the apes are highly frugivorous and fruit dominated their diet throughout this study (Chapter 5). In addition to wild foods, agricultural crops are fully integrated into the annual diet. During the low fruiting season the chimpanzees were able to pursue a fruit-based diet in part by supplementing their natural diet with increased amounts of high-quality fruit cultivars, available year-round. The contribution of agricultural foods in their diet, and the range of cultivars eaten, is most likely increasing. Like chimpanzees at Bossou (Hockings et al. 2009), the Bulindi apes are therefore adapting ecologically to a landscape increasingly dominated by farmland. Unlike other studied communities in mid-western Uganda, insect foods were regularly eaten at Bulindi (Chapter 6). Notably, this community appears to have a ‘culture’ of using sticks to dig up underground bee nests for honey which, prior to this study, has only been described in Central African populations. Whether or not the chimpanzees learnt this behaviour from people, who sometimes also dig up the honey, is uncertain.

Adaptations to the advancing ‘agriculturalisation’ of the landscape and the concomitant rise in contact with people are behavioural as well as ecological. Analysis of the size of nest groups indicated the chimpanzees were more cohesive during months when they fed most heavily on cultivars, perhaps in response to an increased risk of confrontation with farmers (Chapter 7). Adult males display unusually aggressive behaviour towards people, manifest in the intense mobbing of ‘intruding’ researchers in the forest and frequent intimidation and pursuit of villagers encountered in gardens and on roads and footpaths (Chapter 8). The clear consensus among residents is that this confrontational behaviour is a recent phenomenon. Some farmers have responded to increasing encounters with chimpanzees outside the forest and the rise in crop-raiding with aggressive harassment of the apes. Individuals may use dogs to chase chimpanzees from their village, hurl stones at raiding apes, or set large steel traps in an attempt to protect

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[1] See also Arlet and Molleman (2010), who report damage to forest cocoa gardens by wildlife including chimpanzees around the Dja Faunal Reserve, Cameroon.

their sugarcane from chimpanzee depredation. Human-directed aggression by the apes can be regarded as an adaptive response to intensifying competition with people.

An important point to emerge from interviews is that local people at Bulindi live alongside and interact regularly with a large mammal they regard as dangerous and which they fear (Chapter 9). On two occasions during this study a child was attacked by a chimpanzee. This risk of physical aggression places conflict between farmers and chimpanzees (and other great apes) in a different realm from most conflict situations involving smaller-bodied primates, which generally centre around the latter's crop-raiding (e.g. Hill 2005).[2] In this regard human–great ape conflict has parallels with people–wildlife conflicts involving other large and potentially dangerous mammals such as bears or large carnivores (Quigley and Herrero 2005; Kaltenborn et al. 2006). Chimpanzee attacks on humans are rare, but as noted by Hockings et al. (2010: 894) an attack "can elicit much more hostility and panic than less immediately severe but persistent problems, such as crop-raiding."

The deteriorating relationship between chimpanzees and people at Bulindi is not necessarily representative of all situations where these apes live in close proximity to people. For example, chimpanzees at Bossou are habitual crop-raiders and occasionally attack humans (Hockings et al. 2009, 2010), but overall conflict levels appear to be lower than at Bulindi (Yamakoshi 2005; Hockings 2007). This probably reflects villagers' totemic beliefs about chimpanzees that promote tolerance of the apes at Bossou. However, habitat disturbance is evidently a far greater problem at Bulindi. At present it is unclear if the frequency of human–chimpanzee encounters differs between the two sites. The Bulindi data are in line with the emerging view of farmer–chimpanzees interactions elsewhere in Uganda where high-density human populations are destroying the apes' natural habitat (Wrangham 2001; Reynolds et al. 2003; McLennan 2008).

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[2] However, baboons and macaques also show occasional aggression towards people (e.g. Zhao and Deng 1992), and may be feared (Hill 1997).

10.2. Future of Bulindi Forests

The small riverine forests at Bulindi are fast disappearing. During the last decade they have shrunk around the papyrus swamps as farmers seek fertile soil to plant crops, particularly tobacco (Plates 17 and 18). Currently, trees are viewed by local households mainly in terms of their cash value and during this study well over 100 large trees were felled for timber. Although forest owners have legal rights to forest land and resources (Government of Uganda 1998), few trees appeared to be cut in accordance with current forest policy and legislation. For example, forest trees were often harvested with chainsaws; few pitsawyers were licensed; timber permits were allegedly attained in exchange for cash from locally-stationed employees of the National Forest Authority (NFA), who have no jurisdiction over natural forests on private or public land (see below); and permits for clearing land for alternative uses (e.g. agroforestry) were falsely acquired to harvest timber for commercial purposes. In the two years following this study's completion, logging and forest clearance at Bulindi has continued unabated. In particular, much of Kyamalera and Kiseeta forests – two of the most important forests for the chimpanzees – have reportedly been cleared of timber and are being converted to gardens (M. Ssemahunge, pers. comm. 2010). Unfortunately, this is representative of a process of rapid depletion of unprotected forests inhabited by chimpanzees taking place across the region, including within small government reserves controlled by the NFA (McLennan 2008). The illicit timber trade in this part of Uganda is evidently highly organised, and given local insecurity over land tenure few local forest owners can be expected to refrain from selling trees. Unless something is done immediately most unprotected forest not on inundated soils will be cleared for farming in the next few years, and all trees that can be converted to timber will be felled. A similar process of rapid clearance of forest remnants by local communities seems to be occurring elsewhere in western Uganda (Isabirye-Basuta 2004; Chapman et al. 2007).

10.3. Implications of Land-Use Changes for Chimpanzees

Prominent features of the anthropogenic landscape at Bulindi such as roads, footpaths, gardens and villages do not currently constitute significant barriers to chimpanzee ranging (Chapter 7). But as distances separating dwindling forest patches increase, travel will become progressively more costly for the apes. Greater travel distances not only imply reduced foraging efficiency, but an increased risk of encountering traps, hostile villagers and dogs. While travel costs may be offset by the nutritional benefits gained when chimpanzees enter village areas to feed on high-energy cultivars, the advantages of crop-raiding are unlikely to outweigh significantly costs associated with such a risky strategy in the long-term. Theoretically, habitual crop-raiding and confrontational behaviour is maladaptive if it results in the animal's eventual extirpation (McGrew 2007). But the rate of forest destruction at Bulindi, and throughout Hoima District, implies chimpanzees in this region have little alternative.

Land-use changes presently occurring across Hoima District are likely to have additional, as yet undocumented negative consequences for chimpanzees. Unless habitat loss causes immediate declines in resident animal populations, feeding competition between apes and other animals (e.g. baboons and monkeys) will intensify in the short-term. But chimpanzees may also be experiencing increased intergroup competition for resources and space. While there was some indication that Bulindi chimpanzees are currently ranging more widely than previously – presumably in response to habitat disturbance – they are being squeezed into ever-smaller foraging areas within the riverine forests that constitute their core range. In East Africa adult female chimpanzees compete with other females in their community for access to the best quality core areas within the community range (e.g. Murray et al. 2007), but at Bulindi major sections of forest are being felled and cleared. Competition resulting from displacement and crowding could give rise to very high levels of aggression among females (see Townsend et al. 2007). Chimpanzees are a male-philopatric species: males remain in their natal communities while females usually transfer at maturity (Goodall 1986; Nishida 1990; Boesch and Boesch-Achermann 2000). Under certain socioecological conditions, such as major habitat disruption or loss of community males, parous females may also emigrate into neighbouring communities (Emery-Thompson et al. 2006). Yet the potential for female migration may be limited in the heavily human-dominated landscape at Bulindi, despite the apparent mobility of these chimpanzees; adult females were seldom seen outside of forest patches unless accompanied by adult males. An inability to disperse introduces additional problems (i.e. loss of genetic diversity). Additionally, migrating females are unlikely to find more favourable conditions elsewhere since riverine forests across the region are currently subject to the same anthropogenic pressures. The highly territorial nature of male chimpanzees may preclude migration by adult males in the face of habitat loss.

A further implication of the severe habitat disturbance occurring at Bulindi and elsewhere in Hoima concerns the health status of the apes. Anthropogenic environmental changes including forest conversion for agriculture, habitat fragmentation and logging are associated with alterations in host–parasite interactions and increased pathogen transmission rates between humans, primates and livestock (Chapman et al. 2006; Gillespie and Chapman 2008; Goldberg et al. 2008). Stress induced by logging and frequent hostile encounters with people could compromise the apes' immuno-response system, increasing the likelihood of disease (e.g. helminth infections). Alternatively, nutritional benefits obtained through crop-raiding might reduce their susceptibility to infection (cf. Chapman et al. 2006; Weyher 2009). (Note that observations suggested crop-raiding is largely an adult male pursuit, however). Nevertheless, notably high levels of whole leaf-swallowing at Bulindi (Chapter 5), a behaviour linked to the control of helminth parasites (Huffman and Caton 2001), may indicate these chimpanzees are especially vulnerable to intestinal parasite infections (McLennan and Huffman, in prep.).

Chimpanzees at Bulindi and throughout the farm–forest mosaic of northern Hoima are evidently being forced to adapt to rapid habitat change, including a drastic reduction in forest area and loss of large fruit-bearing trees, alterations to forest structure and composition, ever-greater distances across agricultural land between forest fragments, and an overall increase in human activity in and around forests. Figure 10.1 provides a schematic illustration of conflict between farmers and chimpanzees in agriculturalised landscapes outside of protected areas in Uganda. The model implies that an inevitable consequence of these processes is the increased exploitation of human foods by chimpanzees and a sharp rise in human–ape interactions which, as discussed above, grow increasingly negative in character. The eventual outcome is likely to be the apes' extirpation. In sum, the results of this study strongly suggest that, under present conditions, chimpanzees will not survive for long at Bulindi or in similar unprotected forest–farm landscapes regionally without immediate intervention.

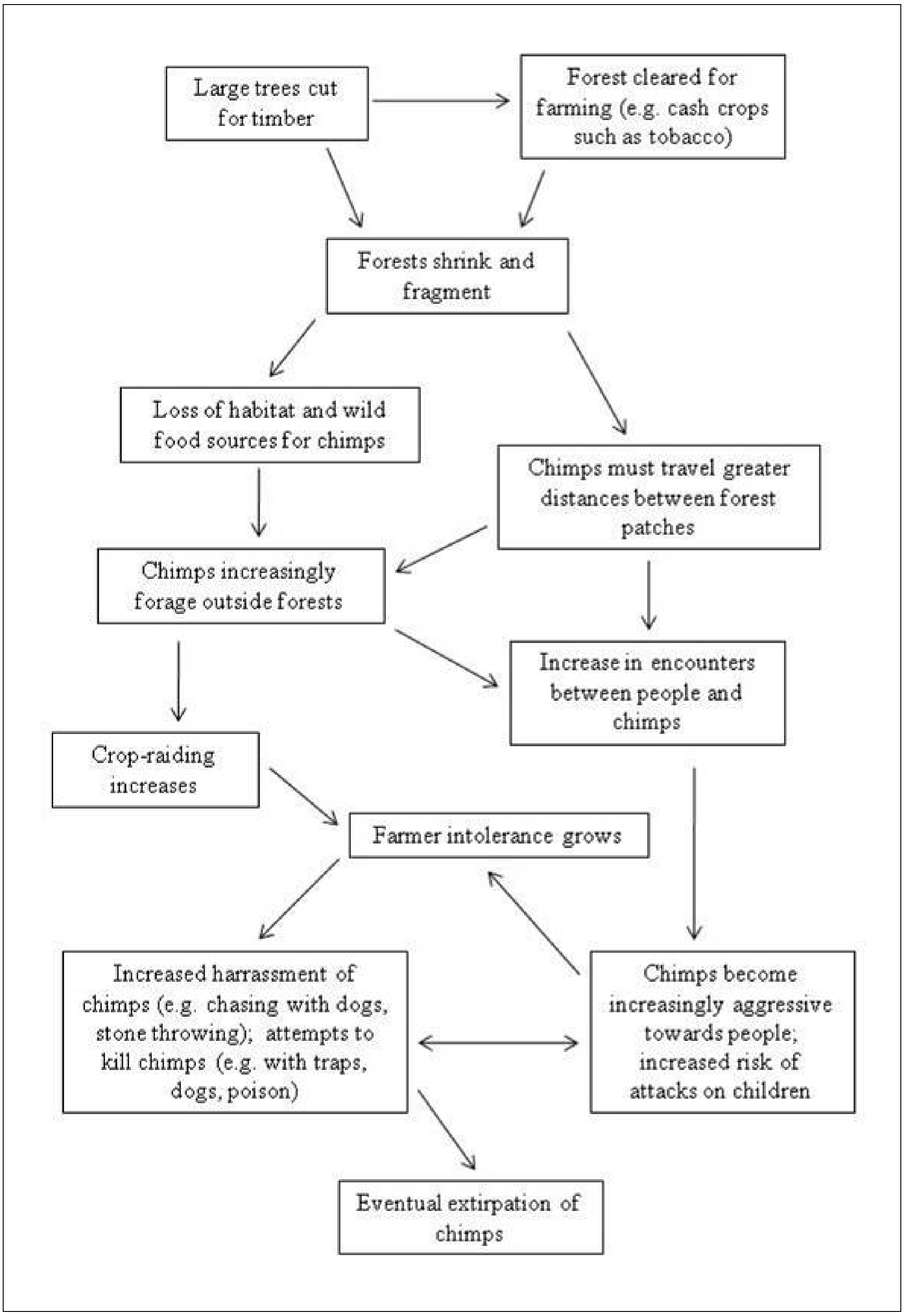

Figure 10.1. Schematic illustration of conflict between chimpanzees and farmers in human-dominated landscapes outside of protected areas in Uganda.

10.4. Why Should We Conserve Chimpanzees in Human-Dominated Habitats?

Chimpanzees are of global conservation concern and across Africa their numbers are fast declining (Caldecott and Miles 2005; Oates et al. 2008). Thus no population is expendable. Despite a growing number of chimpanzee field studies, there remains much to understand about this species. Marked ecological and behavioural – and, in some instances, cultural – differences exist among chimpanzee populations (McGrew 1992; Whiten et al. 2001; Chapter 6). Unlike nearby studied communities in Uganda, the Bulindi apes use tools to dig up subterranean bee nests. Behavioural observations also revealed that individuals in this community perform 'handclasp grooming' (Plates 15 and 19), a cultural behaviour not seen in two decades of research at nearby Budongo (Whiten et al. 2001; Reynolds 2005). These preliminary observations suggest that further research at Bulindi might uncover additional cultural traits. With the conversion of chimpanzee habitat to other land-uses, populations with potentially unique behavioural repertoires are being lost. But funding for conservation is limited. Therefore chimpanzee populations in fragmented agricultural land-use mosaics are necessarily of low priority compared to large populations in major expanses of less-disturbed habitat (Plumptre et al. 2010). However, some outlying populations may play an important role in maintaining gene flow between main forest blocks and protected areas. The unprotected riverine forests of northern Hoima lie between the Budongo and Bugoma forests (Chapter 2), which support important chimpanzee populations (approximately 600 individuals each, equalling about 25% of the national total; Plumptre et al. 2003b). According to the population viability analysis of Edroma et al. (1997), these populations are at low risk of extinction over the course of a century, with a human-induced catastrophe (e.g. disease or war) posing the greatest threat. But since such a catastrophe could feasibly occur in Uganda, the long-term viability of the Budongo and Bugoma populations will be greatly enhanced if managed as a metapopulation. One possibility is to maintain a 'corridor' linking the two forests via Hoima's network of riverine forests, small government reserves and savanna-woodlands (McLennan 2008; Plumptre et al. 2010).

A further factor to consider is that negative interactions between apes and farmers undermine local support for conservation in and around protected areas (Wrangham 2001). In Uganda, cases of chimpanzees attacking people have been reported in the national press (Rwebembera 2004; Tenywa 2006), and occasionally these stories surface in the international media (Smith and Marsh 2003). Therefore conflict between rural farming communities and 'problem' chimpanzees also has the potential to affect adversely national and international public support for conservation of this species. For this reason, it might be short-sighted to disregard all populations inhabiting degraded and fragmented landscapes. But conserving chimpanzees in such habitat entails a troubling dilemma, for in essence we are asking impoverished human communities to share their environment with a large, potentially dangerous wild animal, which they fear. In Uganda, chimpanzees are not perceived by local people to have the same intrinsic value that the international and scientific community assigns to this species. If local people are expected to continue living alongside these intelligent and fascinating animals, the benefits must significantly outweigh the costs.

10.5. Recommendations

The results of this study suggest that the recent destruction of chimpanzee habitat in northern Hoima District, which has given rise to escalating conflict between apes and farmers, has emerged out of a combination of factors including inadequate law and policy enforcement, insecure land tenure, agricultural development initiatives that undervalue natural forest, and poverty. While the following recommendations relate specifically to the present situation in Hoima, many are relevant elsewhere where great apes and humans share a habitat. For more general recommendations regarding human–great ape conflict management, see Hockings and Humle (2009). For information about current strategies to conserve chimpanzees in Uganda, including agencies involved in implementation, see Reynolds (2005) and Plumptre et al. (2010).

Land Tenure and Management Issues

Weak enforcement of wildlife and forestry laws in Hoima District, and in particular the involvement of powerful local figures in illicit logging and its alleged support at all levels of government, presents challenges for conservation. This situation underscores the importance of supporting and empowering local people to manage resources on their land in a manner that is compatible both with poverty alleviation and conservation goals. Since insecurity over land tenure may motivate forest owners to sell trees and clear forest quickly, an important first step is to clarify and secure tenurial rights (Romano 2007). This is especially critical given that some local people at Bulindi evidently believe conservation of chimpanzees and forest will result in a loss of land and access to resources (Chapter 9).

As part of Uganda's recent forestry reforms, governance of forest resources was part-devolved to local district governments and local forest-user groups are encouraged to become more active in forest management (MWLE 2002; Turyahabwe et al. 2007). Further to revenue collection, the District Forestry Services are required to provide advisory services to owners of natural forests outside government reserves, including development of 'sustainable management' plans. To address land tenure issues, owners of private and communal forests are encouraged to register their forests (MWLE 2002; Government of Uganda 2003). Yet no evidence suggested this was happening at Bulindi. Reasons for weak policy implementation regionally may include lack of clear guidelines for registration procedures, management plans and law enforcement; inadequate training and fiscal support; the need for short-term revenue generation from forest produce to fund the District budget; inadequate accountability; or other political factors (cf. Turyahabwe et al. 2007). Conservation organisations should work with the District government and local forest owners to implement policy (e.g. by assisting local people to register their land formally and providing training and advice on sustainable management practices). This would help alleviate anxieties about appropriation of land and resources by conservation projects.

The small government reserves controlled by the NFA in northern Hoima (including Kandanda–Ngobya at Bulindi) are classified as 'production' reserves for development of industrial forest plantations (NFA 2005). Chimpanzees that range within these reserves enjoy no more protection than those on private or communal land (McLennan 2008). Both local government and the NFA must therefore be publicly called upon to take into account the presence of chimpanzees – protected under Ugandan law – in the management of the District's forests. Likewise, policy-makers should consider the environmental impact of agricultural initiatives since degraded and deforested environments may not be conducive to long-term rural development and poverty alleviation. Tobacco firms operating in the region, such as British American Tobacco and Continental Tobacco (Uganda), must be made to conduct environmental impact assessments, performed by independent, external agencies. They should not purchase tobacco where riverine forest has been cleared in order to grow it, and they must provide farmers with materials to build tobacco drying barns to relieve pressure on local forests. Clearly, there is insufficient collaboration between the Ugandan Wildlife Authority (UWA) and officials working in the forestry and agriculture sectors. Certain agricultural and forestry initiatives are currently incompatible with the UWA mandate of endangered wildlife management outside of protected areas.

Alternative Income Sources for Local People

Long-term rural development programmes are needed to offer local people alternative income sources that reduce pressure on unprotected forest. Put simply, the economic returns of maintaining forest must exceed that of other land-uses. As discussed in Chapter 8, ecotourism based on chimpanzee tracking is inappropriate in heavily human-dominated habitats, such as Bulindi, for reasons that include increased likelihood of crop-raiding following habituation, risk of aggression to local people and tourists by emboldened and/or stressed apes (McLennan and Hill 2010), and increased potential for disease transmission. However, development of alternative forms of ecotourism may prove to be more suitable (for example, a roadside cafe to be managed by an association of local households is currently under construction at Bulindi). With appropriate support and training, community income-generating enterprises such as poultry- and bee-keeping, piggeries and fruit-tree growing could provide residents with a viable alternative to selling trees and clearing forest for tobacco. An additional strategy is to explore possibilities for payment for ecosystem services as an incentive for local households to maintain forest on their land. While Plumptre et al. (2010) advocate purchasing private land within the proposed Budongo–Bugoma corridor area, the current sensitivity over land issues at Bulindi suggest this is likely to generate controversy (see also Laudati 2010, who reports local resentment following land purchase by an international conservation organisation around Bwindi-Impenetrable NP).

Alternative Wood Sources

Projects that offer residents an alternative wood source are a priority and are likely to be well received by local households (pers. obs.). For example, establishing tree nurseries and distributing seedlings of fast-growing indigenous species for woodlots outside the forest should help meet future fuelwood and timber requirements (see KCFWP 2006). However, not all residents have sufficient landholdings to plant woodlots at the expense of crops. But it may be feasible to incorporate woodlots into forest restoration programmes, if woodlots are established along forest margins. Other worthwhile projects include promotion of fuel-efficient stoves, which was recently trialled around Kibale NP (KCFWP 2006; Kasenene and Ross 2008), and use of organic fertilisers to help tackle declining soil fertility associated with agricultural intensification (i.e. tobacco farming); the need to establish new gardens on forest land each season might be reduced as a result. The feasibility of introducing suitable alternative energy sources to wood-fuels (e.g. 'biomass briquettes' or cow dung) also needs exploring.

Education and Support

Conservation initiatives must be delivered with a strong, culturally-sensitive educational emphasis. Further to providing information about chimpanzees and their behaviour, and advice and support on environmental issues, education programmes should promote human behaviours that reduce negative interactions with apes and facilitate coexistence (for example, the risk to children from harassing chimpanzees clearly needs widely emphasising; see also Hockings and Humle 2009). An awareness-raising campaign is urgently required to address the problem of chimpanzees being caught in traps in this region. While illegal, 'man-traps' are widely used by farmers to protect crops and are openly sold in local markets. The wildlife authorities need to do more to ensure the use of traps is outlawed. The media could be better utilised to publicise the problem and other conservation issues pertaining to chimpanzees and forests. Projects will need to work with farmers to improve the effectiveness of non-lethal crop-raiding deterrence methods (see Sillero-Zubiri and Switzer 2001; Hill et al. 2002).

Habitat Preservation and Enrichment

One aim of this study was to identify foods that are especially important for chimpanzees in Hoima's riverine forest–farmland mosaic (Chapter 5). At Bulindi, even important foods that are common are at risk of over-harvesting by people, including the *Phoenix* palm, the fruits of which sustain these chimpanzees during much of the year. In the case of the common timber tree *Antiaris toxicaria*, medium to large specimens are being systematically removed, eliminating one of the apes' preferred seasonal fruit sources (Chapter 3). Since many forest trees that provide food for chimpanzees are also valued by people for a variety of uses, sustainable management of these species would benefit local households as well as apes (cf. Kinnaird 1992a; Chepstow-Lusty et al.

2006). Conservation projects should therefore work with local forest owners to protect important food species from over-exploitation. Particular attention should focus on preservation of fallback foods (for example, figs). Participation in community income-generating projects must include the provision that remaining specimens of major food species are not cut.

Effective management of wild forest foods, including enrichment planting, should reduce chimpanzee dependence on crops in the long-term. Nevertheless, certain cultivars are currently among the most important items in the apes' diet at Bulindi and should not be ignored in management plans. In particular, preservation of abandoned forest cocoa *shambas* is imperative; qualitative observations indicated the occurrence of dieback and some replanting is recommended. Since rehabilitation of the cocoa for commercial purposes is incompatible with efforts to reduce chimpanzee–farmer conflict, it is appropriate to compensate the owners of these *shambas*. Guava was the most frequently eaten fruit after figs and should be considered a candidate for forest enrichment planting because (i) small naturalised guava trees already occur in regenerating habitat and around forest edges, and (ii) guava is fast-growing, producing fruit in less than two years (Thaipong and Boonprakob 2005). This could alleviate the problem of chimpanzees travelling into village areas to raid domestic guava trees. Other potential candidates for enrichment planting are fast-growing indigenous species that produce fruits eaten by chimpanzees (e.g. *Maesopsis eminii*, *Ficus* spp.).

Conclusion

If projects are to be effective they must be developed and implemented with the full support of local and national stakeholders (Ancrenaz et al. 2007). A central role must be given to local Ugandans with an interest in conservation and chimpanzees. But change will not happen overnight. Forest and wildlife populations, including chimpanzees, will continue to be lost in the short-term. It may be naïve to assume that by gaining access to alternative income sources local residents will reduce their dependence on remaining forest resources (Hill 2008). Moreover, local communities are not homogenous units, instead comprising individuals, households, clans and villages, whose primary motivation in project participation will often be to maximise their own benefits, whether economic, political or both (Hill 2008; pers. obs.). Conservation programmes may struggle to receive support from officials if project goals are perceived as counter to their professional or personal interests. In addition, conservation agencies and other NGOs compete among themselves for publicity and funding. The challenge is to balance potentially competing interests of all stakeholders and ensure equitable distribution of benefits to recipients. A further constraint is the time required to evaluate the effectiveness of projects given short-term funding cycles (Hill 2008). For example, though community projects have recently been initiated at Bulindi, their immediate effect on reducing overall deforestation rates appear limited. But it is too early to assess their longer-term impact on conservation attitudes and behaviour.

The challenges facing conservation of chimpanzees and other wildlife and their habitats outside of protected areas in Uganda are formidable. With regard to the clearance of forest fragments in the human-dominated landscape surrounding Kibale NP, Chapman et al. (2007: 526) conclude that “reversal of the present trends requires a major conservation effort, on a scale and of a nature that has not been done in the region for any species or habitat to date”, and that “in reality, it is unlikely that a project of such a magnitude will be initiated”. A major problem will be securing funding for such a similarly vast conservation undertaking in Hoima District. Nevertheless, the Budongo–Bugoma corridor through northern Hoima was recently identified as one of East Africa’s Chimpanzee Conservation Units, and thus a priority site for conservation (Plumptre et al. 2010). It is my sincere hope that funds will be forthcoming, so that chimpanzees at Bulindi and elsewhere in this region may yet share a future with people.

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Appendix 1. Tree species recorded in forest plots at Bulindi. For each species the number of stems recorded (≥10 cm DBH), density (stems ha^{-1}), basal area (BA) ha^{-1} (m^2) and mean DBH are shown. Species densities are also shown for individual forest fragments: KLA = Kyamalera, KGA = Kyamusoga, KTA = Kiseeta, KWG = Kaawango, MPA–NKE = Mparangasi–Nyakakonge, KGRO = Katigiro. Tree species nomenclature follows the *Flora of Tropical East Africa*; synonyms commonly used in the literature are given for some species.

Species **(Synonym)**	**Family** **(subfamily)**	**No. Stems**	**Density ha^{-1}**	**BA ha^{-1}**	**Mean DBH**	**Density in Individual Fragments**					
						KLA	KGA	KTA	KWG	MPA–NKE	KGRO
1. *Aidia micrantha* (K. Schum.) F. White	Rubiaceae	1	0.3	0.006	17.2	–	–	–	1.8	–	–
2. *Albizia coriaria* (Welm. ex) Oliv.	Fabaceae (Mimosoideae)	14	3.8	1.349	63.5	7.4	–	–	5.4	3.2	5.0
3. *Albizia glaberrima* (Schumach. & Thonn.) Benth.	Fabaceae (Mimosoideae)	12	3.2	0.439	34.8	7.4	–	–	5.4	2.1	–
4. *Albizia grandibracteata* Taub.	Fabaceae (Mimosoideae)	2	0.5	0.334	88.5	–	–	1.6	1.8	–	–
5. *Albizia zygia* (DC.) Macbr.	Fabaceae (Mimosoideae)	20	5.4	0.546	32.0	6.4	2.4	3.1	3.6	4.3	25.0
6. *Allophylus africanus* P. Beauv.	Sapindaceae	9	2.4	0.042	14.1	1.1	–	6.3	–	–	20.0
7. *Allophylus ferrugineus* Taub. (syn. *A. macrobotrys*)	Sapindaceae	2	0.5	0.004	10.3	–	–	–	–	–	10.0
8. *Annona senegalensis* Pers.	Annonaceae	5	1.4	0.015	11.7	–	–	3.1	–	2.1	5.0
9. *Antiaris toxicaria* Leschen.	Moraceae	129	34.9	2.286	24.4	66.0	21.4	32.8	23.2	20.2	25.0
10. *Antidesma membranaceum* Muell. Arg.	Phyllanthaceae	2	0.5	0.011	15.8	–	–	–	–	2.1	–
11. *Bombax buonopozense* P. Beauv.	Bombacaceae	1	0.3	0.004	14.3	1.1	–	–	–	–	–
12. *Bridelia ndellensis* Beille	Euphorbiaceae	1	0.3	0.032	39.1	–	2.4	–	–	–	–
13. *Celtis africana* Burm. f.	Ulmaceae	4	1.1	0.039	20.4	–	–	–	–	–	20.0
14. *Combretum collinum* Fresen.	Combretaceae	12	3.2	0.043	12.8	1.1	–	3.1	1.8	–	40.0
15. *Combretum molle* G. Don	Combretaceae	6	1.6	0.069	21.3	–	–	4.7	–	1.1	10.0
16. *Croton macrostachyus* Del.	Euphorbiaceae	8	2.2	0.085	21.9	–	–	–	1.8	7.4	–
17. *Croton sylvaticus* Krauss	Euphorbiaceae	2	0.5	0.020	20.2	–	–	–	–	2.1	–
18. *Dictyandra arborescens* Hook. f.	Rubiaceae	11	3.0	0.053	14.7	10.6	2.4	–	–	–	–
19. *Dombeya kirkii* Mast. (syn. *D. mukole*)	Sterculiaceae	4	1.1	0.019	15.1	–	2.4	–	–	1.1	10.0
20. *Dracaena steudneri* Engl.	Dracaenaceae	4	1.1	0.022	15.4	2.1	–	–	–	2.1	–

Cont. overleaf

Appendix 1. *cont*.

Species **(Synonym)**	**Family** **(subfamily)**	**No. Stems**	**Density ha^{-1}**	**BA ha^{-1}**	**Mean DBH**	**Density in Individual Fragments**					
						KLA	KGA	KTA	KWG	MPA–NKE	KGRO
21. *Entandrophragma angolense* (Welw.) C.DC.	Meliaceae	15	4.1	0.187	22.2	4.3	2.4	1.6	8.9	4.3	–
22. *Entandrophragma cylindricum* (Sprague) Sprague	Meliaceae	2	0.5	0.006	11.8	1.1	2.4	–	–	–	–
23. *Entandrophragma utile* (Dawe & Sprague) Sprague	Meliaceae	4	1.1	0.020	14.5	1.1	7.1	–	–	–	–
24. *Erythrina abyssinica* DC.	Fabaceae (Faboideae)	2	0.5	0.008	13.2	–	–	1.6	–	–	5.0
25. *Fagaropsis angolensis* (Engl.) Dale	Rutaceae	5	1.4	0.107	28.3	3.2	–	–	3.6	–	–
26. *Ficus exasperata* Vahl	Moraceae	9	2.4	0.155	26.0	6.4	–	3.1	1.8	–	–
27. *Ficus mucuso* Ficalho	Moraceae	5	1.4	0.164	28.2	–	–	3.1	–	3.2	–
28. *Ficus natalensis* Hochst.	Moraceae	17	4.6	1.012	43.8	1.1	2.4	14.1	3.6	4.3	–
29. *Ficus ovata* Vahl (syn. *F. brachypoda*)	Moraceae	3	0.8	0.226	56.5	1.1	–	1.6	–	1.1	–
30. *Ficus sur* Forssk. (syn. *F. capensis*)	Moraceae	21	5.7	0.446	27.3	3.2	4.8	–	7.1	12.8	–
31. *Ficus vallis-choudae* Del.	Moraceae	6	1.6	0.034	15.9	–	–	–	1.8	5.3	–
32. *Ficus variifolia* Warb.	Moraceae	1	0.3	0.007	18.1	–	–	1.6	–	–	–
33. *Funtumia africana* (Benth.) Stapf (syn. *F. latifolia*)	Apocynaceae	104	28.1	1.312	22.3	28.7	66.7	18.8	35.7	16.0	10.0
34. *Glenniea africana* (Radlk.) Leenh. (syn. *Crossonephelis africanus*)	Sapindaceae	76	20.5	1.338	24.5	30.9	33.3	4.7	26.8	16.0	–
35. *Harungana madagascariensis* Poir.	Guttiferae	5	1.4	0.036	16.6	1.1	–	1.6	–	3.2	–
36. *Khaya anthotheca* (Welw.) C.DC.	Meliaceae	3	0.8	0.029	20.9	–	–	3.1	–	1.1	–
37. *Lannea barteri* (Oliv.) Engl.	Anacardiaceae	1	0.3	0.020	30.8	–	–	–	–	–	5.0
38. *Lannea schimperi* (A. Rich.) Engl.	Anacardiaceae	4	1.1	0.031	17.8	–	2.4	–	–	–	15.0
39. *Lindackeria schweinfurthii* Gilg	Flacourtiaceae	1	0.3	0.002	10.8	1.1	–	–	–	–	–
40. *Lovoa trichilioides* Harms (syn. *L. brownii*)	Meliaceae	45	12.2	0.537	21.8	21.3	9.5	4.7	10.7	11.7	5.0

Cont. overleaf

Appendix 1. *cont*.

Species **(Synonym)**	**Family** **(subfamily)**	**No. Stems**	**Density ha^{-1}**	**BA ha^{-1}**	**Mean DBH**	**Density in Individual Fragments**					
						KLA	KGA	KTA	KWG	MPA–NKE	KGRO
41. *Macaranga schweinfurthii* Pax	Euphorbiaceae	58	15.7	0.861	22.4	14.9	19.0	–	23.2	24.5	–
42. *Maesopsis eminii* Engl.	Rhamnaceae	6	1.6	0.153	32.1	–	–	7.8	–	–	5.0
43. *Margaritaria discoidea* (Baill.) Webster (syn. *Phyllanthus discoideus*)	Euphorbiaceae	17	4.6	0.260	24.1	3.2	2.4	7.8	5.4	2.1	15.0
44. *Markhamia platycalyx* (Baker) Sprague (syn. *M. lutea*)	Bignoniaceae	1	0.3	0.002	10.2	1.1	–	–	–	–	–
45. *Maytenus heterophylla* (Eckl. & Zeyh.) N. Robson	Celastraceae	9	2.4	0.026	11.7	–	–	–	–	9.6	–
46. *Milicia excelsa* (Welw.) C.C. Berg	Moraceae	2	0.5	0.459	82.5	2.1	–	–	–	–	–
47. *Morus mesozygia* Stapf (syn. *M. lactea*)	Moraceae	12	3.2	0.437	31.5	–	4.8	6.3	1.8	1.1	20.0
48. *Multidentia crassa* (Hiern) Bridson & Verdc.	Rubiaceae	1	0.3	0.007	17.8	1.1	–	–	–	–	–
49. *Neoboutonia melleri* (Muell. Arg.) Prain	Euphorbiaceae	24	6.5	0.284	20.8	16.0	21.4	–	–	–	–
50. *Ochna afzelii* Oliv.	Ochnaceae	3	0.8	0.026	20.1	–	2.4	–	–	–	10.0
51. *Oncoba spinosa* Forssk.	Flacourtiaceae	3	0.8	0.009	11.9	–	–	1.6	1.8	1.1	–
52. *Oxyanthus speciosus* DC.	Rubiaceae	14	3.8	0.056	13.4	9.6	–	–	3.6	3.2	–
53. *Parkia filicoidea* (Welw. ex) Oliv.	Fabaceae (Mimosoideae)	15	4.1	0.396	31.2	8.5	–	6.3	–	3.2	–
54. *Phoenix reclinata* Jacq.	Arecaceae	394	106.5	2.804	18.0	126.6	161.9	9.4	85.7	160.6	10.0
55. *Piptadeniastrum africanum* (Hook. f.) Brenan	Fabaceae (Mimosoideae)	15	4.1	0.333	27.5	10.6	4.8	1.6	1.8	1.1	–
56. *Pittosporum mannii* Hook. f.	Pittosporaceae	4	1.1	0.010	10.9	1.1	–	3.1	–	1.1	–
57. *Pseudospondias microcarpa* (A. Rich.) Engl.	Anacardiaceae	69	18.6	2.539	34.9	12.8	47.6	10.9	16.1	22.3	–
58. *Pycnanthus angolensis* (Welw.) Warb.	Myristicaceae	10	2.7	0.131	22.6	1.1	–	1.6	–	8.5	–
59. *Raphia farinifera* (Gaertn.) Hylander	Arecaceae	1	0.3	0.083	62.5	1.1	–	–	–	–	–
60. *Rauvolfia vomitoria* Afzel	Apocynaceae	2	0.5	0.098	47.1	–	4.8	–	–	–	–

Cont. overleaf

Appendix 1. *cont.*

Species **(Synonym)**	**Family** **(subfamily)**	**No. Stems**	**Density ha^{-1}**	**BA ha^{-1}**	**Mean DBH**	**Density in Individual Fragments**					
						KLA	KGA	KTA	KWG	MPA–NKE	KGRO
61. *Rhus natalensis* Krauss	Anacardiaceae	1	0.3	0.006	17.0	–	–	–	–	–	5.0
62. *Rothmannia urcelliformis* (Hiern) Robyns	Rubiaceae	2	0.5	0.007	12.5	–	–	–	3.6	–	–
63. *Sapium ellipticum* (Krauss) Pax	Euphorbiaceae	16	4.3	0.852	46.8	4.3	4.8	4.7	5.4	2.1	10.0
64. *Senna spectabilis* (DC.) Irwin & Barneby (syn. *Cassia spectabilis*)	Fabaceae (Caesalpinioideae)	3	0.8	0.086	36.6	–	–	–	–	3.2	–
65. *Spathodea campanulata* P. Beauv.	Bignoniaceae	6	1.6	0.022	13.0	–	–	7.8	1.8	–	–
66. *Sterculia dawei* Sprague	Sterculiaceae	7	1.9	0.509	48.5	1.1	–	6.3	–	1.1	5.0
67. *Strombosia scheffleri* Engl.	Olacaceae	1	0.3	0.011	23.1	–	–	–	1.8	–	–
68. *Teclea nobilis* Del.	Rutaceae	64	17.3	0.587	19.4	10.6	–	1.6	16.1	45.7	5.0
69. *Terminalia glaucescens* Benth. (syn. *T. veluntina*)	Combretaceae	1	0.3	0.003	12.8	1.1	–	–	–	–	–
70. *Theobroma cacao* L.	Sterculiaceae	115	31.1	0.419	12.8	4.3	95.2	106.3	5.4	–	–
71. *Trema orientalis* (L.) Bl.	Ulmaceae	7	1.9	0.062	17.5	–	9.5	–	3.6	1.1	–
72. *Trichilia dregeana* Sond.	Meliaceae	25	6.8	0.484	26.6	3.2	7.1	14.1	7.1	–	30.0
73. *Trichilia prieureana* A. Juss.	Meliaceae	8	2.2	0.049	16.0	1.1	2.4	–	–	4.3	10.0
74. *Trichilia rubescens* Oliv.	Meliaceae	3	0.8	0.014	14.2	–	–	3.1	–	1.1	–
75. *Trilepisium madagascariensis* DC. (syn. *Bosqueia phoberos*)	Moraceae	224	60.5	3.144	22.1	88.3	81.0	39.1	44.6	60.6	–
76. *Vangueria apiculata* K. Schum.	Rubiaceae	1	0.3	0.004	13.5	–	–	–	–	1.1	–
77. *Vangueria madagascariensis* Gmelin	Rubiaceae	2	0.5	0.014	17.5	–	–	–	–	–	10.0
78. *Vitex doniana* Sweet	Lamiaceae	1	0.3	0.005	16.0	–	–	–	–	–	5.0
79. *Zanha golungensis* Hiern	Sapindaceae	4	1.1	0.142	37.5	4.3	–	–	–	–	–
Total:		1729	467.3	26.486	22.4	535.1	631.0	353.1	373.2	485.1	350.0

Appendix 2. Tree species (≥10 cm DBH) not recorded in plots but which occur at low densities in riverine or hillside forest at Bulindi. Tree species nomenclature follows the *Flora of Tropical East Africa.* Synonyms commonly used in the literature are given for some species.

Species **(synonym)**	**Family**
Alchornea cordifolia (Schumach. & Thonn.) Muell. Arg.[1]	Euphorbiaceae
Allophylus dummeri Baker f *	Sapindaceae
Aningeria altissima (A. Chev.) Aubrév. & Pellegr. * (syn. *Pouteria altissima*)	Sapotaceae
Bridelia micrantha (Hochst.) Baill. *	Euphorbiaceae
Broussonetia papyrifera (L.) Vent.[2]	Moraceae
Caloncoba crepiniana (De Wild. & Th. Dur.) Gilg (syn. *C. schweinfurthii*)	Flacourtiaceae
Chrysophyllum albidum G. Don *	Sapotaceae
Cola gigantea A. Chev. *	Sterculiaceae
Cordia millenii Bak.	Boraginaceae
Ehretia cymosa Thonn. *	Boraginaceae
Entada abyssinica (Steud. ex) A. Rich.	Fabaceae (subfam. Mimosoideae)
Ficus glumosa Del.	Moraceae
Ficus sansibarica Warb. * (syn. *F. brachylepis*)	Moraceae
Ficus sp. *	Moraceae
Ficus thonningii Bl.	Moraceae
Hallea stipulosa (DC.) J.-F. Leroy (syn. *Mitragyna stipulosa*)	Rubiaceae
Mangifera indica L.[2]	Anacardiaceae
Psidium guajava L.[2]	Myrtaceae
Spondianthus preussii Engl. *	Euphorbiaceae

[1] *A. cordifolia* is a common spreading shrub in swamp forest but also occurs as a small tree;
[2] Naturalised exotic;
* Indicates species known at Bulindi from a single specimen only.

Appendix 3. The fate of lost phenology trees (Dec 06–Jan 08). Forest fragments: KLA = Kyamalera, KGA = Kyamusoga, KTA = Kiseeta, KWG = Kaawango, MPA = Mparangasi, KGRO = Katigiro.

#	**Species**	**Forest**	**Month/ Year**	**DBH (cm)**	**Cause of Loss**
1	*Annona senegalensis*	KGRO	Jun 07	20.0	Clearance for garden
2	*Annona senegalensis*	KTA	Dec 07	10.2	Clearance for pine plantation
3	*Antiaris toxicaria*	KTA	Jan 07	61.9	Cut for timber (chainsaw)
4	*Antiaris toxicaria*	KTA	Jan 07	57.0	Cut for timber (chainsaw)
5	*Antiaris toxicaria*	KLA	Jan 07	103.0	Cut for timber (chainsaw)
6	*Antiaris toxicaria*	KTA	Feb 07	46.4	Cut for timber (pit-sawn)
7	*Antiaris toxicaria*	KTA	Mar 07	36.0	Cut for timber (pit-sawn)
8	*Antiaris toxicaria*	KTA	Apr 07	79.2	Cut for timber (pit-sawn)
9	*Antiaris toxicaria*	KTA	Apr 07	94.0	Cut for timber (pit-sawn)
10	*Antiaris toxicaria*	KLA	May 07	100.0	Cut for timber (pit-sawn)
11	*Antiaris toxicaria*	KTA	Dec 07	60.7	Clearance for pine plantation *
12	*Antiaris toxicaria*	KTA	Dec 07	38.0	Clearance for pine plantation *
13	*Entandrophragma angolense*	KLA	May 07	23.8	Cut for pole for pitsaw camp
14	*Ficus exasperata*	KTA	Apr 07	21.3	Crushed by felled *Antiaris*
15	*Ficus ovata*	MPA	Oct 07	88.5	Fell over during storm
16	*Ficus ovata*	KLA	Dec 07	47.2	Burnt dry
17	*Ficus ovata*	KTA	Dec 07	59.4	Clearance for pine plantation *
18	*Ficus sur*	KGA	Jan 07	32.0	Clearance for garden
19	*Ficus vallis-choudae*	KGA	Jan 07	25.6	Clearance for garden
20	*Ficus vallis-choudae*	KWG	Oct 07	101.1	Fell over during storm
21	*Harungana madagascariensis*	MPA	Jan 08	11.5	Clearance for tobacco nursery
22	*Harungana madagascariensis*	MPA	Jan 08	10.3	Clearance for tobacco nursery
23	*Macaranga schweinfurthii*	MPA	Dec 06	72.6	Clearance for tobacco nursery
24	*Morus mesozygia*	KTA	Mar 07	51.7	Fell over during storm
25	*Morus mesozygia*	KTA	Nov 07	23.4	Cut for pole for pitsaw structure
26	*Morus mesozygia*	KTA	Dec 07	38.5	Clearance for pine plantation
27	*Morus mesozygia*	KTA	Dec 07	31.7	Clearance for pine plantation
28	*Parkia filicoidea*	KTA	Dec 07	40.4	Clearance for pine plantation *
29	*Parkia filicoidea*	KTA	Dec 07	46.8	Clearance for pine plantation *
30	*Parkia filicoidea*	KTA	Dec 07	83.4	Clearance for pine plantation *
31	*Parkia filicoidea*	KTA	Dec 07	44.5	Clearance for pine plantation *
32	*Phoenix reclinata*	KTA	May 07	21.7	Cut for pole
33	*Phoenix reclinata*	KLA	Dec 07	23.0	Cut for pole
34	*Psidium guajava*	KGA	May 07	6.1	Cut for pole
35	*Psidium guajava*	KGA	May 07	12.8	Cut for pole
36	*Psidium guajava*	KGA	Dec 07	8.0	Cut for pole
37	*Pycnanthus angolensis*	KGA	Feb 07	47.3	Cut for timber (pit-sawn)
38	*Pycnanthus angolensis*	MPA	Oct 07	21.8	Fell over during storm

Cont. overleaf

Appendix 3. *cont.*

#	**Species**	**Forest**	**Month/ Year**	**DBH (cm)**	**Cause of Loss**
39	*Sterculia dawei*	KTA	Jan 07	80.0	Cut for timber (chainsaw)
40	*Sterculia dawei*	KTA	Jan 07	83.4	Cut for timber (chainsaw)
41	*Sterculia dawei*	KGA	Feb 07	73.7	Cut for timber (chainsaw)
42	*Sterculia dawei*	KGA	Feb 07	58.9	Cut for timber (chainsaw)
43	*Teclea nobilis*	MPA	Feb 07	26.6	Crushed by felled *Trilepisium*
44	*Theobroma cacao*	KTA	Apr 07	16.9	Natural death
45	*Theobroma cacao*	KLA	Aug 07	10.8	*Shamba* cut to discourage chimps
46	*Theobroma cacao*	KLA	Aug 07	11.7	*Shamba* cut to discourage chimps
47	*Theobroma cacao*	KLA	Aug 07	14.1	*Shamba* cut to discourage chimps
48	*Theobroma cacao*	KLA	Aug 07	15.1	*Shamba* cut to discourage chimps
49	*Theobroma cacao*	KLA	Aug 07	15.2	*Shamba* cut to discourage chimps
50	*Trilepisium madagascariensis*	KLA	Jan 07	58.8	Cut for timber (chainsaw)
51	*Trilepisium madagascariensis*	KWG	May 07	15.9	Cut for pole
52	*Trilepisium madagascariensis*	MPA	Jun 07	60.9	Cut for timber (pit-sawn)
53	*Trilepisium madagascariensis*	KTA	Aug 07	46.2	Cut for timber (pit-sawn)
54	*Trilepisium madagascariensis*	KGA	Dec 07	44.5	Cut for timber (pit-sawn)

* Indicates trees felled in December 07 in preparation for a pine plantation, but which were first sawn for timber.

Appendix 4. Description of crop-raiding behaviour by chimpanzees at Bulindi.

Case 1. 20 September 2007

0842. Chimpanzees are heard calling from narrow gallery forest that forms a boundary between Mparangasi and Nyaituma villages. An adult male (KT) is still in his nest in a *Pseudospondias microcarpa* tree at the forest edge, opposite a large banana plantation in Nyaituma village.

0914. A field assistant and I walk through gardens towards the banana. A second adult male (JL) is sitting in a nest in a *Ficus exasperata* tree in the centre of the plantation, some distance from where KT and other chimps are by the river. As we get closer (75 m), JL watches us calmly from his nest. We continue into a cassava garden and stand in front of the plantation, 70 m from KT in his nest. Other chimps are present in the *Pseudopondias* but are obscured by foliage.

0954. We hear *hoos* from behind us. JL has emerged from the banana plantation and stands 50 m from us, hair erect, glaring; he is holding a full bunch of bananas. KT and other chimps in the *Pseudspondias* pant-hoot. JL briefly displays at us, then climbs into the tree and eats banana. Shortly afterwards he displays up through the tree and all the chimps pant-hoot; some are on the ground in vegetation beneath the tree. JL makes a day nest. We are joined by a local man who tells us the chimps want to get at his brewing bananas that are ripening in an underground store just inside the entrance of the plantation, about 70 m from the *Pseudospondias* tree (Plate 16). He says he will have to spend the whole day guarding it. Four chimps nested the previous night deep in the plantation overlooking his homestead (250 m from the forest) and raided his sugarcane as well as some bananas from the store. As we stand talking the chimps pant-hoot and at least four adult males (JL, KT, MR, JK) display at us in the tree; probably they recognise this man as someone who chases them from the banana. There are choruses of pant-hoots at 1019, 1020 and 1029. It appears the apes are frustrated by our presence near the banana store. By 1035 all the males have descended the tree and are out of view in undergrowth by the river.

1045. The local man takes us to where chimps nested the previous night and shows us fresh sugarcane damage 400 m outside the forest. The banana plantation is large and it seems the chimps move freely within it; because of banana wilt the ground vegetation has been allowed to grow, providing the chimps with cover. The man says his children are not safe around the homestead because the chimps come for sugarcane, papaya and banana. He says it is only in the last 1–2 years that they are coming so far out of the forest.

1230. The chimps have been quiet for almost two hours. We approach the *Pseudospondias* tree and collect dung. At 1235 and 1255 the chimps call from across the river (<50 m distant), probably in response to our proximity. We move back into the garden, thinking they want to return to the *Pseudospondias* tree.

1305. Children are heard shouting from gardens across the river on the opposite side of the gallery forest (Mparangasi side) and a dog is barking. We can see four large chimps, probably all adult males, walking purposefully from the forest towards nearby homesteads. There are around six children, a teenage girl and a woman in an adjacent garden. The dog is running towards the chimps and the people are shouting, but the apes appear unconcerned. At 1312 chimps can be seen in the middle of the nearest homestead. We cross the river and join the people in the garden. A young adult male (MR) watches us calmly from the homestead (60 m distant), which is empty because the women and children are in the gardens. At 1315 KT appears from behind a house and, with a papaya fruit in his mouth, begins an impressive charging display towards the forest. He slaps the ground hard about ten times as he charges, and then sits at the forest edge watching us. The dog runs towards him, barking, but he ignores it and then re-enters the forest. An adult female with an infant on her back runs rapidly towards a second homestead >100 m from the forest, followed by a juvenile.

1325. Shouting is heard from the second homestead; an adult male (probably MR) is glimpsed feeding in a guava tree in the grounds of the home. A woman and several children have retreated inside the house, shutting the doors and windows. When we arrive the chimps have just left; there are many half-eaten guavas under the tree. The woman says the chimps usually come on Thursdays, which is a market day, because they know the men are away.

1345. We cross the river through the forest and return to the banana plantation on the other side of the forest. A woman immediately tells us she has just encountered chimps near the underground store and asks for help guarding it. At 1346 a young adult male (JK) appears at the edge of the plantation to monitor us (44 m distant). At 1348 we approach the store. Chimps have tried unsuccessfully to open the entrance to the store, which has several heavy logs piled against it. An adult male (JK?) is partially visible watching us from a jackfruit tree within the plantation (30 m distant). The man whom we met earlier approaches through the banana and the chimp climbs down and disappears. It appears that while some chimps raided guava and papaya from homesteads on the other side of the river, others came for the banana, perhaps seeing we had moved away. However, the man says chimps have also just raided sugarcane at his home on the other side of the banana suggesting at least some apes were hiding in the plantation. Between 1358 and 1453 chimps call several times from near the river behind the *Pseudospondias* tree but they do not return for bananas that afternoon. According to villagers, they also did not return that evening or the following morning.

Appendix 4. *cont*.

Case 2. 20 December 2007

0735. Chimpanzees are heard screaming and pant-hooting from where gallery forest in Mparangasi has been cleared for a rice garden. Two field assistants and I arrive at 0744. The chimps are in isolated trees overlooking gardens on the Nyaituma side of the river. They show no obvious reaction to our arrival (75 m distant); nearby in gardens children are mimicking their calls. Some chimps are in an *Antiaris toxicaria* tree feeding on emerging young leaves. Two adult males (SL and MR) sit in a neighbouring *Pseudospondias microcarpa* tree looking out over farmland. We count six adult males, a female in full estrous, another adult female, an adolescent female, and at least two juveniles and two infants.

0747. The chimps call and scream and some of the males display; the excitement appears to be related to the presence of the estrous female. The female presents to JL (probable alpha male) who inspects her. Several chimps make day nests. Children approach us through the gardens mimicking pant-hoots (no response from the chimps) and a field assistant tells them to go back. Adult males KT and SL sit watching us and the children.

0818. SL descends the tree and some of the males vocalise. KT and MR are watching us intently, and after a moment they also descend. At 0825 they call from a mango tree 100 m away in the middle of gardens. Apparently they had been waiting for the opportunity to go for these mangos. We approach and can see one male (KT) in the crown of the tree peeping at us and eating mangos, which appear to be half-ripe. Meanwhile, those who remained by the river rest in day nests and between 0903 and 0939 the two parties exchange calls. At 0958 there are loud calls and JL displays in the *Pseudospondias* tree, shaking branches at the estrous female. The males at the mango tree rush back through a maize garden to rejoin the group by the river. There follows several minutes of calls, displays and general excitement. By 1012 most of the chimps are out of sight in undergrowth beneath the *Pseudospondias* tree. We stand 50 m away in a rice garden where we are joined by three women, and a boy with a dog. Adult male JL reclines on an exposed branch and idly watches us.

1035. There are grunting sounds at the edge of the rice garden (30 m distant). We move back by 15 m since our proximity might be disturbing chimps resting on the ground (the women are talking rather loudly). A juvenile chimp eating a mango climbs low into a tree to watch us. At 1040 JL appears at the edge of the rice garden (25 m from us), shaking vegetation in mild threat and peering at us over the rice. After about one minute he slowly enters the rice garden and begins screaming loudly. The women make to run but field assistants tell them not to; the boy and the dog have already run off. Cautiously, JL moves through the rice, which reaches to his shoulder. His hair is erect and he is screaming with his face split in a fear-grin. He repeatedly looks at us and then behind him. When he is directly in front of us (15 m distant) he pauses and stands bipedally, screaming. The largest adult male (SL) has now appeared at the edge of the rice garden, also screaming loudly. We assume the chimps want to cross the garden but fear our proximity. JL continues to stand in front of us, alternately screaming at us and screaming at SL. Then he continues walking bipedally through the rice, still screaming. The reason for the males' interest in the rice garden becomes clear: a small cluster of sugarcane is at the centre of the rice garden, 40 m from the edge. As JL nears the sugar he displays briefly, slapping the ground. He then stands by the sugarcane, hair fully erect, looking back at SL. For more than 1 min they stand facing each other across the rice, on either side of us, both with full fear grins, screaming continuously. It seems to us that JL wants SL to join him, but SL – who earlier in the study had been the most fearless of the males – will not cross the garden in front of us. Suddenly JL very quickly snaps off about three canes, and begins walking bipedally back through the rice. When he is immediately in front of us he again pauses, and SL approaches him and presents; JL briefly mounts him. Both have been screaming continuously for more than five minutes; the rest of the party has been silent.

1049. Two teenage girls arrive at the opposite side of the rice garden, drawn by the commotion (~50 m from the males). One of the field assistants motions to them to go back, thinking the chimps may feel surrounded. When the girls turn to run it triggers a display response from the males. SL displays through the rice, away from us but oblique to the retreating girls. JL displays back towards the garden edge where other chimps can also be heard displaying in the undergrowth. Moments later the whole party is seen moving quickly across the river on the Mparangasi side. An adult female (not in estrous) is carrying a stick of sugarcane, which she has apparently obtained from JL.

Note. This encounter occurred at the end of the study when adult males were showing signs of semi-habituation: unlike during the first 12 months of research they rarely charged or threatened us, and instead usually ignored or showed mild interest in us. Nevertheless, the fearfulness of JL and SL – both high-ranking males – on this occasion was remarkable. The males wanted to take sugarcane but in order to do so they had to pass close to us in the open (there were also local women present). Ordinarily, they might try to intimidate people into leaving, through displaying or charging. But they probably knew this would not be effective with us. They also knew from experience that we would not threaten them either. Perhaps for the first time they could take sugarcane in very close proximity to watching adult humans without being chased away, or needing to chase people away. The males' fear-grins and intense screaming may have reflected their anxiety about this unusual situation.

Appendix 5. Chimpanzee attacks on children at Bulindi in 2007. Details of each case are based on local accounts.

Case 1: Attack on 4-year old boy at Kaborogota well (Kyabateke village)

Date and time of Attack: 8 January 2007; early evening, approx. 18.30.

Location: A village well situated within a small pocket of riverine forest used by chimpanzees travelling between Kiseeta and Kyamalera forests.

Circumstances at time of the attack: It appears that chimpanzees had crossed the Hoima–Masindi road from Kiseeta and entered a small strip of forest heading towards Kyamalera where they encountered a group of 4–5 children at the well. According to the eldest child (a 14-yr old girl) the children began to run. In their panic, the youngest child (a 4-yr old boy) fell down and was subsequently grabbed by a 'big' chimpanzee. The children ran and alerted villagers at nearby homesteads, who came with spears and dogs and were able to retrieve the boy. Local accounts were inconsistent, but several villagers claimed the chimpanzee took the boy into a tree. While the eldest girl said the children met the apes unexpectedly, other residents suggested they had been disturbing the animals (e.g. throwing stones). The chimpanzees apparently escaped unharmed.

Injuries: The boy was bitten on the back of his head, right foot, and beneath both armpits. He also sustained cuts on the right side of his abdomen above his rib cage, probably caused by finger-nails. He was treated over several days at a clinic in Hoima town.

Remarks: Judging from the boy's injuries, this was probably not a predatory attack. Although the wounds were serious, the chimpanzee did not attempt to feed on the child or inflict a fatal bite (cf. Wrangham et al. 2000; Kamenya 2002). Apparently, it was the first time a chimpanzee had attacked a child at Bulindi. When field assistants and I met local villagers on 10th January they were calm. Several commented that the animals involved could not have been "our chimps", but must have come from elsewhere (e.g. Budongo) because chimpanzees and people at Bulindi are "used to each other". The incident was reported on local radio on the evening of the incident and the following morning.