

GREAT APE CONSERVATION IN THE MATRIX
INVESTIGATING THE SOCIO-ECOLOGICAL RESPONSES OF CHIMPANZEES
LIVING IN A FOREST-FARM MOSAIC, UGANDA

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Abstract

Behavioural flexibility may be crucial for the long-term persistence of animals in human-modified habitats, such as forest-farm mosaic landscapes. Understanding species' socio-ecological responses to anthropogenic disturbances is essential for developing targeted strategies to ensure their survival in these habitats, particularly where conservation conflicts have arisen. This study investigates the responses of Eastern chimpanzees (*Pan troglodytes schweinfurthii*) in a newly studied site in Uganda with a history of negative human-chimpanzee interactions. I take a comparative approach, evaluating the differences in feeding strategies and activity budgets between chimpanzees in Waibira, a protected, continuous forest block, and Kasongore, unprotected riverine forest fragments surrounded by a large-scale sugarcane plantation, subsistence crop gardens, roads and villages. I followed chimpanzees in both sites over 13 months from July 2015 to July 2016 and recorded their behaviour, species consumed and party composition, size and spread using instantaneous scan samples. I recorded tree species composition and the presence of wild fruits in the forest to determine the impact of human disturbance on the availability of chimpanzee feeding species and to assess how these ecological factors affected chimpanzee behavioural and feeding strategies. Using indirect observations I recorded chimpanzee mango-foraging habits in villagers' crop gardens in Kasongore to investigate how factors relating to risk influence their feeding strategies outside of the forest. In spite of human disturbance, Kasongore forest is rich in chimpanzee feeding species and there was no shortage of wild fruits. Chimpanzees at both sites preferred ripe fruits, but at Kasongore an unprecedented level of foraging on sugarcane was recorded: chimpanzees there spent thirty percent of their overall feeding time consuming sugarcane and adult males spent more time foraging on sugarcane than wild fruits. Kasongore chimpanzees spent less time feeding and more time resting than did those in Waibira, likely as a result of fulfilling their metabolic requirements though foraging on crops. In Kasongore, chimpanzees flexibly responded to the risk of leaving the forest boundary by forming larger parties comprising a higher ratio of males. Chimpanzees foraged heavily on mangos in the village-garden matrix when they were available, regardless of relative high wild fruit availability, and minimised risk of a human encounter by selecting trees which were unguarded and closer to the forest. The results demonstrate that chimpanzees can respond flexibly to risks and changes in human-modified habitats and that, for now at least, they have sufficient resources, when supplemented by crops. The implications for the future of the Kasongore chimpanzee community are discussed. Ultimately, while they may exhibit behavioural flexibility, their long-term survival rests on the tolerance of the humans with which they share a landscape.

For Dad and Murray

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Table of Contents

Abstract.....	iii
Acknowledgements.....	vii
Table of Contents.....	ix
List of Tables	xiii
List of Figures	xv
List of Colour Plates	xvii
List of Abbreviations	xix

CHAPTER ONE INTRODUCTION

1.1 Understanding behavioural flexibility in the Anthropocene	3
1.1.1 Species' responses to human-modified landscapes	4
1.1.2 Why chimpanzees?	6
1.1.3 The Albertine Rift	8
1.2 Overall aims and chapter overview	9

PART ONE

HUMAN ACTIVITIES, FOREST COMPOSITION AND FRUIT AVAILABILITY AT THE STUDY SITES

CHAPTER TWO OVERVIEW OF STUDY SITES, SUBJECTS AND METHODS

2.1 Overview	13
2.2 Study sites and subjects	13
2.2.1 Chimpanzee status	13
2.2.2 Site selection	14
2.2.3 Location.....	14
2.3 Landcape history	15
2.4 Human history.....	16
2.4.1 Population trends and local livelihoods.....	16
2.4.2 Local beliefs and practises	17
2.4.3 Status and management of forests in Uganda	18
2.4.4 Chimpanzee threats	20
2.5 Waibira.....	20
2.5.1 Forest description	20
2.5.2 Climate	22
2.5.3 History of research	22
2.5.4 Chimpanzees	22
2.5.5 Field assistants	23
2.5.6 Human activities	23
2.6 Kasongore	25
2.6.1 Forest Description	25
2.6.2 Climate	25
2.6.3 History of research	26
2.6.4 Chimpanzees	27
2.6.5 Field assistants	28
2.6.6 Human activities	28
2.7 Data collection	36
2.7.1 Study period.....	36
2.7.2 Forest composition and fruit availability	37
2.7.3 Chimpanzee observations.....	37

<i>Location of chimpanzees</i>	38
<i>Focal sampling</i>	39
<i>Scan sampling</i>	39
<i>Ad libitum sampling</i>	41
2.7.4 Habitat types	41
2.8 Data analysis	42
2.9 Ethical considerations	42

CHAPTER THREE FOREST COMPOSITION AND FRUIT AVAILABILITY IN AN UNPROTECTED HUMAN-IMPACTED FOREST AND A PROTECTED FOREST

3.1 INTRODUCTION	45
3.1.1 Forest composition	45
3.1.2 Fruit availability	46
3.1.3 Chapter aims	47
3.1.4 Hypotheses and predictions	47
3.2 METHODS	48
3.2.1 Data collection	48
3.2.2 Data analysis	55
3.3 RESULTS	58
3.3.1 Chimpanzee home ranges	58
3.3.2 Forest composition	60
3.3.3 Phenology	67
3.4 DISCUSSION	71
3.4.1 Chimpanzee home ranges	71
3.4.2 Forest composition	73
3.4.3 Phenology	76
3.4.4 Study limitations	78
3.4.5 Implications of forest loss for chimpanzees	79

PART TWO

CHIMPANZEE ACTIVITY BUDGETS AND DIETS

CHAPTER FOUR DIETARY FLEXIBILITY OF CHIMPANZEES IN A HUMAN-IMPACTED HABITAT AND A PROTECTED FOREST

4.1 INTRODUCTION	85
4.1.1 Feeding strategies	85
4.1.2 Chimpanzee diets	87
4.1.3 Sex differences in diet composition	89
4.1.4 Comparison with neighbouring sites	90
4.1.5 Chapter aims	91
4.1.6 Hypotheses and predictions	91
4.2 METHODS	93
4.2.1 Data collection	93
4.2.2 Data analysis	94
4.3 RESULTS	95
4.3.1 Chimpanzee diets at Waibira and Kasongoire	95
4.3.2 Contribution of different food parts to chimpanzee diets	96
4.4 DISCUSSION	108
4.4.1 Overview of chimpanzee diets at Waibira and Kasongoire	108
4.4.2 Preferred and fallback foods	109
4.4.3 Sugarcane consumption at Kasongoire	111

4.4.4 Non-plant feeding items	113
4.4.5 Study limitations	116
4.4.6 Balanced diets	117

CHAPTER FIVE THE EFFECTS OF LIVING IN A HUMAN-INFLUENCED HABITAT ON THE ACTIVITY BUDGETS OF CHIMPANZEES

5.1 INTRODUCTION	121
5.1.1 Activity budgets: trade-offs for survival.....	121
5.1.2 Habitat quality.....	122
5.1.3 Effect of human foods on behaviour	123
5.1.4 Chapter aims	125
5.1.5 Hypotheses and predictions	125
5.2 METHODS.....	126
5.2.1 Data collection	126
5.2.2 Data analysis	128
5.3 RESULTS.....	129
5.3.2 Activity budget comparison by site.....	131
5.3.3 Influence of sex on activity budgets	131
5.3.4 Effect of fruit availability on activity budgets	132
5.3.5 Influence of sugarcane consumption.....	133
5.4 DISCUSSION.....	134
5.4.1 Chimpanzee activity budgets.....	134
5.4.2 Comparisons with chimpanzee communities across Africa.....	138
5.4.3 Impacts on survival	139

PART THREE

CHIMPANZEE PERCEPTION OF RISK OUTSIDE THE FOREST BOUNDARY

CHAPTER SIX STEPPING ON DANGEROUS GROUND: CHIMPANZEE PARTY RESPONSES WHEN LEAVING THE FOREST

6.1 INTRODUCTION	145
6.1.1 Group dynamics: an overview	146
6.1.2 Party size	146
6.1.3 Party spread	150
6.1.4 Party composition	150
6.1.5 Chapter aims	151
6.1.6 Hypotheses and predictions	152
6.2 METHODS.....	152
6.2.1 Data collection	152
6.2.2 Data analysis	153
6.3 RESULTS.....	155
6.3.1 Party size	155
6.3.2 Party cohesion.....	156
6.3.3 Proportion of males	156
6.4 DISCUSSION.....	161
6.4.1 Party responses to risk.....	161
6.4.2 Socio-ecological factors	163
6.4.3 Study limitations	164
6.4.4 Further research	165
6.4.5 Threat sensitive responses?.....	166

CHAPTER SEVEN PERCEPTIONS OF RISK AND MANGO FEEDING PREFERENCES OF CHIMPANZEES IN A HUMAN-DOMINATED LANDSCAPE MOSAIC

7.1 INTRODUCTION.....	171
7.1.1 Chimpanzees and risk in anthropogenic environments	171
7.1.2 Mangos: seasonal and nutritious fruits	172
7.1.3 Mangos, conflict and conservation.....	173
7.1.4 Chimpanzee mango foraging strategies	174
7.1.5 Study aims.....	175
7.1.6 Hypotheses and predictions	175
7.2 METHODS	176
7.2.1 Study site	176
7.2.2 Methodological considerations/development	176
7.2.3 Data collection	178
7.2.4 Data analysis	181
7.3 RESULTS	182
7.3.1 Mango fruit availability.....	183
7.3.2 Mango tree selection and risk perception.....	183
7.3.3 Tree variety	184
7.4 DISCUSSION	185
7.4.1 Fruit availability	185
7.4.2 Mango tree preferences and responses to risk.....	187
7.4.3 Influence of mango tree variety	190
7.4.4 Study limitations	190
7.4.5 Chimpanzee mango foraging party composition	191
7.4.6 Conservation implications	192

CHAPTER EIGHT CONCLUSION: IMPLICATIONS FOR ANIMALS IN HUMAN-MODIFIED LANDSCAPES

8.1 Summary and analysis of results	197
8.2 Aggressive apes: an obstacle to co-existence	198
8.3 Implications for chimpanzee survival in Kasongoire	200
8.4 Future directions and considerations for studies in human-modified habitats	202
8.5 Final remarks	205

References	207
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Appendices	237
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Appendix 1: Chimpanzee study sites in the Albertine Rift and across Africa, with anthropogenic disturbance ratings and information.....	237
Appendix 2: Waibira chimpanzee list.	245
Appendix 3: Kasongoire chimpanzee list.....	247
Appendix 4: Map of BCFS' trail system in the Waibira chimpanzee home range	249
Appendix 5: Complete species list found in plots at Waibira.	251
Appendix 6: Complete species list found in plots at Kasongoire.....	253
Appendix 7: Shared species and densities at each site.	255
Appendix 8: Contributions to chimpanzee diets at Waibira and Kasongoire per species consumed	257

List of Tables

Table 2.1: Data recorded during instantaneous scan samples.	40
Table 2.2: Habitat type classifications and their descriptions at Waibira and Kasongoire.....	41
Table 3.1: Hypotheses and predictions relating to tree species composition and fruit availability in the Waibira and Kasongoire chimpanzees' home ranges, and the framework for testing them	48
Table 3.2: Chimpanzee home range size (km ²) over the study period.	58
Table 3.3: Summary of species richness and sampling effort at Kasongoire and Waibira.	61
Table 3.4: The 20 most important tree species at Waibira based on Species Importance Values (SIV).....	63
Table 3.5: The 20 most important tree species at Kasongoire based on Species Importance Values (SIV).	64
Table 3.6: The 10 most important tree families at Waibira and Kasongoire based on Family Importance Values (FIV).....	66
Table 3.7: Forest composition at Waibira and Kasongoire according to habitat type.	67
Table 3.8: Trees monitored for fruit availability at Waibira and Kasongoire.	69
Table 3.9: Chimpanzee home ranges and community sizes of study sites across Africa..	72
Table 4.1: Hypotheses and predictions relating to chimpanzee feeding strategies at Waibira and Kasongoire, and the framework for testing them.	92
Table 4.2: Shannon Diversity H' scores of chimpanzee diets per month.	96
Table 4.3: Species consumed and percentage of feeding time (proportion of records) by adult chimpanzees at Waibira and Kasongoire.....	97
Table 5.1: Hypotheses and predictions relating to chimpanzee activity budgets at Waibira and Kasongoire, and the framework for testing them.	126
Table 5.2: Ethogram of chimpanzee activities taken during 15 minute scan samples.	127
Table 5.3: Sampling effort at Waibira and Kasongoire.	129
Table 5.4: Summary of activity budgets from this study and comparisons to other chimpanzee study sites.	138
Table 6.1: Hypotheses and predictions relating to ecological and risk factors predicting chimpanzee party size at Kasongoire and the framework for testing them.	152
Table 6.2: Mean party size, spread and proportion of males ($\pm$ SE) in chimpanzee parties in Kasongoire.	156
Table 6.3: Results of the generalized linear mixed models showing factors influencing chimpanzee grouping patterns, including party size, party spread and the ratio of males in a party.	157

Table 7.1: Hypotheses and predictions relating to chimpanzee mango foraging preferences at Kasongoire, and the framework for testing them.	176
Table 7.2: Mango tree and garden characteristic variables and definitions.	179
Table 7.3: Summary of mango trees and mango stones per tree variety.	185

List of Figures

Figure 1.1: Chimpanzee range and study sites/communities (numbered), with Albertine Rift highlighted	8
Figure 2.1: Map of study sites, Waibira and Kasongoire, in the landscape between Budongo and Bugoma Forest reserves, highlighting neighbouring chimpanzee communities.....	15
Figure 2.2: Satellite image of forest fragments and villages within Kasongoire Parish, with corresponding schematic map highlighting forested areas, village centres and roads.....	26
Figure 3.1: The location of habitat sample plots at (a) Waibira and (b) Kasongoire.	50
Figure 3.2: Waibira chimpanzees' home range during the study period, showing minimum convex polygon (MCP) isopleth estimates at 50, 95, 99 and 100% cores, fixed kernel (FK) isopleth estimates at 50, 95 and 99% and GPS locations.	59
Figure 3.3: Kasongoire chimpanzees' home range during the study period, showing minimum convex polygon (MCP) isopleth estimates at 50, 95, 99 and 100% cores, fixed kernel (FK) isopleth estimates at 50, 95 and 99% and GPS locations.	60
Figure 3.4: Species rarefaction curves for Waibira (a) and Kasongoire (b).	61
Figure 3.5: Distribution of stems in DBH classes; Kasongoire and Waibira.....	65
Figure 3.6: The percentage of surveyed trees which produced ripe fruit (having a ripe fruit score >0) over the study period at Waibira (a) and Kasongoire (b).	68
Figure 3.7: Total monthly ripe fruit availability scores at Waibira.....	68
Figure 3.8: Total monthly ripe fruit availability scores at Kasongoire	70
Figure 4.1: Average time ($\pm$ SE) spent feeding on different food items at Waibira and Kasongoire	101
Figure 4.2: Average proportion of feeding time ($\pm$ SE) spent consuming different food parts by males and females at Waibira and Kasongoire.....	102
Figure 4.3: Average monthly proportion of feeding time spent consuming the most commonly eaten food parts by adult chimpanzees at Waibira.....	103
Figure 4.4: Average monthly proportion of feeding time spent consuming different food parts by adult chimpanzees at Kasongoire.	105
Figure 4.5: Kasongoire chimpanzees' consumption of sugarcane and wild fruit availability.....	106
Figure 4.6: Proportion of feeding time spent on wild fruits versus sugarcane for males and females at Kasongoire.	106
Figure 4.7: Proportion of observation days per month where chimpanzees were recorded as foraging on crops, in villagers' gardens and all crops against wild fruit availability.....	107
Figure 5.1: Monthly variation in Waibira chimpanzees' activity budget.	130

Figure 5.2: Monthly variation in Kasongoire chimpanzees' activity budget.	130
Figure 5.3: Activity budget profiles of chimpanzees at Waibira and Kasongoire during the overall study period showing mean values ($\pm$ SE) across the study period.	131
Figure 5.4: Activity profiles of males and females in Waibira and Kasongoire, showing mean values ($\pm$ SE) across the study period.	132
Figure 5.5: Effect of fruit availability on the activity budget profiles for (a) Waibira and (b) Kasongoire chimpanzees, showing average values ($\pm$ SE) across periods of different wild fruit availability.....	133
Figure 5.6: Mean percent ($\pm$ SE) of daily activity budgets for Kasongoire chimpanzees on days when sugarcane was consumed as compared with days when only wild foods were consumed.	134
Figure 6.1: The influence of a) habitat, b) party activity, c) swollen females and d) wild fruit availability on chimpanzee party sizes at	158
Figure 6.2: The influence of a) habitat, b) party activity, c) swollen females and d) wild fruit availability on chimpanzee party cohesion	159
Figure 6.3: The influence of a) habitat, b) party activity, c) swollen females and d) wild fruit availability on the ratio of males in	160
Figure 7.1: Map showing the distribution of monitored mango trees in Kasongoire.....	178
Figure 7.2: Mango and wild fruit availability in each survey period against the number of mango stones fed on by chimpanzees	183

List of Colour Plates

Plate 1 (on previous page): Chimpanzees (LBE and PAU) foraging on jackfruit (<i>Artocarpus</i>	2
Plate 2 (on previous page): A felled tree (<i>Neoboutonia macrocalyx</i>) with a view over papyrus	12
Plate 3: Pitsawing site in Waibira.....	24
Plate 4: Road at Waibira.	24
Plate 5: A trail used by researchers at BCFS, shown here during a chimpanzee follow at Waibira.	25
Plate 6: Road at Kasongoire..	29
Plate 7: A baboon skin, hung as a deterrent to other baboons for foraging on sugarcane.	30
Plate 8: A cane guards' hut in Kasongoire, in the open gap between the forest and the sugarcane plantation.....	31
Plate 9: Snare in Kasongoire.	32
Plate 10: Mantrap in Kasongoiret.	32
Plate 11: A 'triangle' trap in Kasongoire, dismantled	33
Plate 12: Freshly felled stems, felled by cane guards whilst on their duties and left to collect later.	34
Plate 13: A recently cleared patch of forest in Kasongoire.....	34
Plate 14: A truck leaving Kasongoire forest laden with freshly felled trees, including stems of <i>Pseudospondias microcarpa</i> and <i>Macaranga schweinfurthii</i>	35
Plate 15: Cattle being herded in the open gap between the forest edge and sugarcane plantation.	36
Plate 16 (on previous page): A large party of chimpanzees at Waibira foraging on ripe fruits of <i>Ficus sur</i>	44
Plate 17 (on previous page): A subadult male (BLY) foraging on the pith of mature sugarcane	84
Plate 18 (on previous page): Kasongoire chimpanzees grooming in the open gap between the ..	120
Plate 19 (on previous page): An all-female party travelling with their infants in the open gap	144
Plate 20 (on previous page): View from a fallow field at sunset of the village-garden matrix.	170
Plate 21: Mango feeding trace from a chimpanzee.....	180
Plate 22 (on previous page): A lone male resting in the open gap outside the forest.	196

List of Abbreviations

Abbreviation	Meaning
AO	Aimee Oxley
BA	Basal area
BCFS	Budongo Conservation Field Station
BKJ	Balinda Kiiza Jovan
CF	<i>Cynometra</i> forest
CCFU	Cross-Cultural Foundation of Uganda
DBH	Diameter at breast height
ET	Ecotone forest
FAI	Fruit availability index
FAO	Food and Agriculture Organisation
FIV	Family importance value
H	Shannon-Weaver diversity index
ha	Hectare
IUCN	International Union for the Conservation of Nature
IV	Importance value
JGI	Jane Goodall Institute
KSWL	Kinyara Sugarworks Limited
LC1	Local Chairperson, Level 1 (village)
MAAIF	Ministry of Agriculture, Animal Industry and Fisheries, Uganda
MF	Mixed forest
MH	Morisita-Horn Index of similarity
MFPE	Ministry of Finance, Planning and Economic Development, Uganda
MWE	Ministry for Water and Environment, Uganda
NEMA	National Environment Management Authority of Uganda
NFA	National Forestry Authority, Uganda
NFTPA	National Forestry and Tree Planting Act
SF	Swamp forest
SIV	Species importance value
UBOS	Uganda Bureau of Statistics
UWA	Uganda Wildlife Authority
WWF	Worldwild Fund for Nature



CHAPTER ONE

INTRODUCTION



Plate 1 (on previous page): Chimpanzees (LBE and PAU) foraging on jackfruit (*Artocarpus heterophyllus*) in a crop garden in Kasongoire

1.1 Understanding behavioural flexibility in the Anthropocene

We are in the Anthropocene, a period of rapidly expanding human activities and encroachment on the natural environment (Corlett 2015; Cruzten & Stoermer 2000). Forest loss and fragmentation to make way for conversion to agriculture, roads and settlements for a growing human population are leading causes of species loss in tropical habitats (Arcus Foundation 2015; Barlow et al. 2016; Estrada et al. 2017, 2018; Fahrig 2003; Kupfer et al. 2006; Laurance et al. 2013; Mittermeier et al. 1999; Turner 1996). Many animal species are known to inhabit remnant tropical forest patches, although their survival prospects are often bleak or uncertain (Henle et al. 2004; Kupfer et al. 2006; Laurance et al. 2002). For those species able to persist in these forests, the question remains: how do they survive and what responses or behavioural adaptations do they make in order to cope with these threats?

In reality, everywhere on Earth is affected by human activities, whether directly through land conversion or indirectly through climate change (Jantz et al. 2015; Lewis et al. 2015). Moreover, no two places will be affected in the same way: different sites lie at varying stages along an anthropogenic continuum, and different species will respond to human impacts in diverse ways. As a result of the growing recognition that human activities shape species' behaviour, research on wildlife responses to living in anthropogenic habitats has been increasing over the past decades (Candolin & Wong 2012; Hockings et al. 2015a; Lowry et al. 2013; McLennan et al. 2017; Sih 2013; Tuomainen & Candolin 2011; Wong & Candolin 2015).

The significant reduction in tropical forest cover over the past decades has led to a loss of natural resources. However, human-modified landscapes may also provide new resources and opportunities for animals, principally human foods. Animals in proximity to forest edges may be able to exploit cultivated food outside the forest boundary (Estrada et al. 2012; Hill 2017). However, crop-foraging (commonly referred to as crop-raiding, see Hill 2015 for a discussion on terminology) by wild animals often leads to negative perceptions of wildlife by farmers and increased human-wildlife interactions, in turn resulting in further threats to species' long-term persistence in remnant forests if they are persecuted by their human neighbours.

Where humans pose a direct threat to an animal's survival, for example through hunting or retaliatory aggression from crop-foraging, the risk of fatality from human attack is comparable to that from the risk of predation. Across taxa, animals will exhibit some sort of responses to risk,

whether from wild predators or humans, measured most commonly by observing changes in vigilance behaviour, grouping patterns and/or habitat use (Hill & Lee 1998; Iribarren & Kotler 2012; Laundré et al. 2001; Thaker et al. 2011; Sih et al. 2011). Where tropical forests are shrinking and human populations expanding, intensifying levels of human-wildlife interactions therefore make understanding species' responses to risk in a "landscape of fear" (Laundré et al. 2010) increasingly relevant and important.

Whether and how animals are able to survive in habitats where humans are present and have modified the landscape is determined by their level of behavioural flexibility (McLennan et al. 2017). However, many behavioural ecology studies, even those conducted in habitats impacted by human activities, fail to incorporate an applied conservation dimension. In reaction to the increasing evidence of species' flexible responses to anthropogenic factors, as well as escalating reports of conflicts about wildlife, there is a need to bridge the gap between studies of pure behavioural ecology and their applied conservation (Caro 1999, 2014; Sutherland 1998). Ultimately, through understanding species' flexibility in their responses to an array of human-influenced disturbances and investigating the potential limits of behavioural flexibility, research can help to predict how and whether species will survive in the long-term.

1.1.1 Species' responses to human-modified landscapes

Tropical landscapes have been transformed by humans rapidly over the past decades; where forests still remain they are affected by a myriad of anthropogenic disturbance types (Laurance et al. 2013). These can include setting hunting traps, timber extraction (both small-scale and complete forest clearance), roads and expanding human settlements. Animal responses to human disturbances will vary depending on a variety of factors, including the scale and continuance of the disturbance (e.g. Ancrenaz et al. 2010), whether they are actively persecuted and the resources available to them. The responses shown by a particular species or population depends on species as well as local landscape characteristics.

Dietary modifications are among the most commonly documented responses to habitat alterations (McLennan et al. 2017): animals may incorporate crops into their diets or alter their wild feeding behaviour, potentially changing the quality of their diet. In many human-modified landscapes in the tropics, a wide variety of animal species incorporate crops into their diet, foraging on them during times of wild food scarcity or even as preferred foods, including hippopotamuses (*Hippopotamus amphibious*: Kendall 2011), bush pigs (*Potamochoerus porcus*)

and porcupines (*Hystrix cristata*) (Ango et al. 2017; Hill 1997; Naughton-Treves et al. 1998; Tweheyo et al. 2005; for a review of problematic crop-foraging species in sites across Africa see Naughton-Treves & Treves 2005). Most commonly reported though, and dominating the literature on crop-foraging and human-wildlife interactions, are elephants (African elephants, *Loxodonta africana*: Chiyo et al. 2005; Graham et al. 2010; Naughton-Treves 1998; Asian elephants, *Elephas maximus*: Sukumar 1990; Webber et al. 2011) and nonhuman primates (hereafter referred to as primates; for a recent review of primate crop-foraging see Hill 2017).

Wild animals foraging on crops can be particularly problematic for farmers when the species accounting for the damage illicit fear, due to their large body size and/or aggressive behaviour. Chimpanzees in human-modified habitats are known to have attacked both domesticated animals and people, especially children, in some instances fatally (Hockings & McLennan 2016; Hockings et al. 2010, 2012a). Crop-foraging sloth bears (*Melursus ursinus*) and Asiatic black bears (*Ursus thibetanus*) are also reported to injure and kills humans, including adults (Bargali et al. 2005; Charoo et al. 2011). Where elephants have foraged on crops and caused injury or death of villagers, negative impacts on long-term psychological well-being has been documented (Jadhav & Barua 2012).

The responses of primates to human-modified landscapes have been increasingly studied since the turn of the millennium (McLennan et al. 2017). As an Order, Primates exhibit a high degree of flexibility in their activity budgets, diets, ranging behaviours and direct responses to human presence, including those species considered to be habitat and feeding specialists (Nowak & Lee 2013; McLennan et al. 2017). Some primate species reportedly adjust their activity patterns in response to sharing landscapes with humans with groups inhabiting human-modified habitats often increasing their time spent resting and reducing their foraging time (Altmann & Muruthi 1988; Campbell-Smith et al. 2011; Hockings et al. 2012b; Saj et al. 1999; Strum 2010), likely an effect of fulfilling their energetic requirements on human foods.

Primates are known to utilise a variety of human resources including foraging on crops (Hill 2017), garbage and taking food directly from people's houses (Brennan et al. 1985; Kaplan et al. 2011), using exotic tree species for sleeping and/or nesting (Hoffman & O'Riain 2010; McCarthy et al. 2017) and even opportunistically ingesting alcohol (Hockings et al. 2015b). Human foods may provide an important resource, particularly during periods of wild food scarcity (Campbell-Smith et al. 2011; Hockings et al. 2009; McLennan 2013), an advantage that individuals in more intact

habitats do not have. However, there are often risks to animals accessing cultivated foods: while some have access to abandoned fruit trees (e.g. Hockings et al. 2012b; McLennan & Plumptre 2012), crops are usually found in actively cultivated areas and often guarded by humans to protect them from foraging animals (Hill & Wallace 2012; Linkie et al. 2007; Naughton-Treves 1998). Animals utilising risky anthropogenic habitats therefore require a certain level of behavioural and dietary flexibility in order to adapt and respond to the changes in their environment. This may include the loss of wild resources as well as the introduction of new anthropogenic ones, as well as flexibly responding to physical human activities in the landscape (e.g. timber extraction), some of which may be directed at the primates themselves (e.g. hunting or scaring animals away from crops).

Wildlife responses to anthropogenic disturbances can be extreme enough that animals change their entire time budgets. For example, in a meta-analysis of over 60 species of mammal, Gaynor et al. (2018) found a strong pattern of increased nocturnal behaviour in sites with higher levels of human disturbance. Similarly, Donati et al. (2016) found that higher levels of human disturbance resulted in less diurnal activity in 13 *Eulemur* populations in Madagascar. Elephants and chimpanzees have been recorded foraging on crops at night time (Gunn et al. 2013; Krief et al. 2014), most likely to avoid humans.

1.1.2 Why chimpanzees?

Chimpanzees provide an ideal model to study socio-ecological responses to anthropogenic disturbances because they are known to be a behaviourally flexible species (Hockings et al. 2015a). Chimpanzees can often be an extremely problematic species for local people: they are a large-bodied and cognitively advanced species which forages on crops wherever they are grown in their habitats (Hockings & McLennan 2012) and have the capacity to exhibit aggressive behaviour towards people potentially causing human fatalities (McLennan & Hockings 2016). Chimpanzees are classified as threatened with extinction by the IUCN (Humble et al. 2016a) and are legally protected throughout their range, which can be problematic for local people. In some human-modified habitats, chimpanzees do not avoid areas with high exposure to human activities, particularly in some of the most disturbed sites studied (Bortolamiol et al. 2016; Bryson-Morrison et al. 2017). However, where they are hunted chimpanzees are reported to avoid areas of high potential space overlap (e.g. Bili: Hicks et al. 2012, 2013; Lope: Tutin & Fernandez 1991). Non-avoidance by chimpanzees of humans and human-dominated areas within the landscape can

create complex conservation challenges. The first step to mitigate and manage these challenges is to understand their behavioural responses to the threats they face.

Hockings and McLennan (2012) provide a detailed review of crops known to be consumed by chimpanzees across multiple study sites and highlight site specific differences in the preference or avoidance of different cultivated species (McLennan & Hockings 2014). The authors note that wherever crops are grown in habitats where chimpanzees persist, chimpanzees will certainly forage on them, although certain crops may be ignored, perhaps depending on whether chimpanzees have learnt to forage on them or found them palatable (Hockings & McLennan 2012). In recent years, an increasing number of studies have also focused on chimpanzee responses to human activities and threats, including changes in activity budgets on crop-foraging days (Hockings et al. 2012b), responses to researchers (McLennan & Hill 2010) and road-crossing behaviour (Cibot et al. 2015; Hockings et al. 2006; Sakura 1994).

However, chimpanzee behavioural responses in environments with a very high degree of anthropogenic exposure have been studied at only a few sites (including Bossou in Guinea, Bulindi in Uganda, Caiquene-Cadique in Guinea-Bissau, Sebitoli in Kibale National Park, Uganda; Figure 1.1; see Appendix 1 for information of chimpanzee study sites and human disturbance factors). In reality very few (or no) forests are untouched by humans today, yet long-term chimpanzee research either has been conducted in less-affected sites, or the impact of humans has been ignored or under-played until recently (Hockings et al. 2015a). Since human influences on tropical forests are widespread, particularly in Africa where the human population is predicted to expand considerably in the next decades, understanding the socio-ecological responses of this charismatic and endangered species is extremely important. Such studies will lead to a better understanding of chimpanzee behaviour in sites with varying degrees of human influence and help to determine how and the degree to which they can persist in these environments. This is crucial for evidence-based conservation and with this deeper information we will be better able to inform land management and conservation strategies, both locally to the study area as well as regionally for chimpanzees across their range. Ultimately, it may be possible to identify potential thresholds and triggers beyond which they may not survive. Therefore it is important to further examine how chimpanzees modify their behaviour in human-modified landscapes, and particularly in highly disturbed sites.

1.1.3 The Albertine Rift

The Albertine Rift runs through the heart of East Africa, from the northern tip of Lake Albert in Uganda, down through Western Uganda and Eastern DRC through Rwanda and Burundi, finishing at the southernmost point of Lake Tanganyika in Tanzania and northern Zambia (Figure 1.1). It is an extremely biodiverse region with high numbers of plant, invertebrate, bird and amphibian species, many of which are threatened (Mittermeier et al. 2004; Plumptre et al. 2003, 2007; Stattersfield et al. 1998). Human population density is high in the region, often within close proximity to protected areas (Plumptre et al. 2007). Due to the diverse landscape, this makes the Albertine Rift unique in the broad array of anthropogenic contexts across a variety of habitats. Consequently, it is a fascinating region to study species' responses to human activities, particularly since there are many ways and contexts in which chimpanzees interact with humans. Appendix 1 lists the various sites where chimpanzees have been studied within and outside the Albertine Rift.

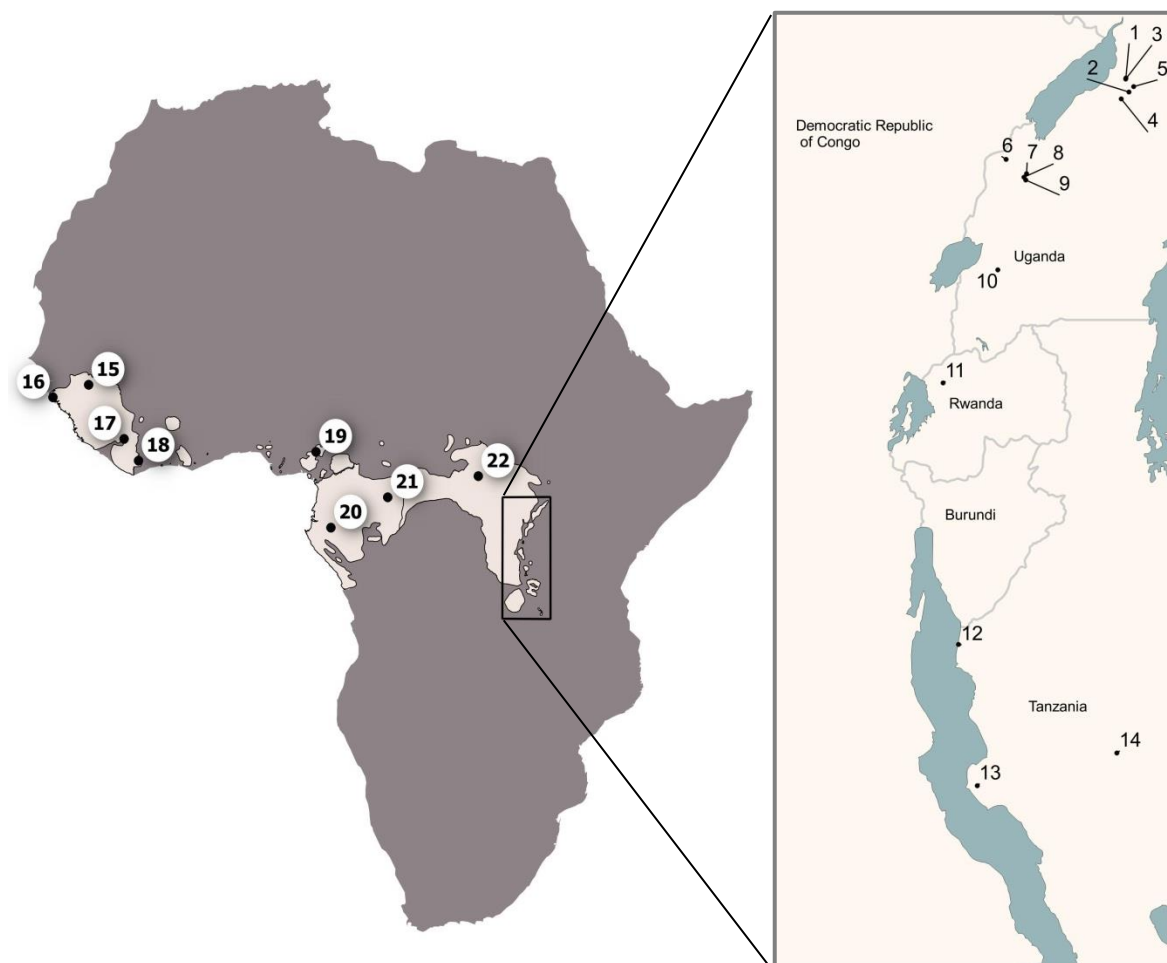


Figure 1.1: Chimpanzee range and study sites/communities (numbered), with Albertine Rift highlighted. For information on study sites, see Appendix 1. 1=Waibira; 2=Kasongoire; 3=Sonso; 4=Bulindi; 5=Kasokwa; 6=Semiliki; 7=Sebitoli; 8=Kanywara; 9=Ngogo; 10=Kalinzu; 11=Gishwati;

12=Mahale; 13=Gombe; 14=Ugalla; 15=Fongoli; 16=Cantanhez; 17=Bossou; 18=Taï; 19=Gashaka; 20=Lopé; 21=Goualougo; 22=Bili.

This study takes place in the northern part of the Albertine Rift East Afromontane Hotspot (Brooks et al. 2004), in and around the Budongo Forest Reserve in Uganda (see Figure 1.1 for location of study sites in relation to chimpanzee study sites across Africa). Within the Albertine Rift, Budongo Forest Reserve has the highest number of tree species and is ranked as ‘medium’ for species endemism and threatened status (including mammals, birds, reptiles, amphibians and plants) in comparison to other Albertine Rift sites (Plumptre et al. 2007), making it a site of significant importance for research.

1.2 Overall aims and chapter overview

The aim of this study is to understand how chimpanzees inhabiting a forest-farm mosaic respond to living in a human-modified landscape and to investigate how specific factors within a human-influenced landscape affect chimpanzee behaviour and grouping patterns. Through this, I address questions around how chimpanzees perceive risk in a potentially hostile environment. I take a comparative approach, whereby I collected data on the socio-ecology of chimpanzees in both minimally disturbed habitat (Waibira) and heavily human-influenced habitat (Kasongire) to assess the differences between the two chimpanzee communities (defined as a group of individuals which “shares a territory over a period of time” [Crockford & Boesch 2003]). The minimally disturbed habitat, acting as a control, is set within an extensive protected forest block; the human-influenced habitat is set within an anthropogenic landscape matrix comprising unprotected riverine forest fragments, villages, villagers’ crop gardens, a large-scale monoculture plantation and roads.

Part One describes the study sites, allowing the reader to contextualise the rest of the study. Chapter Two provides background information on the study sites. The human and physical history of any human-modified landscape will differ to the next. This chapter contextualises the situation in the area this study was set to give the reader a clear picture of the threats that chimpanzees face and the types and scale of human activities. Here I present an overview of methods used in the study. In Chapter Three, I first map the chimpanzees’ home ranges to establish the study area. The main aim of this chapter is to document the forest composition and availability of wild fruits within the chimpanzee home ranges. To understand any differences in the feeding behaviours or activity budgets of chimpanzees in protected versus unprotected forest it was first necessary to establish the food resources available to chimpanzees.

Part Two presents a comparative analysis of chimpanzees between sites, looking at their diets and activity budgets. Chapter Four describes the chimpanzees' diets and compares the feeding strategies of those in forest fragments to nearby continuous forest, exploring the role of a large-scale commercial monoculture crop in the diet of chimpanzees in the forest fragment site. In Chapter Five I examine socio-ecological responses to living in a human-modified environment by comparing the activity budgets of the two chimpanzee communities. The influence of access to sugarcane crops on Kasongore chimpanzee activity is also explored.

In Part Three I focus exclusively on chimpanzees at Kasongore, the disturbed site, to understand chimpanzee perception of risk when outside the forest boundary. In Chapter Six I investigate whether and how chimpanzees modify their grouping patterns in response to leaving the safety of the forest. In Chapter Seven I examine which factors within a 'risky' village-garden habitat influenced chimpanzee foraging on mango trees.

Finally, the implications of the study for conservation and our understanding of wildlife responses to anthropogenic risk are discussed in Chapter Eight. Here I summarise the results and explore their interpretation in the wider context of species flexibility and survivorship in human-influenced habitats.



CHAPTER TWO

OVERVIEW OF STUDY SITES, SUBJECTS AND METHODS



Plate 2 (on previous page): A felled tree (*Neoboutonia macrocalyx*) with a view over papyrus swamp, and swamp forest further in the distance, dominated by wild date palm (*Phoenix reclinata*).

2.1 Overview

This chapter describes the sites where this study was conducted. I highlight relevant background information regarding the human and physical history of the landscape as well as the status of chimpanzees and the threats they face at each site. In this way, I contextualise the situation for humans and chimpanzees in the study sites, which sets the scene for the research and analysis throughout the thesis. This chapter also provides an overview of research methods used in the study, including information on the study sites and chimpanzee communities. Detailed descriptions of methods and methodological considerations are reported in relevant chapters.

2.2 Study sites and subjects

2.2.1 Chimpanzee status

Chimpanzees (*Pan troglodytes*) have the widest geographical range of all extant great ape species with a distribution spanning from Senegal, across equatorial Africa through to western Uganda (Humble et al. 2016a). All four subspecies are classified as threatened on the IUCN Red List: *P. t. schweinfurthii* (Plumptre et al. 2016), *P. t. troglodytes* (Maisels et al. 2016) and *P. t. ellioti* (Oates et al. 2016) are classified as Endangered, and *P. t. verus* (Humble et al. 2016b) is classified as Critically Endangered.

Eastern chimpanzees (*P.t.schweinfurthii*) are the most numerous of the four subspecies, with the majority of animals found within the Democratic Republic of Congo. Around 5000 individuals are estimated to exist in Uganda, of which over 1000 are found in the Budongo and Bugoma Forest Reserves, which hold over 500 individuals each (Plumptre et al. 2003). The unprotected corridor forests between these two reserves contain a smaller, but significant, population of chimpanzees. A 2003 census (Plumptre et al. 2003) estimated that there were just 69 individuals in these forests, but subsequent studies showed the number was much higher. McLennan (2008) made an estimate of 260 individuals based on extrapolating his preliminary survey results across the forested areas between the reserves. A later study based on genetic evidence by McCarthy et al. (2015) corroborated this higher estimate, finding a population of 256-319 individuals in the corridor fragments.

Chimpanzees are a protected species: they are listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) and it is illegal to hunt or kill a chimpanzee in Uganda (Uganda Wildlife Statute, Section 50(1), 1996), though arrests and prosecutions are very rare.

2.2.2 Site selection

The location and study sites were chosen because they offered the opportunity to conduct a comparative study between two chimpanzee communities enabling me to make an assessment of how chimpanzees in a human-modified habitat behaved as compared with those with minimal/no human disturbances. The two sites were close enough together that I was able to travel between them (30-80 minute drive, depending on season). The proximity of the two sites also ensured that the behaviour of the chimpanzee communities should be comparable: there are known behavioural differences in chimpanzee populations across subspecies and sites, as well as differences in cultural repertoires (Whiten et al. 1999). Close proximity rules out any major genetic differences that might affect behaviour, although it appears that behavioural differences across chimpanzee populations are spread “culturally”, rather than genetically (Gruber et al. 2012; Whiten et al. 1999). Therefore it was important to ensure there was a high level of geographical proximity between the study sites to control for other potential factors explaining differences in behaviour between the two communities.

2.2.3 Location

This study was conducted at two sites in Masindi District in mid-western Uganda, focusing on two separate chimpanzee communities: Waibira and Kasongoire (Figure 2.1). There are several communities of chimpanzees within the Budongo-Bugoma corridor (McCarthy et al. 2015; see Figure 1.1), and within this broad study area the various chimpanzee communities experience a spectrum of human habitat disturbances. The two chimpanzee communities vary markedly in terms of their anthropogenic exposure and status of forest protection. The Waibira community is located around 5 km north of the southern edge of the Budongo Forest Reserve and experiences low current exposure to anthropogenic disturbances. They range entirely within Budongo Forest Reserve and do not come into contact with the villages around the borders. The Kasongoire community is located around 15 km south of Budongo outside the reserve in privately owned forests and experiences high exposure to anthropogenic disturbances, including large- and small-scale agriculture, roads and human settlements. The Kasongoire chimpanzee community is part of the same regional population of chimpanzees as those found in Budongo Forest Reserve, meaning

that they are close enough together that any genetic differences will only minimally affect their behaviour.

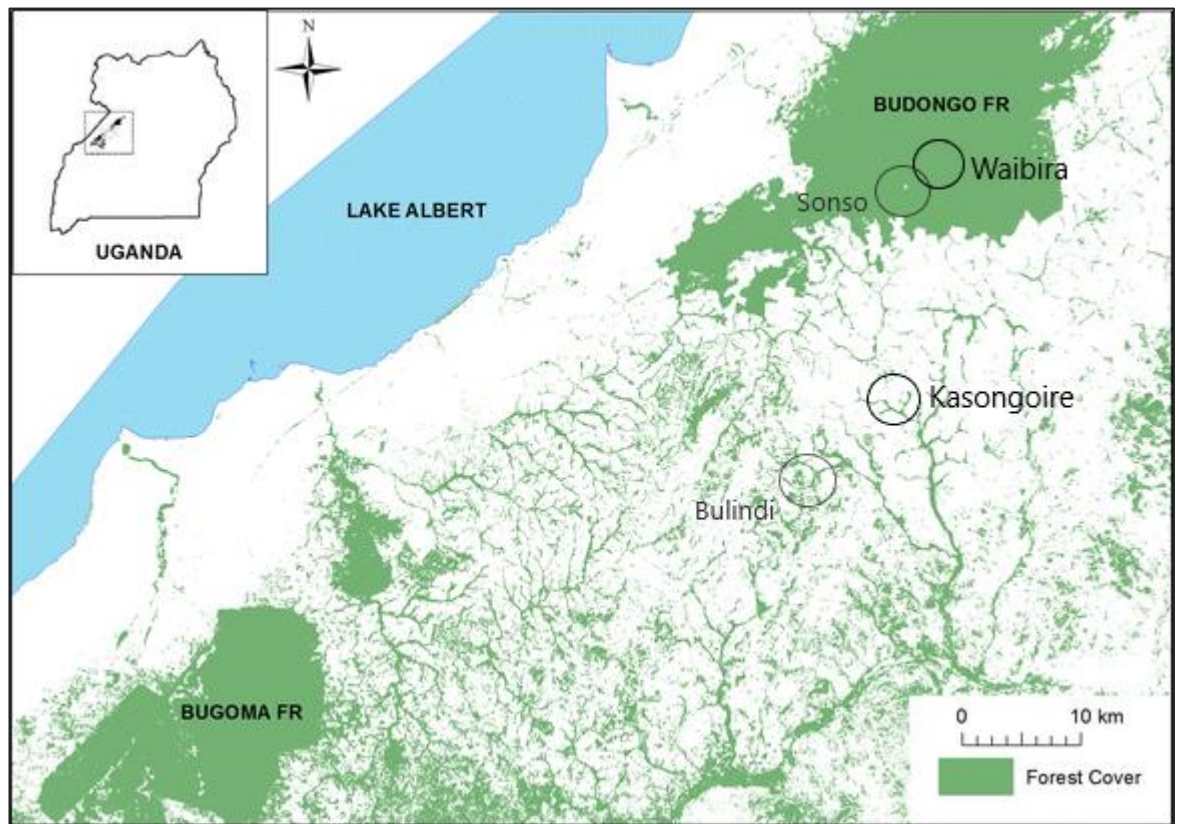


Figure 2.1: Map of study sites, Waibira and Kasongoire, in the landscape between Budongo and Bugoma Forest reserves, also highlighting neighbouring chimpanzee communities, Sonso and Bulindi (modified from McCarthy et al. 2015).

2.3 Landcape history

Forests, of varying types, cover 4.9 million hectares in Uganda, comprising 24% of the country's total land cover (FAO 2008). Of this, 81% is woodland, less than 1% is plantations (likely higher since these figures were issued) and around 19% is tropical high forest (FAO 2008). Dependence on agriculture combined with a rapidly growing human population (see Section 2.5.1 below) means a large amount of land is required for planting crops: forty one percent of the country's land cover is used for subsistence agriculture (FAO 2008).

Over the past few decades, Uganda has experienced the highest level of annual forest loss within the Albertine Rift (Ryan et al. 2017). Around 60% of Uganda's remaining forests are unprotected and between 1990 and 2015 over 80% of these privately owned forests were cleared (MWE 2016). In the area around Budongo Forest Reserve, there was a net loss of 8.2% (4,680 hectares)

of forest cover between 1988 and 2002 (Mwavu & Witkowski 2008). From 2010 onwards, deforestation rates appear to have slowed in this area, but this has been attributed to the fact that “almost all” of the unprotected forests had already been cleared in the preceding decades (Twongyirwe et al. 2015).

2.4 Human history

2.4.1 Population trends and local livelihoods

Uganda has the joint sixth highest human population growth rate in the world with an overall growth rate of 3.3% (World Bank 2017). In Masindi district, the growth rate between 1991 and 2002 was higher than the national average at over 4%, falling to 2.8% between 2002 and 2014 (UBOS 2014). The rate of urbanisation in Masindi is relatively high (10.1%). Uganda’s population is projected to grow by 10 million in a decade up to 2025, reaching an estimated 46.7 million people (UBOS 2014).

In the areas where this study was conducted, the average household size in Nyabeya parish (the parish on the southern border of Budongo Forest Reserve) is five people per household and in Kasongore parish it is 4.8 people per household (UBOS 2011). Local livelihoods rely primarily on subsistence agriculture: in Nyabeya agriculture accounts for 58% of household livelihoods, and in Kasongore parish 87% of households rely on agriculture as their main source of income and living (UBOS 2011).

In Africa, small-scale subsistence farming plays a major role in deforestation, although globally, large-scale commercial agriculture is the leading cause of forest loss (Arcus Foundation 2015). As a result of increasing pressures on land use from a growing population, the area of land per capita has dramatically decreased. In the villages to the south of the Budongo Forest Reserve, the average size of a landholding almost halved within just a decade around the turn of the millennium with a median size of 0.37 hectares by 2005 (Babweteera et al. 2012). Additionally, the Masindi landscape has been transformed in the past decades by the expansion of large-scale agriculture, specifically sugarcane (Reynolds et al. 2003), under the management of Kinyara Sugarworks Ltd. (KSWL), which is the second largest producer of sugarcane in Uganda. Between 1988 and 2002, sugarcane land cover increased by 1745% to cover 12,039 hectares (Mwavu & Witkowski 2008). Sixty percent of sugarcane is grown by outgrowers (private individuals who

cultivate the crop and sell to KSWL; Zommers et al. 2012). A combined effect of growing commercial agriculture at the same time as expanding subsistence farming has had a dramatic impact on Uganda's forests. In the area where this study was conducted this has led to not only reduction in forest cover but also frustration and insecurity from local people regarding land tenure (pers. obs.).

2.4.2 Local beliefs and practises

The study sites, both on the border of Masindi district, lie within the Bunyoro Kingdom. Traditionally, Banyoro people were horticulturalists and herders, using the land to feed cattle, exploiting the forest minimally and routinely burning the perimeter as a means to control the tsetse fly population (Paterson 1991). By the beginning of the 20th century, when Uganda had become a British protectorate, this burning practice was stopped to allow the forest to expand and Budongo Forest was managed and modified for timber extraction. After the burning ceased the tsetse fly population became prolific which was one of the drivers that led to the end of traditional of cattle herding within the Bunyoro around Budongo (Naughton-Treves 1999; Paterson 1991). Additionally, the population of Bunyoro suffered from decades of population decline around the turn of the century as a result of severe malnutrition and disease outbreaks during and following British conquest, which had been particularly brutal in the Bunyoro Kingdom (Doyle 2006).

An influx of workers for waged jobs to the Budongo sawmill in the 1950s and 1960s, as well as more recently (1990s to present) at Kinyara Sugarworks Ltd. (KSWL), led to a high level of ethnic diversity in the area. Over 56 ethnic groups live within Masindi District, with the Banyoro representing the largest proportion of the population (30%) (UBOS 2007). Babweteera et al. (2011) report that minority ethnic groups were often settled on marginal land bordering Budongo Forest, providing a buffer for the Banyoro people and any problematic wildlife coming out of the forest. However, this means that tribes which may be more likely to hunt bushmeat were then placed directly next to the forest (Hill 1997; Naughton-Treves 1999).

Banyoro people do not traditionally eat primates (McLennan 2008). McLennan & Hill (2012) report that some residents of Bulindi (93% Banyoro tribe) believe that their family will receive bad luck or even die in return for killing a chimpanzee. With the exception of reports from one Banyoro clan (CCFU 2018), Banyoro people do not report holding totemic beliefs about

chimpanzees (McLennan & Hill 2012), unlike some sites in West Africa where chimpanzees are considered sacred (e.g. Bossou in Guinea, Hockings 2009).

While chimpanzees are generally not targeted by hunters for meat in Uganda, Plumptre et al. (2003) found evidence of the highest level of bushmeat hunting in the area around and inside Budongo and Bugoma Forest Reserves as compared with other areas where chimpanzees persist in Uganda. Levels of hunting were highest at the forest edges where the population density is higher, particularly around the southern border of Budongo forest. Later surveys in the corridor forests between the two reserves found lower levels of poaching, but reported that logging was “rampant” (McLennan 2008; Plumptre et al. 2011).

2.4.3 Status and management of forests in Uganda

Governmental reforms around the turn of the century and the creation of the Forestry Service introduced a new form of land ownership, the majority of which became either land of the Protectorate, which needed a permit, or privately owned (Hamilton 1987). In 1900, a Memorandum of Agreement between the British colonialists and chiefs of the Kingdom of Buganda transferred a proportion of forests to the British administration, dividing other forests between chiefs. Prior to this forests had been managed by communities and animist beliefs and rules within tribes had limited most exploitation (Turyahabwe & Banana 2008). Around the same time a law aimed to protect and control the over-exploitation of forests (Turyahabwe & Banana 2008). Over the succeeding decades further agreements transferring ownership of forests were made between other tribes.

In 1930, when Uganda was a British Protectorate, Budongo Forest was a major site for timber extraction and export. Four sawmills were established within the forest and had become the largest in Uganda by 1960 (Reynolds 2005), one of which is today the site of the Budongo Conservation Field Station in the centre of the Sonso chimpanzee community’s home range. After independence from British rule in 1961, the sawmills transferred ownership and were managed by an Asian-based company. In the following decade under the rule of Idi Amin, large swathes of foreigners were expelled and the sawmills closed (Paterson 1991).

At the same time that the sawmills were thriving, cash crops including mango, coffee, tea and sugar were brought to the areas surrounding Budongo Forest, largely by colonists (Turyahabwe & Banana 2008). However, the majority of the agricultural sector in Uganda was and continues to be

dominated by subsistence farmers. More recently, the Ugandan government passed a “Plan for Modernisation of Agriculture” aiming to convert a certain level of the country’s subsistence agriculture into a commercial economy (MAAIF & MFPED 2000). Since the 1990s the Ugandan government has repeatedly given rights to public land to private companies, including for commercial plantation of sugarcane and palm oil, as well as to the National Forestry Authority (NFA) for the plantation of pine and eucalyptus (Turyahabwe & Banana 2008). Most recently, the National Forest and Tree Planting Act (NFTPA) of 2003 aims to safeguard forests and encourage the planting of new forest (NFTPA Section 2).

There are different classifications of forested land in Uganda, which differ in their level of protection and administration and management. Central Forest Reserves are under the administration and management of the NFA, the functions of which are to “provide forest products, amenity and recreation, conserve biodiversity, ameliorate climate, stabilize soils, and protect water catchments and steep slopes, riverbanks and lakeshores” (Obua et al. 2010, p. 854). Budongo Forest is an example of a Central Forest Reserve, meaning that it has protected status which is monitored by NFA rangers (although sporadically). The exceptions are that there is one compartment (the forest is divided on the map into blocks with codes) whereby a certain limited level of timber harvesting is permitted, and fuelwood collection of dead and fallen branches is allowed within a certain area nearby the village at the entrance to the track into the forest. Other timber extraction is punishable by law. Unusually, Budongo Forest is managed by both NFA and Uganda Wildlife Authority (UWA) since there is an ecotourism site within the reserve which falls under the remit of UWA (MWE 2016).

In privately owned forests, such as the forest fragments in Kasongore, some laws exist to manage and protect forests, but these are limited and poorly enforced. Within the original law in 1900, it was written that clearing vegetation within 90 metres of a water source (a river, stream or lake) was prohibited without a permit, even on privately owned land (Turyahabwe & Banana 2008). This law still stands today, although the distance has been reduced to 30 metres for an unlisted river such as those found in many tropical forests (NEMA 2000) and the law has not been enforced, particularly in unprotected forests. The nature of logging in private forests, even if illegal (i.e. by a water source) is such that it can be undetectable without regular inspection and it is practically very difficult for a single District Forestry Officer to monitor such a large area. Unfortunately, even where deforestation is clearly visible from roads, action is not taken. The only exception to this may be if the private landlord has a personal grievance about the loss of their

forest, in which case the usual method of solving the dispute would be to go to the local village chairperson (LC1) for mediation without involving the law.

2.4.4 Chimpanzee threats

The IUCN Action Plan 2010-2020 for eastern chimpanzees confirms that the conversion of forest to agriculture is the leading cause of the species' decline (Plumptre et al. 2010). Chimpanzees within the Albertine Rift face a variety of threats, including hunting traps (snaring and mantraps), roads, persecution (including retaliatory killings for crop damage), habitat and resource loss and the loss of habitat connectivity and therefore dispersal opportunities (see Appendix 1 for threats across chimpanzee study sites). Further information on the specific human activities at each site is described in the following section.

2.5 Waibira

2.5.1 Forest description

The Waibira chimpanzees' home range is found within the Budongo Forest Reserve (1°37'–2°00'N, 31°22'–31°46'E). The Forest Reserve covers 793 km² of moist semi-deciduous forest and grassland, of which 482 km² is continuous forest. Budongo Forest is classified as a medium-altitude, semi-deciduous forest (Langdale-Brown et al. 1964), generally undulating but with occasional steep hills and lying at an average altitude of 1100 m.

Within Budongo Forest, four forest types were classified by Eggeling (1947) in the first in-depth study of the habitat: colonising, mixed, and *Cynometra* forest, all of which are successional stages of *Cynometra* (ironwood) forest, the latter being the most mature successional stage. Another forest type found only around rivers and streams, swamp forest, is edaphic *Cynometra* forest. Eggeling (1947) also described two other habitat types, shrubland and grassland, although these are generally found on the outskirts of the forest rather than the interior.

Colonising, or early successional, forests can be further broken down into either *Maesopsis* forest or woodland forest. The former grows on better soils and is dominated by *Maesopsis eminii*, forming 50 to 80 percent of the canopy, with *Calconcoba schweinfurthii* often growing below as a subdominant species and common trees include those in the genera *Olea*, *Margaritaria* and *Celtis* (Paterson 1991). Woodland forests are found on poorer soils and also host trees in the *Olea*,

Phyllanthus and *Calconcoba* genera, the latter often dominating the understorey (Paterson 1991). “Mixed forest” is used in this study to describe both colonising forest and Eggeling’s description of mixed forest, following the field method procedure of Budongo Conservation Field Station (BCFS) for habitat data collection.

Cynometra forests in Budongo are unusual in that they are characterised by monodominance (Reynolds 2005). *Cynometra alexanderi* can account for up to 35 percent of all trees and 90 percent of large trees (Eggeling 1947). The understorey is dominated by *Lasiodiscus milbraedii*. Other species include *Strychnos mitis*, *Celtis wightii* and *Celtis milbraedii*. This forest type, in its truly climatic form, is limited to the north-eastern most section of Budongo Forest Reserve showing a gradient of succession from the southwest, which holds a much higher proportion of colonising and mixed forests (Eggeling 1947; Plumptre 1996). Here, I use the term “*Cynometra* forest” to describe patches of forest distinctly dominated by *Cynometra alexanderi*, although these patches may not be fully representative of the original meaning of the term, which refers to a distinct successional stage.

During the period when Budongo Forest was under the management of the sawmills, mahoganies were the primary target species for timber extraction in Budongo Forest (*Khaya* spp. and *Entandrophragma* spp.) which grow primarily in mixed forest. Trees and lianas with no commercial value or those that affected the growth of valuable species, such as *Cynometra* forests and strangling figs (*Ficus* spp.), were treated heavily with arboricide which after decades of regeneration has altered the forest composition (Plumptre 1996; Reynolds 2005).

Even with its history of logging Budongo Forest has the highest number of tree species recorded at any Albertine Rift site (Plumptre et al. 2003, 2007; Reynolds 2005). Within the Waibira chimpanzee home range, the compartment was selectively logged in the mid-1960s with around 36 m³ ha⁻¹ timber extracted, of which 23 m³ ha⁻¹ were mahoganies (Plumptre 1996). Arboricide treatment to eliminate non-target timber species was administered in this compartment (Plumptre 1996). Despite the considerable reduction in cover of *Cynometra*-dominated forest since the 1960s, pockets of *Cynometra*-dominated forest occur frequently within the Waibira home range: in this study referred to as the habitat type “*Cynometra* forest”. See Table 2.2, Section 2.7 in this chapter for a full list of habitat types and definitions used in this study.

2.5.2 Climate

Rainfall is bimodal: two wet seasons occur from March to May and from September to November where monthly rainfall is above 150 mm. There is a distinct dry season from December to February when the area usually experiences less than 50 mm of rain per month, and a transitional dry season between June and August. Annual rainfall is 1200-2000 mm with average daily temperatures of 28°C (19°C min to 32°C max; Reynolds 2005).

2.5.3 History of research

Studies of chimpanzees in Budongo Forest began in the 1960s with initial behavioural studies of chimpanzees in Busingiro, in the south west of the Budongo Forest Reserve (Reynolds 1963; Reynolds & Reynolds 1965; Sugiyama 1968) and a population survey in the early 1970s (Albrecht 1976). After some decades, chimpanzee studies resumed and have been on-going within Budongo Forest since 1991 (Reynolds 2005), but until recently long-term research had been restricted to the Sonso chimpanzee community. BCFS were keen to study a neighbouring community to Sonso chimpanzees in order to answer a broader and comparative array of research questions (Figure 2.1). BCFS identified Waibira as the best neighbouring community to habituate to human presence as there were at that point two adult females in Waibira that had transferred from the neighbouring Sonso community. Habituation efforts with the Waibira community began in 2011 by teams of BCFS field assistants and volunteers, coordinated by Dr. Catherine Hobaiter. The high speed of the habituation process was facilitated by socially learnt habituation whereby other chimpanzees in the community were more relaxed around humans in the presence of the already habituated Sonso females (Samuni et al. 2014). The community reached an appropriate level of habituation to begin full-time study by mid-2014 (C. Hobaiter, 2014, pers. comm.): this study is the first doctoral research study at Waibira.

2.5.4 Chimpanzees

The Waibira community comprises 80 individuals, including 22 adult males and 29 adult females (see Appendix 2 for community composition and age/sex classes). At the beginning of this study's pilot phase (September 2014) 76 individuals were formally identified, with all individuals being identified and named by the end of May 2016 (with the exception of infants <1 year old). During the study 2 females gave birth to infants and during the pilot study one infant died. Data were collected from 53 independent individuals, rising to 54 by the end of the study as one juvenile male started travelling independently of his mother. Twenty three individuals (19%) in the

community are permanently disfigured due to snare injuries, as is the case for other chimpanzee populations in Uganda (Hashimoto 1999; Reynolds 2005; Quiatt et al. 2002; Waller & Reynolds 2001; Wrangham & Mugume 2000).

2.5.5 Field assistants

All observational data on Waibira chimpanzees were collected by myself. A team of three field assistants employed by BCFS, each assigned to work with a student researcher, were trained to follow and identify Waibira chimpanzees and collect long-term data for BCFS. Field assistants did not collect behavioural data that contributed to this study. BCFS have a policy that international researchers are not permitted in the forest alone. Due to unforeseen circumstances (my field assistant became ill in the first week of my data collection and was unable to work for the duration of the study) I had to fit with other researchers' schedules which impacted data collection.

Fruit availability data were collected by the BCFS phenology team who were highly experienced in identification of flora and trained in phenological monitoring. However, data were not collected in the Waibira home range until November 2015 due to logistical issues at BCFS. Data from tree composition surveys were collected by myself, a team of local men and Gophine Erickson (GE), an experienced botanist and head of the Habitat and Phenology Team at BCFS.

2.5.6 Human activities

The Waibira chimpanzees are located within Budongo Forest Reserve and do not share a forest edge with a village or crops, meaning that this community is relatively undisturbed and acts as the control community for comparison with the high level of disturbance witnessed in Kasongore. However, while there is a much lower level of human disturbance and activity in this area as compared with Kasongore, the forest is still affected by a number of human activities including snare traps and pit-sawing sites (Plate 3). As part of the BCFS snare removal program, a team had been patrolling part of the Waibira home range prior to this study, confirming the presence of snares and pit-sawing sites. The rate of snare occurrence in the forest compartments in the Waibira chimpanzee range is among the lowest in all the surveyed compartments (Reynolds 2005), although the high incidence of snare injuries suggests that snaring is still an issue.

One road runs through the Waibira home range (Plate 4), although this road was never used by vehicles and was not connected to any available roads. It had been established as part of an

ecotourism project which never materialised, and was last maintained in February 2014 (Yersin et al. 2017). Trail maintenance teams employed by BCFS would keep trails in the grid system clear (Appendix 4), working in teams of two or three using pangas (machetes) to cut back new growth. They were present in the Waibira home range one or two days a month. Due to the large area they covered it was very unusual to see them while following chimpanzees.



Plate 3: Pitsawing site in Waibira. A large (>80 cm DBH) *Cordia milenii* stem had been felled.

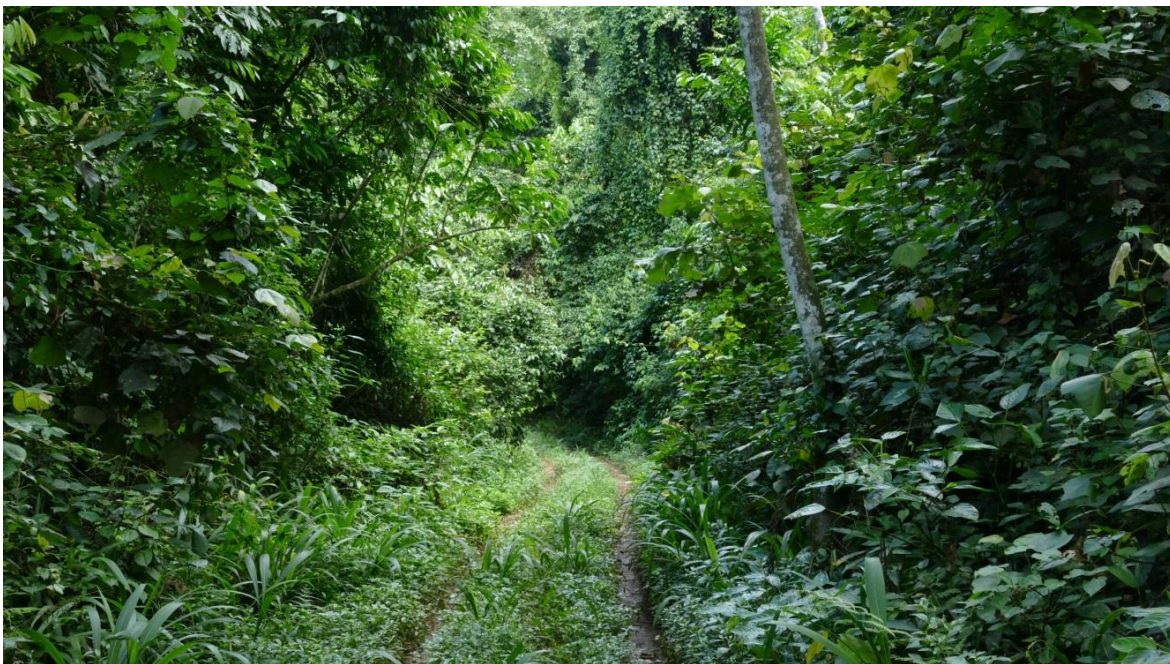


Plate 4: Road at Waibira.



Plate 5: A trail used by researchers at BCFS, shown here during a chimpanzee follow at Waibira.

2.6 Kasongoire

2.6.1 Forest Description

Kasongoire forest fragments are primarily riverine corridor forests that historically linked Budongo and Bugoma Forest Reserves (separated by 50 km). The landscape between the two reserves was originally a mosaic of grassland interspersed with gallery forest and savannah woodland and was never one continuous block of forest, as in Budongo Forest Reserve. However, the riverine forests which are important for chimpanzee populations have now largely been disconnected from each other as a result of human encroachment (McLennan 2008), dividing the landscape into patches of fragments and creating a landscape mosaic of woodland savannah, riverine forest and small- and large-scale agriculture (Figure 2.2).

2.6.2 Climate

Overall seasonal rainfall patterns are the same as at Budongo, although Kasongoire may be slightly drier, as was the case in the neighbouring site, Bulindi (McLennan 2010; Figure 2.1). As a result of being further from the continuous forest block, daily temperatures will likely also reach slightly higher than those within Budongo Forest Reserve (McLennan 2010).



Figure 2.2: Satellite image of forest fragments and villages within Kasongoire Parish, with corresponding schematic map highlighting forested areas, village centres and roads.

2.6.3 History of research

While this was the first in-depth study on the Kasongoire chimpanzee community, local people in the village have experience of some previous research activity, assistance and interest in them and the chimpanzees, although this has predominantly been short-term in nature. The chimpanzees were previously the subject of two short-term studies by scientific researchers, with projects involving collecting hair (Carlitz et al. 2016) and faecal samples (McCarthy et al. 2015). These studies both made preliminary observations of the chimpanzees but neither conducted an in-depth study which followed the chimpanzees over a long period of time. Additionally, two studies used social survey techniques to assess villagers' reports and attitudes to chimpanzee foraging (Jeary, unpubl.; Vogel 2013).

The Kasongoire chimpanzees were previously partially habituated for tourism purposes beginning in 2008 (see Section 2.6.7 for further information). In response to increasing reports of chimpanzee crop-foraging problems in Kasongoire, a survey was conducted in 2012 by BCFS and the WWF. A local research assistant observed chimpanzees for 41 days in April and May 2012 taking basic demography and activity budget data. This was complemented by surveys determining the economic status of villagers, their crop uses and reported crop-foraging by all animals (WWF/BCFS 2012).

During the data collection period of this study, Jane Goodall Institute (JGI) Uganda delivered an alternative livelihoods and sensitisation program that ran from January-December 2015. The purpose of the project was to deliver sources of income that would reduce Kasongire villagers' reliance on the forest, including providing crop seeds, goats and pigs, beehives (and training) and establishing a tree nursery. Education sessions discussed the reasons behind chimpanzee conservation and how to behave when/if involved in an interaction with a chimpanzee.

BCFS has a veterinary team that responds to situations if chimpanzees are injured or face potential serious injury; principally if a chimpanzee is caught in a mantrap or snare. Between the pilot and main study data phases a team was called out and darted a chimpanzee (believed to be the subadult BLY) and successfully removed the snare. The team on this occasion also found the decomposing carcass of a chimpanzee in the forest, although the identity of this individual is not known, nor was it possible to ascertain whether this individual died of natural or human-inflicted causes. BCFS has also delivered community sensitisation sessions in Kasongire and is known by villagers as the local organisation working towards chimpanzee conservation.

2.6.4 Chimpanzees

By the end of the study period, the Kasongire chimpanzee community comprised 42 individuals: 11 adult males and 15 adult females (see Appendix 3 for community composition and age/sex classes). Since the beginning of the pilot study six females gave birth (four during the main data collection), and two infants died (one between the pilot study and main data collection period and one during the main data collection). Two subadult females identified during the pilot were not seen during the main data collection period, presumably because they had dispersed. Two males disappeared during the study: one which was seen on only one occasion, and the other a core member of the adult male group. At the end of the study's pilot phase (December 2014) 24 individuals were formally identified, with all individuals being identified by the end of May 2016. Data were collected from 28 independent individuals, rising to 29 by the end of the study as one juvenile male started travelling independently of his mother. Seven individuals were known to have injuries from wire snares, and a further three individuals were caught in mantraps following the end of the study period, two of whom lost a limb.

2.6.5 Field assistants

I sought and hired one primary field assistant over the course of the study, named Balinda Kiiza Jovan (BKJ). He was a boda-boda driver (motorbike taxi) living in the nearby town of Kabango, but from Kasongore village. He is a well-respected young man locally with many relations living there. While he was not originally trained in any data collection skills, he had known the forest since he went hunting with his father as a young boy. He was trained during this study in all relevant skills including behavioural observations and tree identification and quickly became proficient in data collection, following chimpanzees and chimpanzee identification, as well as having a high level of natural enthusiasm and motivation.

Two other field staff from Kasongore were employed to assist with other work. Godfrey Darren worked as a part-time field assistant covering some periods when I was collecting data at Waibira, although he did not collect any data himself. He assisted with vegetation plots and tree renumeration. Godfrey decided he wanted to go back into education and was replaced by Tumwesige Benald (TB). TB had a Diploma in Forestry from the Nyabyeya Forestry College and assisted in plot renumeration and was trained to follow chimpanzees in my absence with BKJ, although did not collect systematic data on chimpanzees. After the initial set up, Ben took the lead on data collection for monitoring mango trees when BKJ and I were following the chimpanzees (Chapter 7). An international MSc graduate, Marika Roma (MR), assisted in data collection during the first few months. Inter-observer reliability tests were performed regularly to ensure consistency in data collection between everyone collecting data (AO, BKJ, TB, MR).

GE was instrumental in identifying trees for phenology monitoring. He and a Makerere University student, Alfred Afeku (who had previously worked with the phenology team at BCFS) both assisted with vegetation sampling plots. Two other men from Nyakfunjo (the village neighbouring Budongo Forest Reserve), who were both experienced in sampling trees, assisted with transect cutting and measuring trees.

2.6.6 Human activities

Kasongore forest shows evidence of ongoing human disturbance with remnant riverine forest patches distributed between human settlements, crop gardens and the large-scale sugarcane plantation owned by KSWL. Kasongore parish comprises 8 villages (Figure 2.2) set within the landscape mosaic. The terrain is gently undulating. Patches of riverine forest lie at the lower altitudes, originally connected by a landscape-wide system of streams but some of which are now

isolated through forest loss. A range of hills runs through the centre of the parish. The hills are dominated by savannah-woodland which is burnt seasonally and also used by humans for crop gardens, and a commercial pine plantation (overseen by the NFA). Chimpanzees were known to live mainly in the riverine forest but were reported by local villagers to range on the hills previously, although they were reported to do that less frequently during this study (B. K. Jovan, 2015, pers. comm.).



Plate 6: Road at Kasongoire. This road cuts through the chimpanzees' core range and is used by trucks transporting sugarcane (left) and workers to and from the factory (amongst other vehicles). Chimpanzees cross this road regularly (right).

Roads

Several roads connect the villages, some of which run directly through the forest in the chimpanzee community's home range. These roads can experience a high traffic load since they are used by KSWL trucks bringing sugarcane to the factory and transporting workers (Plate 6). Traffic levels depend on the workload required to maintain nearby sugarcane blocks (e.g. during periods of weeding and harvesting traffic will increase). All roads are made from maram (a local red clay) rather than tarmac and the main roads used by sugarcane trucks are maintained by KSWL. Despite seasonal deterioration they are maintained to a standard where vehicles can drive at speeds of up to 80 km per hour. Other transport includes occasional motorbikes and, less frequently, cars.

Cane guards

KSWL employs cane guards to ensure that the sugarcane is protected against foraging animals deemed pests. Chimpanzee sugarcane foraging is tolerated by KSWL meaning that, in theory, cane guards are not allowed to chase away chimpanzees. Guards typically deter animals by shouting, hitting two sticks together or hitting a tree with a stick, throwing stones, bushwhacking through the forest after animals with a panga (machete), or with dogs. Baboons are chased the most frequently and violently and on occasion several were caught, killed, skinned and their skins hung up to deter other animals (Plate 7). While chimpanzee sugarcane foraging is officially tolerated by KSWL, it is likely that guards sometimes deter and chase them as they do not like having to clear up the feeding remains (C. Asiimwe, 2015, pers. comm.).

Cane guards contractually work from dawn until dusk, although generally they were at their posts from around 7.30 am until 5 pm. Each guard patrols around 500-800 m of forest edge and has a hut constructed of a wooden frame and thatched roof and sides (Plate 8). Materials to construct the huts come directly from the forest and it is each guard's responsibility to maintain their stations. Guards often cook lunch together using the local traditional method, meaning they harvest and gather wood from the forest and often leave their stations at lunch time.



Plate 7: A baboon skin, hung as a deterrent to other baboons for foraging on sugarcane.



Plate 8: A cane guards' hut in Kasongoire, in the open gap between the forest and the sugarcane plantation.

Hunting traps

Cane guards lay various traps to catch small animals: snares (usually made of wire but occasionally nylon or rope), traditional 'triangle' traps and occasionally mantraps (Plates 9-11). The guarding behaviour exhibited at each post will depend on the personality and resources of the particular guard, likely influenced by cultural factors. For example, one Congolese guard set a range of wire snares not seen anywhere else and made arrows; several guards used a 'triangle trap' to catch cane rats (Plate 11); other guards do not use traps and use other tactics such as teaming together to flush baboons out by chasing them from both sides of the forest.

It has been illegal to set mantraps as non-selective vermin control since 2002 (Reynolds 2005), but reports of mantraps in the area still exist and they are known to be used at other nearby sites (McLennan et al. 2012). BCFS has an amnesty collection where those with mantraps can hand them in. During this study, local people were aware that setting mantraps was illegal, although mantraps were found in the forest.



Plate 9: Snare in Kasongoire. This one is made from string and uses a structure with a very small piece of cassava inside. Snares are most commonly placed along the trails of animals in the bush.



Plate 10: Mantrap in Kasongoire. Usually a sign will be erected made of wood, or, on this one occasion a sheath of maize, to alert other humans. This medium-sized trap in Kisagura village was placed directly in the middle of a human trail. It was set: we dismantled and retrieved it.



Plate 11: A 'triangle' trap in Kasongoire, dismantled. Used mainly by cane guards for catching edible rats for consumption. A piece of cassava is placed underneath attached to a string which triggers the trap to fall on the prey.

Logging

Local people use the forest to harvest small trees (between 10-20 cm in diameter) as poles for constructing houses in the village (Plate 12). Trees are also cut down and left to dry and later collected for fuel wood (i.e. for cooking), although many people gather fallen wood from their gardens as this is more convenient and perhaps due to fears of entering the forest (this is predominantly a job performed by women). There is also evidence of pit-sawing at Kasongoire, with five individual sites discovered over the course of this study. The majority of these were set up during the period between the pilot and the main study period, with one during the main study itself. The two sites that were in operation during the study were abandoned, likely as a result of our presence.



Plate 12: Freshly felled stems, felled by cane guards whilst on their duties and left to collect later.

Several acres of forest were cleared entirely during the study period (Plate 13). Large-scale clearing events such as these were always several kilometres from the main village and were cleared for planting of crops. Occasionally trees were felled by chainsaws but mostly trees were cut with axes and left standing and then burnt until they fell. Despite the law prohibiting clearance of forest next to water sources, the law is not enforced: during this study, most large-scale forest clearances in the area occurred next to streams.



Plate 13: A recently cleared patch of forest in Kasongoire. This clearance, around three acres in size, was discovered when we followed the chimpanzees there, on the periphery of their home range. Some trees (mostly *Psuedospondias microcarpa*) have been burnt to allow easier felling. It is likely that burning the trees was also to make charcoal.



Plate 14: A truck leaving Kasongoire forest laden with freshly felled trees, including stems of *Pseudospondias microcarpa* and *Macaranga schweinfurthii*. The men driving the truck informed us that they had permission from the private landowner (although this cannot be confirmed) and that they were taking this to Bulima, a nearby town where no forest is remaining.

Additionally, men come from nearby towns, where the forest has already been depleted, to harvest wood from the forest at Kasongoire (Plate 14). From speaking with some of the men I found out they use the wood for various purposes, including for burning to make local alcohol and selling as construction poles and fuel wood in the towns. Similarly, cane guards often (i.e. almost daily) harvest trees to sell to make extra money.

Tourism

Kasongoire chimpanzees were previously partially habituated for a private tourism venture. Local residents in Kasongoire felt that they did not benefit from the tourism and accused the individual of swapping the original chimpanzees for ‘aggressive, brown-faced’ chimpanzees (WWF/BCFS 2012). As a result, the tourism project was halted on 18th April 2012. Groups of tourists were still seen occasionally by local people, including on two instances in the first month of this study.

Plantation forestry

There is a pine plantation on the hill, disconnected from the riverine forest where the chimpanzees mainly range. The plantation is on government-held land and managed by the NFA, although it is run by a Kenyan firm. The creation of this plantation displaced those originally living

on this land, which has now become a central forest reserve. This has created tensions locally and alleged land grabs continue to persist to the present day. Local people are upset because they have had to vacate their land and also have not been provided with job opportunities as the management is sub-contracted.

Livestock

Cattle are grazed on the grass around the forest border, in the open gap between the forest edge and the sugarcane (Plate 15). Occasionally they are herded through the forest along trails which cross the stream in order to get from one side to the other more efficiently.



Plate 15: Cattle being herded in the open gap between the forest edge and sugarcane plantation.

2.7 Data collection

2.7.1 Study period

Fieldwork was conducted over 13 months between July 2015 and July 2016. An 11 week pilot study was conducted between October and December 2014 to assess suitable methods, gauge chimpanzee habituation levels and begin with chimpanzee identification. In the pilot phase I also made logistical arrangements for the main study period, including formally asking for permission to conduct research from local leaders at the Budongo Sub-County and Kasongore Parish. Between July 2015 and May 2016, data collection was divided equally between the two study locations and chimpanzee communities, Waibira and Kasongore, with alternate two week periods

spent collecting data at each site. I travelled fortnightly between the two sites to collect behavioural and habitat data with one main local research assistant at each site. In Kasongoire data collection was continued in the remaining fortnight by the research assistant. In June and July 2016 I worked solely in Kasongoire. Community meetings were held in Kasongoire during the pilot study, on arriving back for the main data collection period, at the half-way point and before leaving. The aim of these meetings was to keep local people informed and involved as much as possible with the progress of the research, as well as to maintain good relations with them.

2.7.2 Forest composition and fruit availability

Measuring forest species composition

Plots were established to assess tree species composition and diversity at each site. Square plots measuring 10 x 10 m were established every 100 m along a transect line, with the exact layout being different between sites due to the different forest shapes. I sampled all trees over 10 cm in diameter at breast height (DBH) that fell within a plot, recording the name of the species and its DBH. Using these data I calculated the species richness and diversity found at each site and created species rarefaction curves to extrapolate estimated species richness. I calculated species densities, created species and family importance values and assessed the level of overlap between forest composition in Waibira and Kasongoire.

Phenology

Monthly surveys were conducted to record the availability of wild fruits at each site. The fruit trail method was used (Chapman et al. 1994), recording fruits from specific trees on a scale from 0 to 4, 0 denoting no fruits and 4 denoting 76-100% of the tree covered by fruit. A fruit availability index (FAI) was created, extrapolating scores from each species with their corresponding tree density and DBH from the sampled vegetation plots.

2.7.3 Chimpanzee observations

Data on chimpanzee behaviour, party composition and feeding were collected using a mixture of scan and *ad libitum* sampling (Altmann 1974). Chimpanzees in each community were followed for a minimum target of eight days per month. In Waibira, logistical issues with staff meant that the minimum number of days was not always met (average four days per month). In Kasongoire, this target was exceeded every month (average 10 days month), except for a short period when a brief pause in chimpanzee follows was requested by BCFS directors in response to their concerns over our safety in a new site.

Individuals from both chimpanzee communities were assigned a name with a corresponding code. At Waibira, chimpanzees had already been assigned names by BCFS, whereas at Kasongoire my team assigned names to identify chimpanzees. Only adult males and females were focal subjects during follows, although every individual was assigned a name. Age groups were defined as per Goodall (1986): infants (0–4 years), juveniles (5–9 years), sub-adults (males: 10–15 years, females: 10–14 years) and adults (males: 16 years, females: 15 years). Since the exact ages of many chimpanzees at both sites were not known, estimates were applied based on physical appearance (see Appendices 2 and 3 for lists of chimpanzees and age/sex classifications at each site). Behavioural data were collected from adult individuals as a result of them displaying independent behaviour (without any dependence on the mother). Where sub-adult males travelled independently from their mother for a number of months, they were included in party scans as independent individuals.

Location of chimpanzees

I searched for chimpanzees with an assistant from around 6.30 am, when chimpanzees would leave their night nests. Chimpanzees were located using one or more of the techniques described below.

- Vocalisations. We often located chimpanzees initially by following the direction or location of the sound of the morning pant hoot chorus.
- Night nests or previous known location. If chimpanzees were followed the previous evening, we would commence in or near the area where they nested or were known to have last been.
- Feeding trees. We would often locate chimpanzees directly in specific trees during times when certain favoured feeding trees had an abundance of food (usually fruit, but not always). This was particularly the case at Waibira, since the home range was much more extensive than at Kasongoire. Additionally, the topography at Waibira meant that vocalisations often did not carry over the larger hills.
- Local reports (at Kasongoire only). In the event we were unable to locate chimpanzees, we would ask the sugarcane guards whether they had seen or heard them recently. Guards often moved between their guarding station and that of their neighbour's, meaning that a reliable transfer of knowledge on the chimpanzees' whereabouts could often be obtained, and across distances that vocalisations would not travel. At Waibira, more than one team of observers may have been in the home range at the same time and would try to communicate when locating the chimpanzees. However, due to the

topography, radio or cellular phone contact was almost impossible. If another team had successfully encountered chimpanzees while searching, this could only be communicated as far as a loud human “hoot” could carry, around 200-500 m. Therefore, transferring knowledge of chimpanzees’ location at Waibira was difficult and often impossible.

At Waibira, the working schedule required field assistants to leave from base camp at 6 am, meaning that we would reach the chimpanzees’ home range from 6.30 am onwards, locating chimpanzees as soon as possible (Hobaiter et al. 2017). The schedule there meant that we would usually leave the forest by 5 pm and it was rare to follow chimpanzees to nest. At Kasongore, we would also arrive in the forest at 6.30 am and leave by 6.30 pm, since we travelled there by road.

Focal sampling

Individual animals chosen from a randomised list each day were the subject of 60 minute continuous focal samples. Only adult males and females were the subject of focal samples. When chimpanzees were found at the beginning of each day a focal animal would be chosen at random, based on the individuals available in the party and the overall monthly bias of males and females. Chimpanzee habituation levels of both communities improved during the study period but chimpanzees were often lost due to the difficulty of following them in thick forest. This was particularly the case at Kasongore, since the habitat there included patches of inundated swamp forest and papyrus swamp which were difficult to pass through. When chimpanzees were lost the same techniques used at the beginning of the day were used to relocate them.

Due to challenges keeping sight of focal individuals, focal data that were collected were not of an adequate enough sample size and were therefore not analysed. However, the method of sampling a focal individual was an important methodological detail as it ensured party composition was sampled systematically (e.g. rather than follow a central male, male, mixed and female parties comprising central and peripheral individuals were more likely to be sampled evenly).

Scan sampling

Instantaneous scan samples were recorded at 15 minute intervals (Newton-Fisher 1999). I recorded the identity of all dependent individuals within a party and the party spread (distance in metres between the two furthest individuals in the party). A party was defined as all individuals associating within a 30 m diameter (Hockings et al. 2012b), although on occasions where the

party of chimpanzees was clearly a cohesive unit but spread over more than 30 m, all party members were included.

The activity of all individuals in the party was recorded during each scan as per the ethogram described in Chapter 5, Section 5.2.1. For ranging data, I collected a GPS point for each scan on a Garmin GPS unit (model 60x at Kasongoire and 62sx at Waibira). For each scan where chimpanzees had moved further than 10 metres a new GPS point was created and the corresponding number was noted. This allowed for discrepancies in GPS accuracy of up to 10 m error. Information about habitat type was also recorded during scans. Categories of habitat type are explained in the following section (see Table 2.2 for habitat type classifications and definitions). If one or more than one adult chimpanzee was recorded as feeding during a scan, I recorded the species and part consumed, recording data separately for males and females. If individuals were feeding on more than one species or part, I recorded the species and feeding item consumed by the majority of individuals. Anogenital swelling stage was recorded daily for all observed adult females. These were recorded on a scale from 0-4, with 0 denoting no swelling at all, and 4 being maximally swollen. Observer reliability of distance judgements was tested and recalibrated at regular intervals until all observers had a maximum error of 5 m.

Table 2.1: Data recorded during instantaneous scan samples.

Data variable	Description
Focal	Focal individual name code
Party spread	Recorded in metres
GPS point	Number generated by waypoint on GPS
Activity	For each individual in party: F=feed, R=rest; T=travel; G= groom; O=other. Kasongoire additional code: S= sugarcane feeding
Feeding species	Code of feeding species
Feeding part	UF= unripe fruit; RF=ripe fruit; YL=young leaves; ML=mature leaves; PI=pith; IN=insects; SD=seeds; HY=Honey; ME=Meat
Habitat type	CF= climax forest; MF= mixed forest; SF= swamp forest; ET= ecotone forest; SAV= savannah-woodland; PAP= papyrus swamp; CLE= clearance
Human activity	0=absent, 1=present
Human activity details	Tree stumps, snare, road, house, crop (large-scale, garden, plus species if known)
Human presence	0= no human present; 1= audio contact only, no human physically present but can be clearly heard; 2= human present but passive – not directing attention or actions towards chimpanzees; 3= human present and actively directing behaviour towards chimpanzees.

Ad libitum sampling

When chimpanzees were feeding on species in between scans, this would be noted for a more complete inventory of dietary composition. If chimpanzees left the forest to enter crop gardens this was noted because we did not follow chimpanzees to gardens (see Section 2.9). Anthropogenic landmarks and notable signs of human habitat use were recorded on an *ad libitum* basis and their location marked on the GPS receiver to map human activities throughout the chimpanzee home ranges (see Table 2.1 for list and definitions of all landmarks and activities). It was not possible to mark every single tree stump at Kasongoire (they were too numerous) but large stumps, pit-sawing sites, snares and mantraps were all mapped.

Table 2.2: Habitat type classifications and their descriptions at Waibira and Kasongoire.

Site	Habitat type	Code	Description
Waibira	<i>Cynometra</i> forest	CF	<i>Cynometra</i> -dominated forest, drained soil, often/usually on elevated ground. High, closed canopy.
	Mixed forest	MF	Intermediate forest rich in mahoganies and fruit trees favoured by chimpanzees (Reynolds 2005). Closed canopy, occasionally dense with lianas. Most common forest type (Plumptre 1996).
	Swamp forest	SF	Occasionally waterlogged, always next to streams, usually near to clay pits.
Kasongoire	Mixed forest	MF	Drained soil, between swamp and forest edge. Closed canopy.
	Swamp forest	SF	Permanently waterlogged, usually next to streams. In wet seasons inundated and flooded from streams overflowing. Dominated by <i>Phoenix reclinata</i> palms.
	Ecotone forest	ET	Usually found on the forest edge and regenerating from forest clearance or fire, sometimes found in forest interior between mixed forest and savannah-woodland patches. Characterised by thick terrestrial vegetation (e.g. <i>Lantana camara</i> , <i>Acanthus eminens</i>) and not dominated by any tree species. Open canopy.
	Savannah-woodland	SAV	Drier and exposed habitat, grassy with low tree density. Dominated by <i>Acacia</i> spp. and tall grasses. Open canopy.
	Papyrus swamp	PAP	Completely waterlogged swamp, with little or no trees. Dominated by <i>Cyperus papyrus</i> , mixed with strangling lianas.
	Clearance	CLE	Open area usually on the forest edge cleared by humans by deforesting and/or burning, typically for starting agriculture. If left will become ecotone forest.

2.7.4 Habitat types

Habitat type was recorded in botanical plots (Section 2.7.2) and during behavioural scans (Section 2.7.3). Mixed and swamp forests were found at both Waibira and Kasongoire, although were different in their characteristics due to natural differences between the two forests. At Waibira the habitat classifications used follow Eggeling's (1947) habitat descriptions at Budongo; at

Kasongore classifications broadly follow that of McLennan and Plumptre (2012) for riverine forest fragments at Bulindi.

2.8 Data analysis

Individual statistical tests are described in each chapter. I tested data for normality using the Kolmogorov-Smirnov test and non-parametric tests were used when data did not meet the assumptions of normality. Significance was set at 0.05. All statistical analyses were performed using SPSS Version 24 (IBM Corp. 2014).

2.9 Ethical considerations

An array of ethical considerations placed limitations on following chimpanzees out of forests into adjacent croplands due to negative local perceptions linking researchers to crop-feeding and potentially dangerous animals (Hockings & Humle 2009; McLennan & Hill 2013). The methodological approach developed by this study was designed to deal with this, while still answering important questions regarding primate responses to human modifications and activities within the landscape. All BCFS protocols regarding following primates and causing minimal disturbance in the forest were adhered to (e.g. not cutting trails without prior planning and permission). Regular community engagement ensured that local people understood the purpose of my research.

Debates around studying animals in human-modified landscapes have discussed the ethical implications of following animals and collecting data in croplands and have generally concluded it is not appropriate to do so (Gruen et al. 2013). From the human perspective, local people can perceive that the researcher is escorting or bringing the animals to their crop gardens, and then watching as the animals consume and destroy their crop. This can then lead to a breakdown in trust of the local people towards the researcher and hamper conservation goals in the long-term. From the animals' perspective, especially those with high cognitive abilities like chimpanzees, if they become accustomed to foraging on crops with the researchers standing by, they may feel more protected when in what is a risky environment, where humans may in future instances persecute them for destroying their crops. Consequently in this study, chimpanzees were not followed into crop fields. Instead, data were collected on party composition prior to animals leaving the forest and entering crops in local people's gardens. However, sugarcane foraging by chimpanzees is tolerated by KSWL and with their permission I observed chimpanzee behaviour in sugarcane plantations.



CHAPTER THREE

FOREST COMPOSITION AND FRUIT AVAILABILITY IN AN UNPROTECTED HUMAN-IMPACTED FOREST AND A PROTECTED FOREST



Plate 16 (on previous page): A large party of chimpanzees at Waibira foraging on ripe fruits of *Ficus sur*.

3.1 INTRODUCTION

Forest composition and the availability of wild fruits are known to influence the socio-ecology of wild primates (Chapman et al. 1995; Robbins & Hohmann 2006; Struhsaker 1969), shaping animals' activity and grouping patterns, as well as potentially influencing the use of human-grown food resources where they are available to wild animals. Logging in tropical forests affects the size, density and distribution of trees, which will influence the availability of resources for primates (Donati et al. 2011). Seasonal changes in availability may drive animals to consume foods of lower nutritional value when preferred foods are not available, particularly for frugivorous species (Donati et al. 2011). Resource scarcity can lead to behavioural adaptations and presents opportunities to understand a species' flexibility (van Schaik et al. 1993).

Surveys to document the composition and density of tree species were required since these data were lacking for the home ranges of the Waibira and Kasongoire chimpanzee communities. Monitoring fruiting phenology was needed in order to compile data on available food resources, their availability and distribution. In this chapter I first calculate and map the home ranges of chimpanzees at both sites, since information on where they range directly informs the location of habitat sample plots. I then describe the forest composition at Waibira and Kasongoire and the availability of wild fruit at each site. These data are used to inform future chapters including chimpanzee feeding behaviour (Chapter 4), activity budgets (Chapter 5), grouping patterns (Chapter 6) and use of cultivated fruits (Chapter 7).

3.1.1 Forest composition

The flora of Budongo Forest as a whole has been studied previously (Eggeling 1947; Paterson 1991; Plumptre 1996), whereas forest composition specifically in the home range of Waibira chimpanzees was unknown. The forest composition at Kasongoire had not been documented prior to this study. Therefore, habitat surveys were conducted at both sites and these data establish the tree species present in this habitat and their densities and draw direct comparison between sites.

Kasongoire is situated only 12 km to the south of the Budongo border, yet, as described in Chapter 2, the habitat is considerably different to that found within the Budongo Forest Reserve. Budongo Forest is classed as semi-moist deciduous forest, whereas forest in Kasongoire is riverine

gallery forest set in a landscape mosaic. Some species are common in forests throughout the region (McLennan & Plumptre 2012) and the two sites are extremely close geographically, so a certain level of species overlap is expected. At the same time, the two forests exhibit fundamental differences as a result of habitat type since tree species composition in riverine forest will naturally differ from that in semi-moist deciduous forest. The compositional difference between Budongo and Kasongore forests is likely further exacerbated by human encroachment, since the harvest of large tree species can cause dramatic changes to species composition, as was the case at Tana River in Kenya (Moinde-Fockler et al. 2007).

A previous study has documented forest composition in the riverine corridor forests outside of Budongo Forest, conducted in Bulindi, 7 km southwest (at the nearest point) of Kasongore (McLennan & Plumptre 2012; see Figure 1.1, Chapter 1). From the data available at Bulindi, riverine forest differed markedly in tree composition and chimpanzee feeding trees to Budongo. Species richness (the number of species inventoried) was much greater in the continuous, protected forest at Budongo than that of the riverine forest fragments in Bulindi. Species diversity (the relative abundance and evenness of species, factoring in species richness) was also slightly higher at Budongo, although Bulindi had a moderate level of diversity, likely as a result of the various habitat types there. Unsurprisingly, the two forests had a low level of species overlap. Important chimpanzee food tree density was higher in Bulindi than in Budongo, largely due to the large proportion of swamp forest at Bulindi, which is dominated by wild date palm, *Phoenix reclinata*. Similarly, Reynolds et al. (2003) note that Kasokwa Central Forest Reserve, another fragmented forest south of Budongo Forest, is dominated by *P. reclinata* palms in addition to *Pseudospondias microcarpa*, a species also common in Bulindi. Additionally, trees belonging to the Moraceae family were found at higher density in Bulindi than in Budongo, which may be important for chimpanzee feeding behaviour since fruits in this family, including figs, are consumed heavily by chimpanzees (Tweheyo & Lye 2003; Wrangham et al. 1993). Given the geographical proximity and similarity in forest type, Kasongore forest was expected to be very similar in composition to Bulindi.

3.1.2 Fruit availability

Spatio-temporal fluctuations in forest food resources at Kasongore and Waibira could explain key differences between the two chimpanzee communities. Chimpanzees are primarily ripe fruit specialists, although they are known to consume a wide variety of food types (Wrangham et al. 1998; Newton-Fisher 1999; Tutin et al. 1997; Watts et al. 2012a; Yamakoshi 1998). Therefore,

phenological surveys were conducted each month to assess wild fruit availability at both sites to determine factors affecting chimpanzees' food preferences and time budget strategies.

An inverse relationship was found between rainfall and fruit availability at neighbouring sites: in recent studies at Bulindi and Budongo, peaks in fruit availability were reported in the dry season, generally between December and March, with lean periods falling during the wettest months, April and May and again from August until December (Fawcett 2000; McLennan 2013). Other studies in Budongo have found the reverse, with higher fruit availability occurring during wetter months (Newton-Fisher 1999; Tweheyo & Babweteera 2007). Since the location of these studies are within a 15 km radius of my study sites and represent both forest types, I expected Waibira and Kasongire to experience similar patterns of fruit availability to one another. However, other studies have found considerable differences in forest composition and fruit availability in forested areas within Kibale National Park that are 15 km apart (Chapman et al. 2003; Potts et al. 2011). Therefore, some level of heterogeneity in fruiting was also expected between the two sites in this study.

3.1.3 Chapter aims

In this chapter I aim to:

- Establish the study area by mapping the home ranges of chimpanzees at Waibira and Kasongire.
- Provide an inventory of tree species within the chimpanzee home ranges.
- Characterise the forest and assess forest composition (tree species diversity and dominance) and compare between the sites.
- Assess wild fruit availability at both sites.

3.1.4 Hypotheses and predictions

Table 3.1 outlines the hypotheses and predictions tested in this chapter.

Table 3.1: Hypotheses and predictions relating to tree species composition and fruit availability in the Waibira and Kasongoire chimpanzees' home ranges, and the framework for testing them

Hypothesis	Prediction	Analysis
Forests in human-modified habitats will exhibit composition and phenological differences to those less impacted by humans.	1. There will be a low level of similarity in forest composition between Waibira and Kasongoire; 2. Tree species richness will be higher in Waibira than in Kasongoire; 3. Tree species diversity will be higher in Waibira than in Kasongoire; 4. The basal area of trees will be significantly greater in Waibira than in Kasongoire;	1. I test the level of similarity in tree species composition between forests using the Morisita-Horn Index of similarity, where 0=no similarity and 1=complete. Scores under 0.3 are determined as low (McLennan & Plumptre 2012). 2. I count the number of tree species at each site using data from botanical plots to determine which forest contains the higher species richness. 3. I use the Shannon Weaver Diversity Index (H') using data from botanical plots to determine which forest has a greater tree species diversity. 4. I calculate the average basal area (BA) per plot at each site using tree DBH measurements. I will use a Mann Whitney U test to determine if the BA of trees is significantly greater at Waibira than at Kasongoire.

3.2 METHODS

3.2.1 Data collection

Chimpanzee home ranges

Ranging data were collected by marking the location of chimpanzees on a Garmin GPS unit every 15 minutes during instantaneous group scans, as described in Chapter 2, Section 2.7. GPS accuracy was kept below 10 m. Due to the nature of the irregular size and shape of the forest at Kasongoire, monthly recces of peripheral areas were carried out from November 2015 to July 2016 and signs of chimpanzees were noted and the GPS location recorded. These included recent nests, feeding traces and knuckle prints. Additionally, reports from local villagers of chimpanzees in peripheral areas or the village-garden matrix were followed up on and if signs were found and recent chimpanzee presence could be confirmed then the GPS location was recorded.

Forest composition

As a result of the contrasting size and shape of the two forests and the differing levels of existing transect networks at each site, the layout of the sample plots was designed in the most replicable way possible. Furthermore, consideration was given to working efficiency as well as minimising disturbance to the forest created by conducting the surveys, such as creating paths and cutting small saplings.

The Waibira chimpanzee community ranges within Budongo Forest Reserve, a large contiguous forest block with an existing grid system of walkable trails established by BCFS. This grid system (Appendix 4) was set up to facilitate research on the chimpanzees and covers the majority of the known Waibira home range. In contrast with Budongo, the forest in Kasongire meanders along the course of streams and the width of the forest ranges from 300 m to less than 100 m at some points meaning a grid system is not practical there. It was also important not to establish a permanent grid system because it might encourage increased access and use of the forest by local people. With these factors in mind, I used a replicable and efficient design for the habitat surveys, using available trails in Waibira without placing a plot directly on a path and creating paths of least disturbance at Kasongire.

Square plots have been shown to capture fewer species compared with rectangular plots (Bonham 1989). However, square plots were the most practical shape in this study for the following reasons. Firstly, to cover a minimum target area of three hectares rectangular plots measuring 10 x 20 m would have been too close together to avoid possible spatial autocorrelation. Secondly, 20 x 50 m rectangular plots were considered too large since the forest fragments at Kasongire are not sufficiently large enough and the course of the forest meanders with the streams, meaning this size would too often have a large proportion of the plot outside the forest edge. Therefore square plots of 20 x 20 m were the most practical size and shape, and considering the total area covered it was thought that the trade-off of potentially capturing fewer species than in rectangular plots would be out-weighed by the large area covered.

Plots were established every 100 m along a transect line at both sites. The layout of the transects differed between sites as shown in Figure 3.1 and as described below. At both sites, transects ran parallel or perpendicular to one another at intervals of 500 m to standardise and replicate the design between both sites as much as possible. Transects were cut using a compass bearing and the three pole method (a series of poles arranged in a straight line to help maintain the bearing: see McLennan 2010). This was assisted by following a line on a Garmin handheld GPS unit, which

was plotted prior to the survey using Garmin Mapsource for accuracy and to give a baseline to follow in the field. Transects that needed to be cut were done so with minimal disturbance: there was no need to create a permanent transect so no trees were cut and only a walkable line was created to aid the enumeration team to get from one plot to the next. The position of transect lines and plots at each site are shown in Figure 3.1.

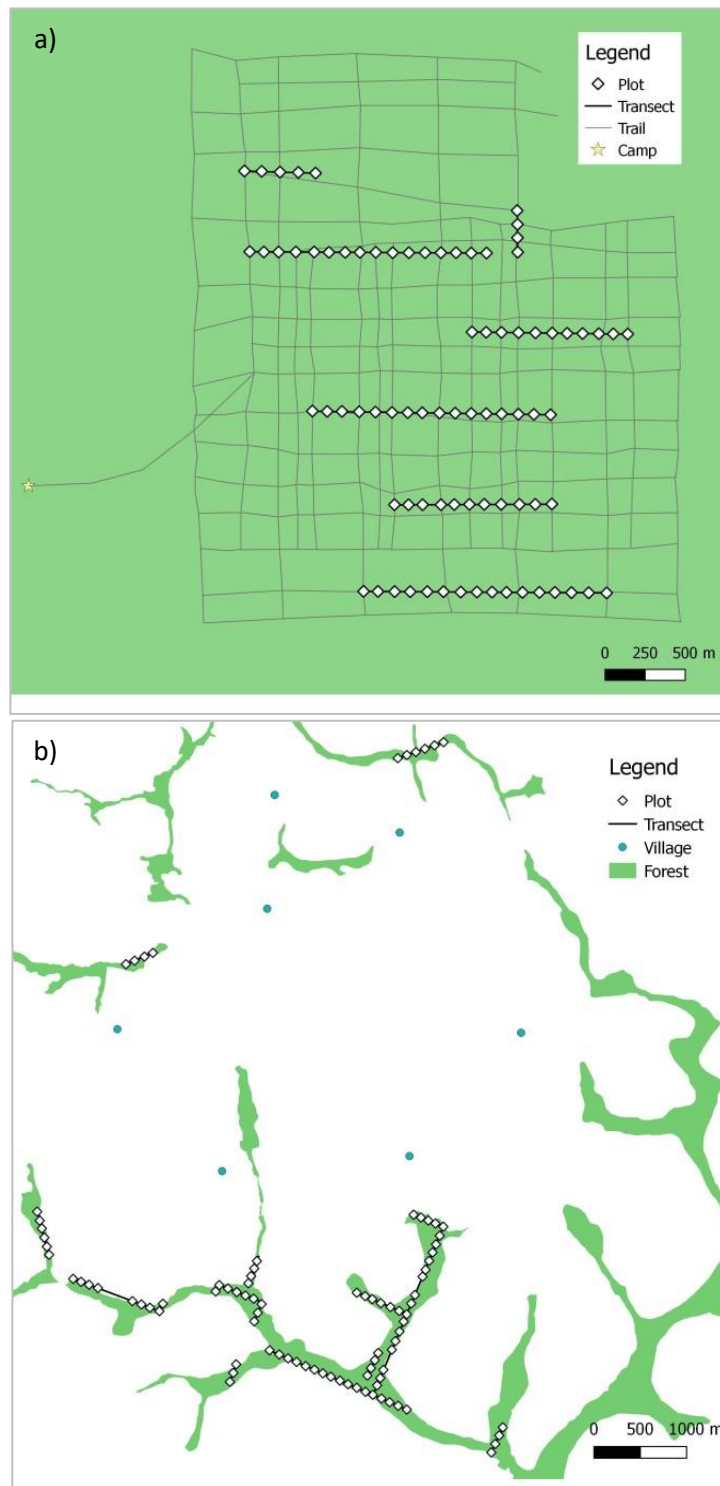


Figure 3.1: The location of habitat sample plots at (a) Waibira and (b) Kasongoire.

The centre point and corners of each plot were marked with flagging tape. Tree species and DBH, recorded at 1.3 m from ground level, were recorded for all trees ≥ 10 cm DBH ($n=2624$). For very large and buttressed trees, DBH was measured above the buttress, or estimated in the eight cases where this could not be physically reached. For multi-stemmed trees, the DBH of the largest stem was recorded at breast height (1.3 m) from the intersection of the stems. The habitat type of each plot was recorded as per the classifications described in Chapter 2, Table 2.2. Occasionally, plots lay on an ecotone where two forest types were present. In these cases, the forest type that covered the majority of the plot was recorded. The percent cover of terrestrial vegetation within the plot was recorded and, where identifiable, the dominant species was noted.

At Waibira, each transect line was between 1 and 1.5 km in length with plots established every 100 m. The starting point and length of each transect was determined by picking a number and letter at random at the beginning of the survey, corresponding to the numbering system of the existing grid. I would write the numbers and letters down and ask a member of the team to point on the paper with their eyes closed. The trail system within the Waibira home range had paths 2-3 m wide: plots were placed on the north-eastern corner of the plot starter mark to avoid an established trail falling within a plot. When the minimum number of plots was completed (a target of 70, based on covering a minimum of 3 hectares) further plots were established, the starting points selected at random. To sample as many areas as possible and avoid spatial overlap, transects ran from east to west, with the additional plots established along north-south transects.

Due to the irregular forest shape at Kasongore the design outlined above had to be modified slightly. At Kasongore, the perimeters of the forest fragments were plotted by following the forest edge on foot and drawn using the “track log” function on a Garmin GPS unit. Two main transects were placed along the longest lines of best fit within the forest perimeter, perpendicular to one another. To increase the number of plots and keep to the same systematic method, further transects were established every 500 m along these at 90° (Figure 3.1). All transects ran until they reached the forest edge and plots were established every 100 m. Transects sometimes ran through waterlogged areas: if a plot lay on a waterlogged area data were still recorded to capture the different habitat types, although at Kasongore, often there would be few or no trees recorded, especially in papyrus swamp.

At Kasongore, further plots were established outside the core of the chimpanzees’ range after 70 plots had been established. These were often in forest patches within Kasongore Parish that the

chimpanzees visited (or were reported to visit) occasionally, so were within their home range but outside of what appeared to be their core range during the study. These areas were primarily forested but occasionally comprised other habitats, including savannah-woodland. The same method was used for establishing the additional transects and plots: plots were placed at 100 m intervals or at perpendicular transects every 500 m according to changes in shape of the forest.

I established a total of 78 plots in Waibira covering an area of 3.1 hectares and 91 plots covering an area of 3.62 hectares in Kasongoire. In Bulindi, McLennan (2010) found that a similar coverage of plots in a similar habitat and area was a sufficient level of sampling, based on species accumulation curves. Initially, the same number of plots was established in each site, but adding plots in other forest patches at Kasongoire increased the area covered, which had the additional benefit of describing more of the habitat since tree composition at this site had not previously been recorded. The total transect length at Waibira of 7850 m was equivalent to a plot every 100.6 m and at Kasongoire was 9350 m, equivalent to a plot every 102.7 m.

Habitat type was recorded in botanical plots, as per the classifications outlined in Chapter 2, Section 2.7.3. The area covered, species richness, tree stem density and average DBH for each habitat type was calculated. Mixed and swamp forests were found at both Waibira and Kasongoire, although were slightly different in their characteristics due to natural differences between the two forests.

Phenology

Estimating fruit availability

Chimpanzees show preferences for ripe fruit, consequently the availability of known fruit trees was recorded, since the abundance of fruit (rather than other food types, such as leaves) is likely to influence ranging and grouping patterns (Anderson et al. 2002; Basabose 2004; Mitani et al. 2002). The availability of other food parts including leaves and flowers were recorded, but from these fruit trees only. In Kasongoire, it was particularly important to record wild fruit availability since seasonal fluctuations and periods of natural fruit scarcity may influence chimpanzee feeding on cultivars (Hockings et al. 2012b; McLennan 2013).

Of the common methods for estimating fruit availability, there are two systematic methods: phenology transects, where all trees are monitored along randomly positioned belt transects; and fruit traps, measuring fruit fall from trees under randomly and systematically placed traps. The

fruit trail method is non-systematic and involves selecting specific trees and monitoring them periodically. Chapman and colleagues (1994) found that the fruit trail method is well suited for time-constrained studies and can give a good estimation of habitat-wide availability if the tree density can be extrapolated. It is as reliable as the phenological transect method which is thorough but measures all trees and is therefore more time-consuming (Chapman et al. 1992; Chapman et al. 1994).

Since the aim of this study is to monitor availability of chimpanzee foods, it was not necessary to use a method which randomly or systematically recorded habitat-wide fruit availability. Additionally, this study was relatively time-constrained, working between 2 field sites. Therefore, the fruit trail method was the most appropriate in this study as it enabled the team to monitor specific trees in an efficient way. Using the values for basal area and tree density of species sampled across the chimpanzees' range from the plot data (this chapter), a habitat-wide estimate of fruit availability is then created.

Many tree species are patchily or very sparsely distributed, sometimes depending on habitat type but also through natural differences in tree distribution. Additionally, some fruit trees are found at a very low density meaning that the few individuals of specific tree species which I wanted to target for monitoring would likely be missed out if using phenology transects or fruit traps. This strengthened the argument for using the fruit trail method which ensured that specific trees were included.

Kasongoire

Chimpanzee food tree species were selected based on personal observations, feeding observations, chimpanzee food species recorded at other sites and advice from BCFS field assistants. During the pilot study (October-December 2014), some wild fruits were confirmed as being fed on by the chimpanzees. McLennan (2013) provides a list of feeding trees fed on by the Bulindi community in a similar riverine mosaic fragmented habitat around 10 km further west/southwest: many of these species were included for phenological monitoring in this study.

A target of 15 and a minimum of 10 individuals from 23 species were initially identified for monitoring, as per McLennan (2013). Some species were found in very low densities and more individuals were included as they were discovered over the course of the study as the chimpanzees ranged into new areas. Initially 127 individual trees were identified for monitoring during the first month of phenological surveys in August 2015, rising to 170 by December 2015

and 180 by January 2016. One tree was cut down during the survey period meaning that 179 trees were included in the analysis. Table 3.8 presents the tree species monitored at each site.

At Kasongoire phenology surveys ran from August 2015-July 2016 (i.e. 12 consecutive months). Trees were monitored in the second week of every month. During the final two months at Kasongoire phenology surveys were conducted fortnightly to complement the mango-feeding data collection (Chapter 7). Phenology surveys were carried out by AO and BKJ.

For each tree the level of cover for leaves (young and mature) and fruit (unripe and ripe) was recorded on a scale of 0 to 4, where 0 is absent, 1 is between 1 and 25% of the canopy covered; 2 is 26 to 50% cover, 3 is 51 to 75% cover, and 4 is 76 to 100% cover (Hockings et al. 2012b). Whether the tree was flowering was recorded in binary form (0/1) rather than quantified. This was because flowers do not usually form an important part of chimpanzee diets (with the exception of the Sonso community, see Newton-Fisher 1999) so the purpose of monitoring flowering was not to quantify or make an availability index but to monitor the number of trees that might shortly come into fruit. Trees that were cut down during the study were recorded and where possible another individual of that species was added to the fruit trail and monitored for the remainder of the study.

Waibira

Waibira chimpanzees' diet was previously recorded by BCFS staff during the habituation process and was also expected to be similar to that of the neighbouring Sonso community, which has been studied extensively since 1990. Therefore the same species monitored for phenology surveys in the Sonso area were monitored in this study, with the exception of species which were absent from Waibira (e.g. *Broussonetia papyrifera*, some *Ficus* spp.). A target of 15 trees from 14 species were identified for monitoring and a total of 154 trees were included in the analyses (Table 3.8)

At Waibira the fruit trail method recorded fruit availability each month using a 0-4 scale as described above. At Waibira the study ran from July 2015-May 2016; however, due to delays at BCFS in beginning phenology surveys in the Waibira community's home range, data were only available from November 2015-May 2016 (7 months). Phenology surveys were conducted monthly by the BCFS phenology team led by GE. I accompanied GE on surveys at Budongo during the pilot and the main study in addition to GE joining surveys in Kasongoire to ensure inter-observer reliability.

3.2.2 Data analysis

Chimpanzee home ranges

Chimpanzee home ranges were calculated using fixed kernel (FK) analysis. The benefit of FK in this study is that it can allow for meaningful comparison between sites. While home range analyses using minimum convex polygons (MCP) are often used for comparative studies, the weakness of using MCP is that they often bias home range estimates by including areas that are never visited (Powell 2000). In the case of Kasongoire this might lead to an extremely distorted home range area due to the irregular forest shape: if the analysis included peripheral ranging areas in forest fragments that are kilometres away, then the area under the polygon would include the entire landscape in between, including several village centres. However, in the interest of creating a varied and comparable analysis, I performed the analysis using both MCP and FK to calculate chimpanzee home ranges. Cores of 50%, 95% and 99% were selected for both methods, in addition to 100% for MCP to show the maximum total overall area used by chimpanzees. For the FK analysis I used least squares cross-validation as the smoothing modifier and contours fitted to locations in order to ensure that the several locations far away from the core area were included at Kasongoire. To avoid temporal autocorrelation, the first GPS location every two hours was used in the analysis. Home ranges were analysed using Ranges9 (Kenward et al. 2014) and plotted using mapping tools in Quantum GIS 2.18.0 (QGIS Development Team 2016).

Forest Composition

Tree species richness

Species richness is an important baseline index of community structure, although it is inevitable that community-wide tree species richness will be underestimated since it is impossible to record and measure all trees within the area (Colwell et al. 2004; Gotelli & Colwell 2001). Sampling a large enough area should ensure that as many species as possible are recorded, although this will still create an underestimation of the real value. From personal observation, in both sites some species were present but did not fall within the plots. Since sampling data can inevitably only document the presence of a species and not the absence, species rarefaction is useful to estimate the number of species by modelling expected species based on the discovery rate of new species within the sampled area (Gotelli & Colwell 2011). Species rarefaction curves are also a good way to see how thorough and accurate the sampling effort made was by comparing modelled expected species richness with actual samples.

Species rarefaction curves plot the probability of finding new species in a sampled area based on the actual species accumulation data: for every next sample (plot) it will model the likelihood of discovering a new species based on the actual incidence that new species were found as the sample area increased. As further species are found the curve rises, sharply at first and then more slowly as less common species are added. Eventually the curve reaches an asymptote when no further species are expected to be found, and thus this value is the expected species richness predicted by the model.

Several models have been developed to create a more accurate estimation of species richness based on rarefaction. The non-parametric Chao2 and second-order Jackknife indices were found to be the most accurate estimators of asymptotic species richness (Colwell & Coddington 1994) and were used in this study. Species rarefaction curves and the Chao2 and second-order Jackknife indices for species richness were computed by *EstimateS* Version 9.1.0 (Colwell 2013), with 95% confidence intervals. Reported values are based on 100 permutations.

Forest structure and composition

For each species and family, I calculated the total number of stems and overall frequency (the number of plots species were present in per total plots sampled), density (stems per hectare) and basal area (BA) $\text{m}^2 \text{ ha}^{-1}$. Using DBH measurements from trees in sample plots (unit=cm), I calculated the BA of trees (unit= m^2) using the following formula:

$$\text{BA} = \pi * (\text{DBH})^2 / 40000$$

I then calculated the relative frequency (the frequency of occurrence as a percentage of the sum of all occurrences), relative density (the percentage of stems per species of the total number of stems per hectare) and relative dominance (the percentage basal area per species of the total basal area per hectare).

Importance values (IV) for species (SIV) and families (FIV) show a measure of overall ecological importance within the community per species and family. IVs were calculated for each species and family by summing their relative frequency (for species) or diversity (for families), relative density and relative dominance to provide a comparative measure of ecological importance (Curtis & McIntosh 1951).

Species diversity in forest composition within both Waibira and Kasongore (Prediction 4) was assessed using the Shannon-Weaver index (H'), which accounts for both the abundance and evenness of species present in the community. This was calculated from the equation:

$$H' = -\sum p_i \ln p_i$$

where p_i is the proportion of the sample that belongs to the i th species (Shannon & Weaver 1963).

Comparison of forest fragments

Similarity of forest composition between Waibira and Kasongoire was assessed using the modified Morisita–Horn index (Prediction 1). The Morisita index of similarity is recommended above others as it can cope with differences in sample size (Wolda 1981) and the modified variant of the index by Horn (Horn 1966) adds in the component of abundance, allowing the index to calculate species overlap including relative abundance of each species. The index (MH) is calculated from the equation:

$$MH = 2 \sum (a_{ni} \times b_{ni}) / (d_a + d_b) aN \times bN$$

where a_{ni} is the number of individuals of the i th species at site a , b_{ni} is the number of individuals of the i th species at site b , aN is the total number of individuals at site a , and bN is the total number of individuals at site b ; d_a and d_b are calculated as:

$$d_a = \sum a_{ni}^2 / aN^2, d_b = \sum b_{ni}^2 / bN^2$$

The Morisita-Horn index returns a value between 0 and 1, with 0 denoting no overlap, and 1 denoting identical forest composition. The Shannon-Weaver diversity and Morisita–Horn similarity indices were computed with *EstimateS*. To compare the difference in tree biomass between the two sites, the average basal area per plot was calculated and compared using a Mann-Whitney U test (Prediction 5).

Phenology

A ripe fruit availability index (FAI) for each month was calculated as follows:

$$FAI = \sum F_{km} \times D_k \times S_k$$

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 DBH of adult trees of species k (McLennan 2013). Ripe fruit scores were first weighted according to the number of trees surveyed. To calculate the availability of fruit from adult trees (trees which will bear fruit), immature trees were eliminated according to a minimum reproductive size threshold, and the density and DBH of stems were recalculated accordingly (as per McLennan 2010). Results from all monitored species are shown in this chapter. Values of FAI each month are expressed in this chapter as the absolute FAI score, in order to compare fruit availability of the monitored species between the two sites. From these values, categories of “high” ($FAI > 1000$), “medium” ($FAI = 500$ –

999) and “low” (FAI<500) were created for analyses in future chapters. In future chapters where phenology data are used, at Kasongoire species which were not observed being fed on by chimpanzees despite abundant fruit are excluded from fruit availability values since chimpanzees were never observed feeding on those species. At Waibira, species not observed being fed on by chimpanzees were left in the fruit availability values. This is because the very low sample of feeding observations at Waibira meant it was possible that chimpanzees did consume them but observations were missed. While some feeding species at Kasongoire were also likely missed, it made sense to exclude them due to the much larger sample of observations of observations there. In Chapter 7, values are expressed as an index as a weighted proportion of 100 where the month with the highest value=100, as per Fawcett (2000) and McLennan (2013).

3.3 RESULTS

3.3.1 Chimpanzee home ranges

The home and core range sizes of the two chimpanzee communities during the study period varied considerably between sites (Table 3.2; Figures 3.2 & 3.3). From the fixed kernel analyses, the total (99% FK) home range size was larger at Kasongoire than at Waibira, but the reverse was found for core ranges: Waibira chimpanzees used a core range (50% FK) of 0.89 km², split into two areas (Figure 3.2), while Kasongoire chimpanzees used one central core range of 0.67 km² (Figure 3.3). GPS locations recorded outside this area at Kasongoire show that the total home range was much larger than this, but due to the large sample of GPS points, this was missed even in FK analysis using 99% cores. Minimum convex polygons showed this total ranging area to cover almost 25km² at Kasongoire.

Table 3.2: Chimpanzee home range size (km²) over the study period.

<i>Method</i>	FK			MCP			
<i>Cores</i>	50 %	95 %	99 %	50 %	95 %	99 %	100 %
Waibira	0.89	4.69	6.28	1.52	4.62	5.87	6.10
Kasongoire	0.67	2.24	7.82	0.82	1.98	9.34	24.99

After sorting the data using GPS locations every two hours to avoid temporal auto-correlation, 135 GPS locations were analysed to calculate the chimpanzees’ annual home range from a total of 863 over 10 months of data collection. At Kasongoire, 508 GPS locations were analysed over 13

months from a total of 2847, of which 2490 were from instantaneous scan samples, 162 were from nests and 195 were from feeding traces.

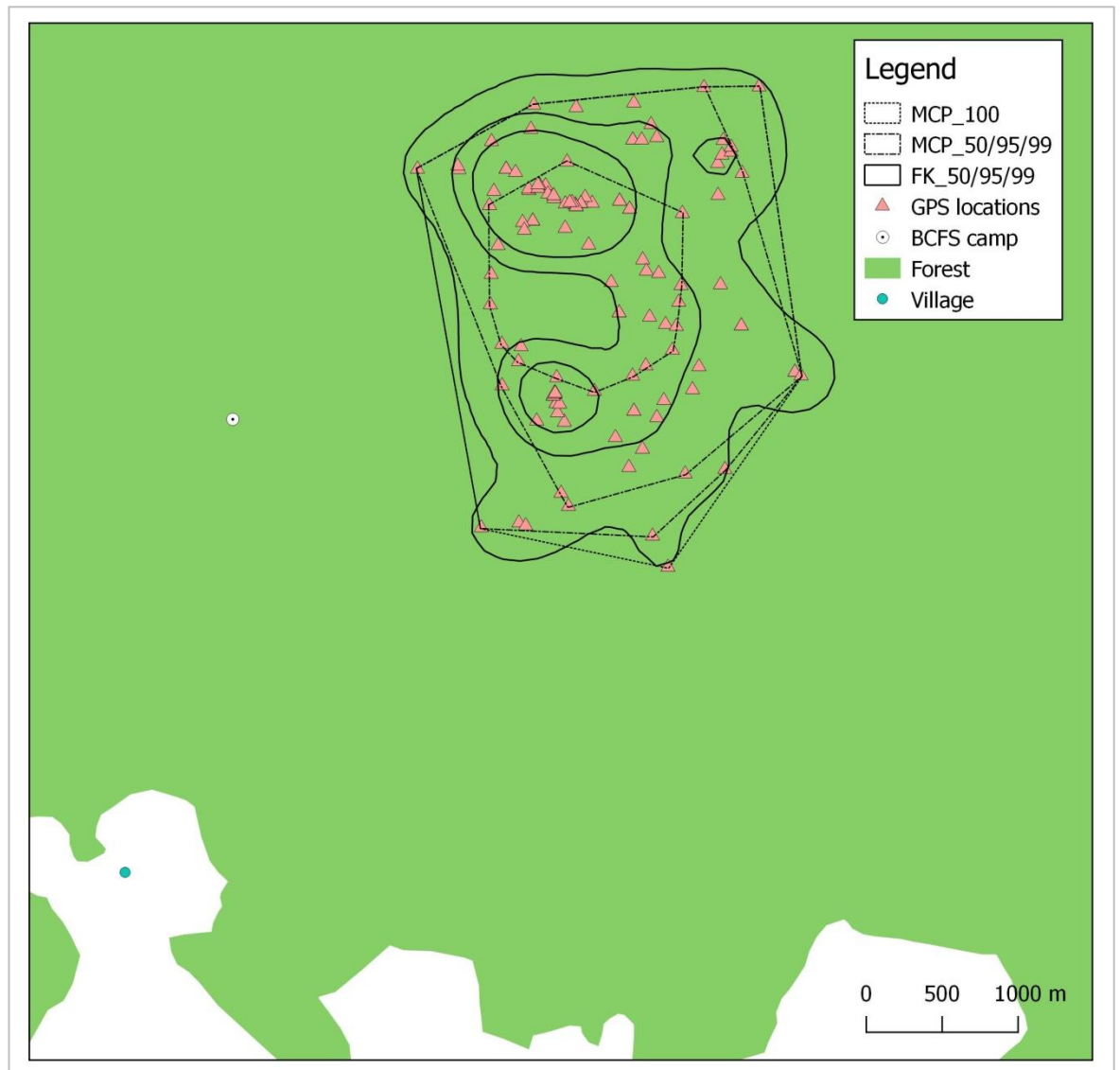


Figure 3.2: Waibira chimpanzees' home range during the study period, showing minimum convex polygon (MCP) isopleth estimates at 50, 95, 99 and 100% cores, fixed kernel (FK) isopleth estimates at 50, 95 and 99% and GPS locations.

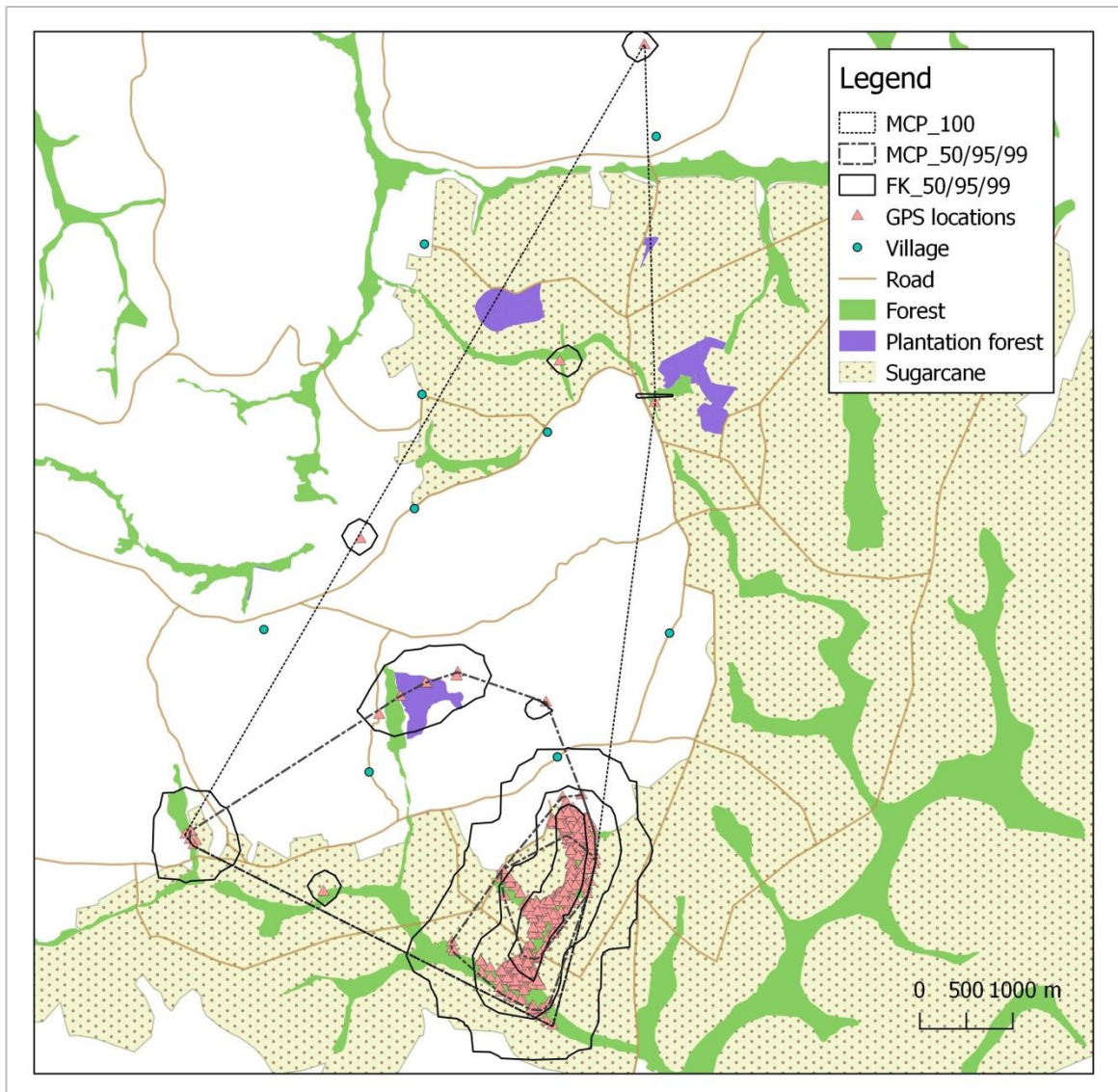


Figure 3.3: Kasongoire chimpanzees' home range during the study period, showing minimum convex polygon (MCP) isopleth estimates at 50, 95, 99 and 100% cores, fixed kernel (FK) isopleth estimates at 50, 95 and 99% and GPS locations.

3.3.2 Forest composition

Species richness

At Kasongoire, a total of 1140 stems ≥ 10 cm DBH were recorded in 91 plots, comprising 89 species belonging to 31 families. At Waibira a total of 1484 stems ≥ 10 cm DBH were recorded in 78 plots, comprising 92 species belonging to 32 families. There were two unidentified species in plots at Kasongoire and one at Waibira. See Table 3.3 for a summary and comparison between sites. Full species lists for each site are presented in Appendices 5 (Waibira) and 6 (Kasongoire).

In support of Prediction 1 the Morisita-Horn value of similarity was 0.255, denoting a low level of compositional similarity between the two forests. Thirty-four species were found in both sites,

with few found at similar densities (see Appendix 7 for a list of shared species between sites). Kasongoire and Waibira had only two species in common from the top 20 species: *Ficus sur* and *Croton sylvaticus*.

Table 3.3: Summary of species richness and sampling effort at Kasongoire and Waibira.

	Kasongoire	Waibira
No. stems	1140	1484
No. plots	91	78
Area sampled (ha)	3.64	3.12
Stem density	313	476
Total BA (m ²)	16	35
Shannon H'	2.87	3.17
Species richness*	89 (94)	92 (96)
Chao2	161	118
Jackknife2	157	131
Morisita-Horn	0.255	

* Value presented is the species richness found within sampled area. In parenthesis, additional species noted outside of plots are included to present total observed species richness.

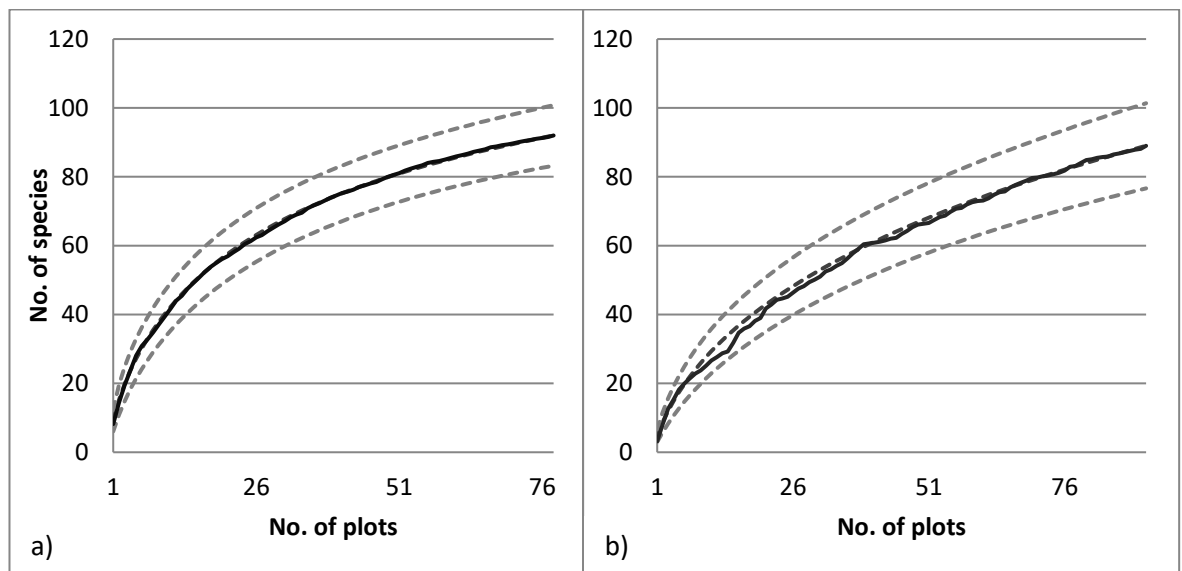


Figure 3.4: Species rarefaction curves for Waibira (a) and Kasongoire (b). Solid line=actual species richness; dark dashed line=rarefaction curve; light dashed line=confidence intervals.

Figure 3.4 shows the sample-based rarefaction curve with 95% confidence intervals and the actual species accumulation curve. Neither slope reaches an asymptote. The rarefaction curve for Kasongoire does not level off even after the full 91 plots and a single individual of a new species

was recorded in 44 percent of plots (n=40). The rarefaction curve for Waibira slope begins to level off towards the end of the sampling effort (78 plots), and much more so than that for Kasongoire. There was a much lower number of new plots where an individual of a new species was found at Waibira (n=24). The confidence intervals are also larger for Kasongoire, as shown by the dashed lines. Accordingly, the Chao 2 and second Jackknife estimated greater species richness at Kasongoire than at Waibira, contrary to Prediction 2 (Table 3.2). Tree species diversity (a measure of richness and evenness) was greater at Waibira however, supporting Prediction 3, with an H' Index of 3.17 at Waibira compared with 2.89 at Kasongoire.

Tree biomass

Average basal area (BA) per plot was significantly higher in Waibira than in Kasongoire (U=1637, Z=-4.979, p<0.001) with BA covering 35 m² ha⁻¹ at Waibira and 16 m² ha⁻¹ at Kasongoire, upholding Prediction 4. Average DBH for all trees was similar, although overall significantly higher at Waibira than at Kasongoire (U= 652152, Z=-6.669, p<0.001): mean DBH of all trees was 23.2 ±SD 20.3 cm at Waibira (range: 10.03-206.9 cm) and was 22.5 ±SD 14 cm at Kasongoire (range: 10.03-184.6 cm).

The distribution of stem sizes at both sites is shown in Figure 3.5. The majority of stems at both sites fell in the smallest DBH class: 61% of all stems at Kasongoire and 66% at Waibira were between 10-20 cm. Trees with very large stems were rare at Kasongoire: only three individuals measured over 100 cm DBH. The individual with the largest DBH at Kasongoire was an *Antiaris toxicaria* measuring 185 cm, and the other two individuals over 100 cm were *Pseudospondias microcarpa* (127 cm) and *Parkia filicoidea* (108 cm). At Waibira large trees were more common and of the 19 trees over 100 cm DBH, 12 were *Cynometra alexandrii*, the largest of which measured 207 cm. Other large individuals included *Pseudospondias microcarpa* (121 cm), *Alstonia boonei* (165 cm), *Khaya anthotheca* (181 cm) and three *Ficus* species.

Species composition

The family with the highest importance value at Kasongoire, Arecaceae, reflects the results of species importance: *Phoenix reclinata* dominates with 391 stems (34% of all stems) and a density of 107.4 stems per hectare. Similarly, at Waibira the high percentage of trees in the Ulmaceae family reflects the dominance of *Celtis spp.* (21% of all stems). Tables 3.4 and 3.5 present the results for the 20 most important species at each site.

Table 3.4: The 20 most important tree species at Waibira based on Species Importance Values (SIV), showing for each species: number of stems ≥ 10 cm found in all plots, percentage of plots the species occurred in, density and basal area (BA) per hectare, relative frequency (RF), relative density (RD) and relative dominance (RDo).

Species	Family	No. Stems	% Plots	Density ha ⁻¹	BA (m ²) ha ⁻¹	RF	RD	RDo	SIV
<i>Cynometra alexandri</i>	Fabaceae	95	61.5	30.4	9.6	6.7	6.4	27.2	40.3
<i>Celtis mildbraedii</i>	Ulmaceae	195	82.1	62.5	3.9	8.9	13.1	11.0	33.1
<i>Lasiodiscus mildbreadii</i>	Rhamnaceae	289	76.9	92.6	1.6	8.4	19.5	4.4	32.2
<i>Funtumia elastica</i>	Apocynaceae	151	67.9	48.4	1.5	7.4	10.2	4.3	21.9
<i>Rinorea ardisiaeflora</i>	Violaceae	121	43.6	38.8	0.5	4.7	8.2	1.5	14.4
<i>Celtis durandii</i>	Ulmaceae	48	38.5	15.4	2.3	4.2	3.2	6.6	14.0
<i>Celtis zenkeri</i>	Ulmaceae	60	39.7	19.2	0.9	4.3	4.0	2.5	10.9
<i>Alchornea laxiflora</i>	Euphorbiaceae	63	41.0	20.2	0.3	4.5	4.2	0.8	9.5
<i>Khaya anthotheca</i>	Meliaceae	16	17.9	5.1	1.4	1.9	1.1	3.9	6.9
<i>Margaritaria discoidea</i>	Euphorbiaceae	23	20.5	7.4	0.9	2.2	1.5	2.5	6.3
<i>Ficus sur</i>	Moraceae	20	16.7	6.4	0.9	1.8	1.3	2.5	5.7
<i>Alstonia boonei</i>	Apocynaceae	8	9.0	2.6	1.5	1.0	0.5	4.2	5.7
<i>Chrysophyllum albidum</i>	Sapotaceae	21	20.5	6.7	0.7	2.2	1.4	1.9	5.5
<i>Croton sylvaticus</i>	Euphorbiaceae	25	19.2	8.0	0.6	2.1	1.7	1.6	5.3
<i>Tapura fischeri</i>	Dichapetalaceae	22	24.4	7.1	0.2	2.6	1.5	0.4	4.6
<i>Trichilia prieuriana</i>	Meliaceae	18	20.5	5.8	0.1	2.2	1.2	0.4	3.8
<i>Ricinodendron heudelotii</i>	Euphorbiaceae	6	6.4	1.9	0.8	0.7	0.4	2.3	3.4
<i>Trichilia rubescens</i>	Meliaceae	19	14.1	6.1	0.1	1.5	1.3	0.4	3.2
<i>Ficus variifolia</i>	Moraceae	4	5.1	1.3	0.7	0.6	0.3	2.0	2.9
<i>Albizia glaberrima</i>	Fabaceae	7	9.0	2.2	0.5	1.0	0.5	1.4	2.8

Table 3.5: The 20 most important tree species at Kasongoire based on Species Importance Values (SIV), showing for each species: number of stems ≥ 10 cm found in all plots, percentage of plots the species occurred in, density and basal area (BA) per hectare, relative frequency (RF), relative density (RD) and relative dominance (RDo).

Species	Family	No. Stems	% Plots	Density ha ⁻¹	BA (m ²) ha ⁻¹	RF	RD	RDo	SIV
<i>Phoenix reclinata</i>	Arecaceae	391	53.8	107.4	3.1	11.2	34.3	19.2	64.7
<i>Pseudospondias microcarpa</i>	Anacardiaceae	98	50.5	26.9	2.6	10.5	8.6	16.2	35.3
<i>Macaranga schweinfurthii</i>	Euphorbiaceae	119	31.9	32.7	1.3	6.6	10.4	7.9	24.9
<i>Neoboutonia macrocalyx</i>	Euphorbiaceae	72	16.5	19.8	0.4	3.4	6.3	2.7	12.4
<i>Sapium ellipticum</i>	Euphorbiaceae	27	17.6	7.4	1.0	3.7	2.4	6.0	12.0
<i>Syzygium guineense</i>	Myrtaceae	33	17.6	9.1	0.9	3.7	2.9	5.4	12.0
<i>Funtumia africana</i>	Apocynaceae	35	23.1	9.6	0.4	4.8	3.1	2.2	10.1
<i>Bridelia micrantha</i>	Phyllanthaceae	33	16.5	9.1	0.3	3.4	2.9	1.9	8.2
<i>Ficus vallis-choudae</i>	Moraceae	21	9.9	5.8	0.6	2.1	1.8	3.7	7.6
<i>Antiaris toxicaria</i>	Moraceae	5	3.3	1.4	0.9	0.7	0.4	5.8	7.0
<i>Blighia unijugata</i>	Sapindaceae	20	14.3	5.5	0.3	3.0	1.8	1.9	6.7
<i>Pycnanthus angolensis</i>	Myristicaceae	14	14.3	3.8	0.3	3.0	1.2	2.0	6.2
<i>Trilepisium madagascariensis</i>	Moraceae	22	15.4	6.0	0.1	3.2	1.9	0.8	6.0
<i>Croton sylvaticus</i>	Euphorbiaceae	14	14.3	3.8	0.2	3.0	1.2	1.3	5.5
<i>Morus mesozygia</i>	Moraceae	10	6.6	2.7	0.4	1.4	0.9	2.4	4.6
<i>Tabernaemontana holstii</i>	Apocynaceae	17	9.9	4.7	0.1	2.1	1.5	0.5	4.0
<i>Myrianthus holstii</i>	Moraceae	22	5.5	6.0	0.1	1.1	1.9	0.8	3.8
<i>Parkia filicoidea</i>	Fabaceae	6	5.5	1.6	0.3	1.1	0.5	2.0	3.6
<i>Ficus sur</i>	Moraceae	10	11.0	2.7	0.1	2.3	0.9	0.4	3.6
<i>Voacanga thouarsii</i>	Apocynaceae	11	5.5	3.0	0.1	1.1	1.0	0.8	2.9

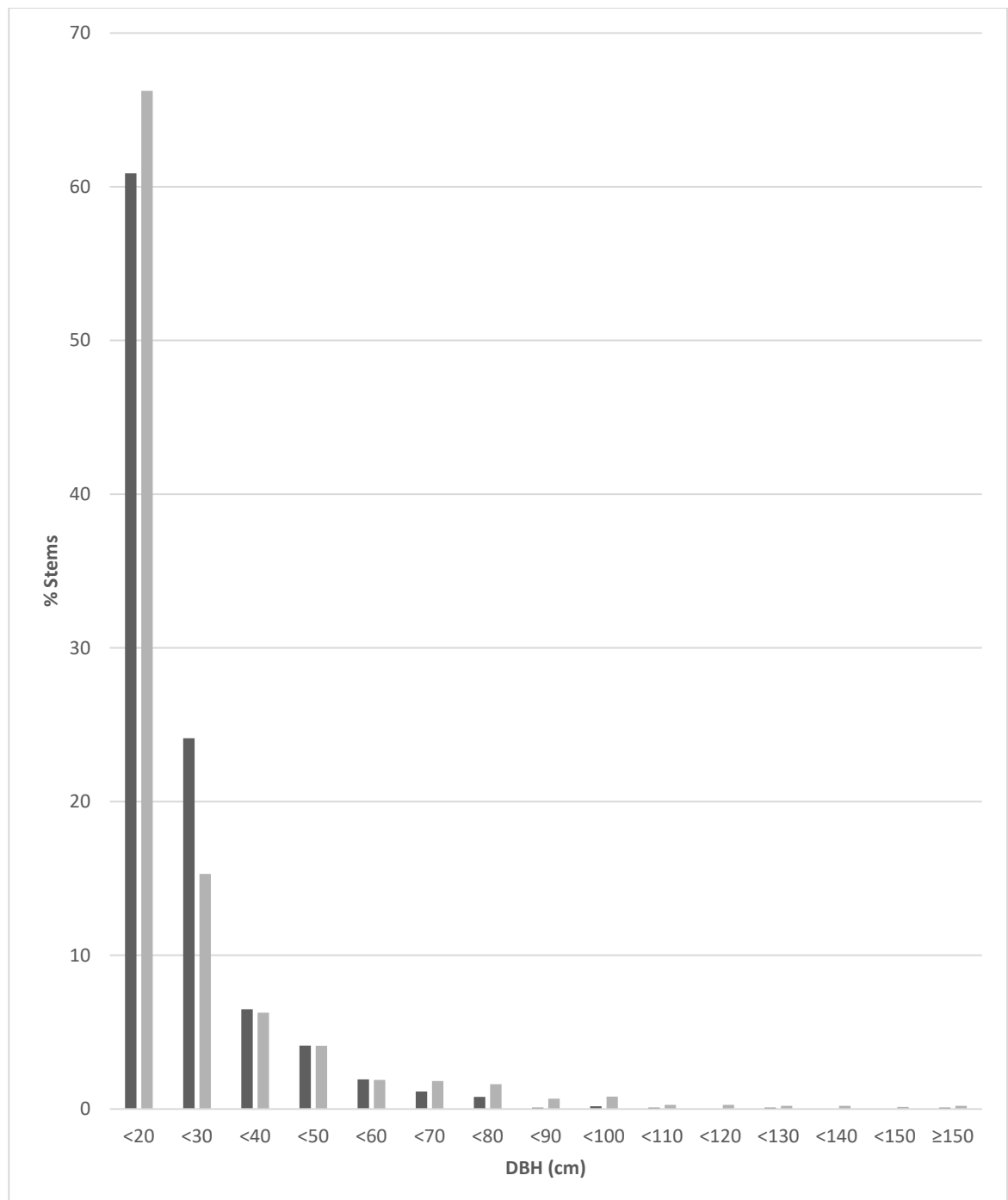


Figure 3.5: Distribution of stems in DBH classes; Kasongoire (dark grey) and Waibira (light grey).

Of the 15 Moraceae species found at Kasongoire, six occurred at very low densities in one plot with one or two single stems (five *Ficus* spp. and the naturalised alien species *Broussonetia papyrifera*). Therefore, while the number of species belonging to the Moraceae family is high, not all were common species, nine were *Ficus* species and 11 were observed feeding trees for Kasongoire chimpanzees during this study.

Table 3.6: The 10 most important tree families at Waibira and Kasongoire based on Family Importance Values (FIV), showing for each family: number of species and stems ≥ 10 cm, percentage of plots occurred, the density and BA ha⁻¹, relative diversity (RDi), relative density (RD) and relative dominance (RDo).

Family	No. Species	No. Stems	% Plots	Density ha⁻¹	BA (m²) ha⁻¹	RDi	RD	RDo	FIV
<i>Waibira</i>									
Ulmaceae	6	323	91.0	103.5	7.4	12.9	21.8	20.9	55.6
Fabaceae	7	114	71.8	36.5	10.9	10.2	7.7	30.9	48.8
Rhamnaceae	2	296	78.2	94.9	2.1	11.1	20.0	6.0	37.1
Apocynaceae	3	167	74.4	53.5	3.0	10.5	11.3	8.6	30.4
Euphorbiaceae	10	137	70.5	43.9	2.9	10.0	9.3	8.2	27.4
Moraceae	9	68	42.3	21.8	2.7	6.0	4.6	7.6	18.2
Violaceae	1	121	43.6	38.8	0.5	6.2	8.2	1.5	15.8
Meliaceae	8	61	43.6	19.6	1.9	6.2	4.1	5.3	15.6
Sapotaceae	6	46	33.3	14.7	0.9	4.7	3.1	2.7	10.5
Dichapetelaceae	1	22	24.4	7.1	0.2	3.5	1.5	0.5	5.4
<i>Kasongoire</i>									
Arecaceae	1	391	53.8	107.4	3.1	13.4	34.4	19.2	66.9
Euphorbiaceae	11	253	59.3	69.5	3.5	14.7	22.2	21.7	58.6
Moraceae	16	111	44.0	30.5	2.8	10.9	9.8	17.1	37.7
Anacardiaceae	1	98	50.5	26.9	2.6	12.5	8.6	16.2	37.3
Apocynaceae	5	65	34.1	17.9	0.6	8.4	5.7	3.6	17.8
Myrtaceae	1	33	17.6	9.1	0.9	4.4	2.9	5.4	12.7
Fabaceae	11	25	22.0	6.9	0.7	5.4	2.2	4.1	11.7
Phyllanthaceae	1	33	16.5	9.1	0.3	4.1	2.9	1.9	8.8
Sapindaceae	2	21	15.4	5.8	0.3	3.8	1.8	2.1	7.7
Myristicaceae	1	14	14.3	3.8	0.3	3.5	1.2	2.0	6.7

Table 3.6 presents the results for the 10 most important tree families. Moraceae had a much higher family importance value, number of stems, and density in Kasongoire than Waibira and of the 20 species with the highest species important values in Kasongoire, six belonged to the Moraceae family. At Waibira, only two of the 20 most important species belonged to the Moraceae family. Despite this, the basal area of trees in the Moraceae family was almost the same and the percentage of plots was comparable, indicating that at Kasongoire there was a

higher density of immature individuals. This was reflected in the difficulty of finding a minimum of 10 individuals of each species to monitor in phenology surveys at both sites, but particularly at Kasongoire (see section below, Table 3.8).

Habitat types

The habitat at Kasongoire is composed primarily of swamp forest (37.4%) and mixed forest (29.7%; Table 3.7). While mixed forest covered a smaller area of the total sampled habitat, it had a higher total BA than swamp forest, showing that larger trees were often found in this habitat type. At Waibira mixed forest dominated (83.3% total area). *Cynometra* forest was much patchier (as described by Plumptre, 1996), although BA per plot in *Cynometra* forest is considerably higher than mixed forest. Twelve plots at Kasongoire contained no trees at all; seven in papyrus swamp, one in ecotone forest, one in savannah-woodland and three were in cleared forest. At Waibira there were no plots without a single stem.

Table 3.7: Forest composition at Waibira and Kasongoire according to habitat type. PAP=papyrus swamp; MF=mixed forest; ET=ecotone forest; SF=swamp forest; SAV=savannah-woodland; CLE=Clearance; CF= *Cynometra* forest.

Habitat type	Waibira			Kasongoire					
	MF	CF	SF	PAP	MF	ET	SF	SAV	CLE
Species richness	86	31	34	4	45	13	37	3	3
% total stems	79.9	13.9	6.2	2.2	39.2	4.2	53.1	0.7	0.6
Avg DBH	23.0	22.5	26.0	23.8	23.5	24.7	20.4	15.9	19.6
±SD	±19.5	±20.6	±28.3	±15.5	±16.6	±18.8	±10.2	±5.6	±7.0
Plots/habitat	65	8	5	9	27	13	34	3	5
%Total area	83.3	10.3	6.4	9.9	29.7	14.3	37.4	3.3	5.5

3.3.3 Phenology

Overall ripe fruit availability of monitored species was higher at Kasongoire when comparing study months where data are available. At Kasongoire, all species produced fruit during the study period, with the exception of one species (*Trilepisium madagascariensis*) which was excluded from the analysis because it was represented by a single stem. At Waibira, six out of 14 monitored species did not produce ripe fruit during the monthly surveys: in five cases the trees were surveyed to have unripe fruits, but by the following month had finished fruiting, and one species did not produce any fruit at all. As a result, some species for which chimpanzees consumed the fruit yielded a ripe fruit score of zero across months. On average, 40% of surveyed trees produced ripe fruit each month at Kasongoire, compared with only 13% at Waibira (Figure 3.6). This is

reflected in the low fruit scores at Waibira (Figure 3.7). Table 3.8 presents a list of species monitored, the months with ripe fruit recorded as available and whether they were observed chimpanzee feeding species during this study.

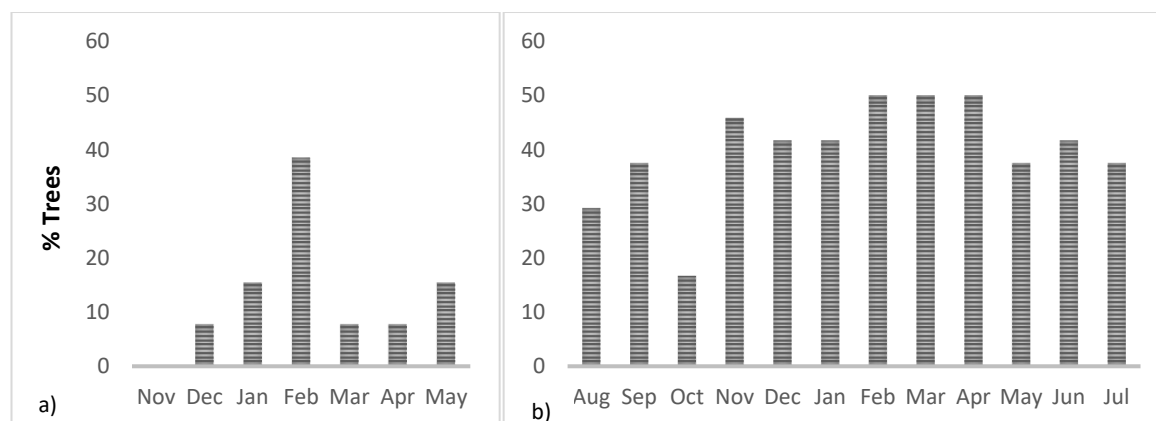


Figure 3.6: The percentage of surveyed trees which produced ripe fruit (having a ripe fruit score >0) over the study period at Waibira (a) and Kasongoire (b).

Waibira

Generally, a low level of fruit availability was recorded at Waibira during the period monitored. Fruiting of observed chimpanzee feeding species peaked in the dry season, with a spike in January (Figure 3.7) when *Cynometra alexandrii* was super-abundant. Moraceae availability remained low throughout the study months.

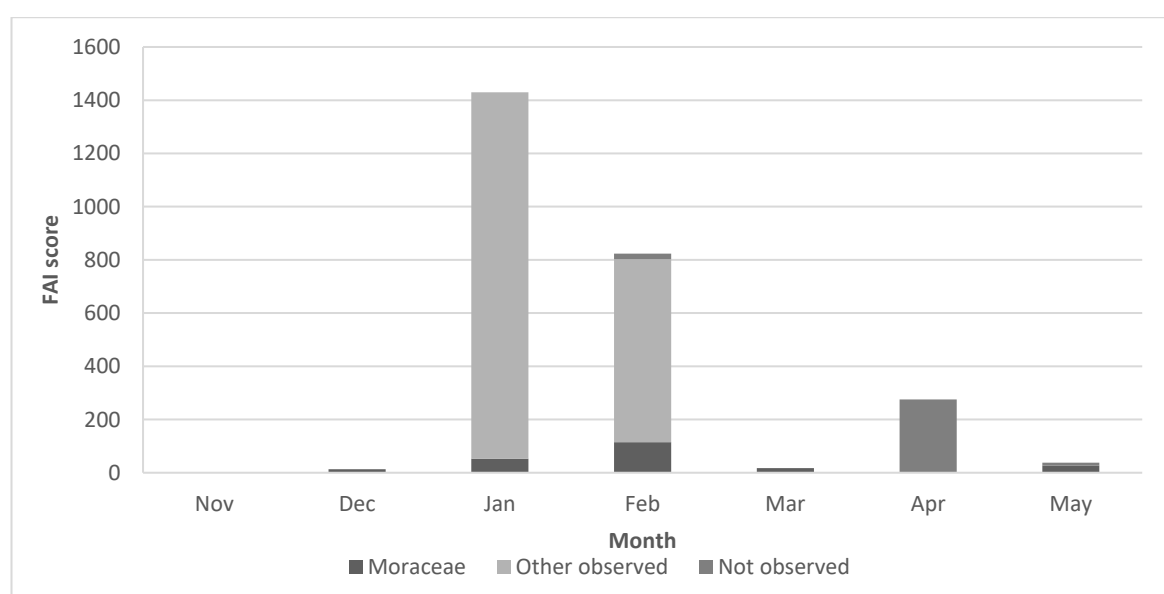


Figure 3.7: Total monthly ripe fruit availability scores at Waibira, broken down into: species from the Moraceae family ("Moraceae"), species (not Moraceae) that chimpanzees were observed feeding on ("other observed") and species that chimpanzees were not observed feeding on ("not observed").

Table 3.8: Trees monitored for fruit availability at Waibira and Kasongoire.

Site	Species	No. trees ¹	Months RF ²	Fruiting cycle ³	Fruit fed on? ⁴
Waibira	<i>Calconcoba schweinfurthii</i>	15	1	Annual	✗
	<i>Celtis durandii</i>	15	1	Continuous	✗
	<i>Celtis mildbraedii</i>	15	0	Annual	✗
	<i>Cola gigantea</i>	2	0	Annual	✗
	<i>Cordia millenii</i>	15	0	Annual	✓
	<i>Croton sylvaticus</i>	15	0	Sub-annual	✗
	<i>Cynometra alexanderi</i>	15	2	Sub-annual	✓
	<i>Ficus exasperata</i>	13	1	Asynchronous	✓
	<i>Ficus mucoso</i>	6	0	Asynchronous	✓
	<i>Ficus sur</i>	15	4	Asynchronous	✓
	<i>Ficus variifolia</i>	5	0	Asynchronous	✓
	<i>Maesopsis eminii</i>	15	0	Sub-annual	✗
	<i>Mildbraediodendron excelsum</i>	6	1	Annual	✗
	<i>Morus mesozygia</i>	2	2	Annual	✓
Total		154			
Kasongoire	<i>Aningeria altissima</i>	4	2	Annual	✓
	<i>Antiaris toxicaria</i>	9	4	Annual	✓
	<i>Cola gigantea</i>	9	8	Annual	✓
	<i>Croton sylvaticus</i>	10	2	Sub-annual	✗
	<i>Ficus bubu</i>	11	9	Asynchronous	✓
	<i>Ficus exasperata</i>	1	2	Asynchronous	✓
	<i>Ficus natalensis</i>	5	4	Asynchronous	✓
	<i>Ficus saussureana</i>	10	4	Asynchronous	✓
	<i>Ficus sur</i>	8	8	Asynchronous	✓
	<i>Ficus vallis-choudae</i>	10	10	Asynchronous	✓
	<i>Khaya anthotheca</i>	2	1	Annual	✗
	<i>Macaranga schweinfurthii</i>	8	4	Annual	✗
	<i>Maesopsis eminii</i>	10	5	Sub-annual	✓
	<i>Morus mesozygia</i>	12	4	Annual	✓
	<i>Myrianthus holstii</i>	10	4	Asynchronous	✓
	<i>Parkia filicoidea</i>	8	3	Annual	✓
	<i>Phoenix reclinata</i>	10	9	Continuous	✓
	<i>Pseudospondias microcarpa</i>	10	7	Sub-annual	✓
	<i>Pycnanthus angolensis</i>	8	11	Continuous	✗
	<i>Sterculia dawei</i>	4	4	Annual	✓
	<i>Syzygium guineense</i>	10	1	Annual	✓
	<i>Trilepisium madagascariensis</i>	1	0	Sub-annual	✗
	<i>Voacanga thouarsii</i>	10	9	Sub-annual	✗
Total		180			

¹Number of trees surveyed during the final month. Range 127-180 (Kasongoire only); the same number of trees were monitored at Waibira each month (154).

²Number of monthly surveys ripe fruit (RF) were recorded.

³Defined according to Newstrom et al. (1994): Annual=one major fruiting cycle in 12 months; Sub-annual=more than one fruiting cycle in 12 months; Continuous= unripe or ripe fruit produced year-round with breaks lasting <1 month; Asynchronous= fruits irregularly year round (predominantly *Ficus* spp.).

⁴Based on observations (direct and feeding traces) during this study.

Kasongoire

Phoenix reclinata is by far the most abundant species in Kasongoire (Table 3.5). However, the high density of this species heavily influenced the overall fruit availability values meaning that one individual tree of *P. reclinata* with a low level of ripe fruit (e.g. score of 1) significantly increased the overall FAI when extrapolating the FAI score for all species across the study area. To illustrate this, Figure 3.8 displays the ripe fruit scores, with *P. reclinata* displayed separately. Including all observed feeding species, fruit availability peaked in November. However, if *P. reclinata* was excluded as a result of its hyper abundance, FAI scores of chimpanzee feeding species were highest in February.

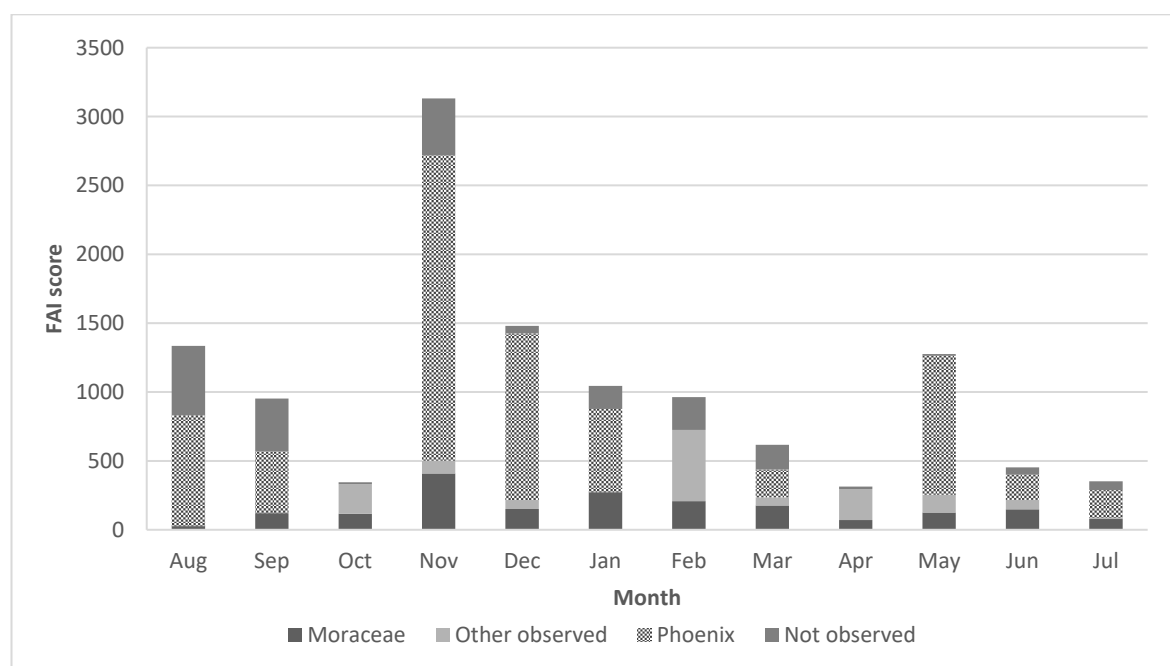


Figure 3.8: Total monthly ripe fruit availability scores at Kasongoire, broken down into: species from the Moraceae family ("Moraceae"), species (not Moraceae) that chimpanzees were observed feeding on ("other observed"), *Phoenix reclinata* ("Phoenix") and species that chimpanzees were not observed feeding on ("not observed").

3.4 DISCUSSION

3.4.1 Chimpanzee home ranges

From the results of both the minimum convex polygon and fixel kernel analyses, Kasongoire chimpanzees were found to use a larger total home range area than those at Waibira, a result of less frequently visited areas outside the main forest block at Kasongoire being spatially segregated due to the nature of the fragmented landscape. Waibira chimpanzees utilised a larger core area than did those in Kasongoire, likely due to the limited area within the forest at Kasongoire. This could be explained by the fact that chimpanzees at Waibira must find resources over a larger range within the continuous forest block, whereas Kasongoire chimpanzees are restricted to the riverine strip which they generally re-use regardless of resource availability, with small parties travelling considerable distances on rare occasions.

Chimpanzee home range analyses for both Waibira and Kasongoire using fixed kernel analysis returned small values as compared with previous studies, particularly at Kasongoire. At Waibira, comparing the results with the neighbouring community there is a remarkable level of similarity between the two home range sizes: adult male chimpanzees at Sonso were found to have a total home range of 6.89 km² (Newton-Fisher 2003) and core range of 1.48 km² using fixed kernel analyses. When running the analysis using MCP, the results for Waibira chimpanzees' total home range area returned similar results. This implies that the Waibira total home range value may be genuinely representative of the chimpanzees' habitat use, although there are more chimpanzees in the Waibira community than Sonso, meaning I would have expected them to use a larger area. Additionally, the 6.89 km² range of Sonso chimpanzees is the smallest reported chimpanzee home range of all studies (Table 3.9 for a comparison of chimpanzee home range sizes in long-term study sites).

For Kasongoire chimpanzees, their total home range area appears to be much smaller than expected when using FK, despite a large sample size: with the exception of Newton-Fisher's (2003) study in Sonso, it is the smallest home range reported across study sites (Table 3.9). However, when comparing homerange size of chimpanzees at Kasongoire to that found at Bulindi using MCP, it appears that Kasongoire chimpanzees range over a similar total area to those in neighbouring forest fragments: McLennan (2010) reported overall confirmed home range size of 21 km² and a core range of 4.6 km² for chimpanzees at Bulindi, very similar results to those reported in this study. Additionally, the 100% MCP home range results of this study are not

particularly unusual when comparing to those recorded for fragment chimpanzees in Cantanhez, Guinea-Bissau (Vieira et al. 2019).

Table 3.9: Chimpanzee home ranges and community sizes of study sites across Africa. Table modified from Morgan et al. (2006), Bertolani (2013) and Vieira et al. (2019).

Site	Comm.	Method ²				Source
	Size ¹	MCP	FK	GC	Oth	
<i>Kasongoire</i>	42	24.9	2.2	-	-	<i>This study</i>
<i>Waibira</i>	80	6.1	4.7	-	-	<i>This study</i>
Bulindi	25 [^]	21	-	-	-	McLennan 2010
Cadique-Caiquene	35 [^]	-	-	-	7.9	Bessa et al. 2015
Fongoli	32	-	-	-	63	Pruetz 2006
Gombe	23*	-	-	13	-	Wrangham & Smuts 1980
Goualougo	54	19.2	17.3	-	-	Morgan et al. 2006
Kahuzi-Biega	23	-	-	12.8	-	Basabose 2005
Kibale - Kanyawara	41	14.9	-	8.5	-	Chapman & Wrangham 1993
Kibale - Kanyawara	50	37.8	-	-	-	Wilson et al. 2007
Kibale - Kanyawara	48	27.4	16.2	26	-	Bertolani 2013
Kibale - Ngogo	143	27.7	19.5	29.3	-	Amsler 2009
Madina	-	19.5	8.5	15.5	-	Vieira et al. 2019
Mahale	-	19.4	-	-	-	Nishida 1979
Sonso	56	9.7	9.2	-	-	Fawcett 2000
Sonso	42	6.8	6.9	-	-	Newton-Fisher 2003
Tai (1982)	74	18.1	-	-	-	Boesch & Boesch-Achermann 2000
Tai (1989)	66	23.7	-	-	-	Boesch & Boesch-Achermann 2000
Tai (1995)	29	15.5	-	-	-	Boesch & Boesch-Achermann 2000
Tai (Northern)	35	10.5	-	-	-	Herbinger et al. 2001
Tai (Middle)	11	9.0	-	-	-	Herbinger et al. 2001
Tai (Southern)	63	13.5	-	-	-	Herbinger et al. 2001

¹Number of individuals in the community including all age/sex classes, except entries with a * denoting independent individuals only. [^]Denotes estimated community size (non-habituated).

²Method of analysis: MCP=Minimum convex polygon; FK=Fixed kernel (95%); GC=Grid cell; Oth=Other, including faecal and feeding traces.

It is important to note that in a highly fragmented habitat, using MCP as a method of home range analysis will dramatically increase the size of the range size since the area under the polygon from

the furthest points are included in the estimation (Powell 2000; Vieira et al. 2019). However, chimpanzees do occasionally travel to areas between forest fragments since they are highly mobile in the matrix. This highlights a benefit of using multiple methods for the sake of comparison, even if it is difficult to use an analytical method which produces values that are reflective of the true home range size.

3.4.2 Forest composition

Forest species composition varied considerably between Kasongoire and Waibira habitats, which was expected considering the two forest types are different, regardless of influences from human activities. The Morisita-Horn Index returned a low value of species overlap between the two study sites, providing a similar value to the comparison made between nearby Bulindi and Budongo (Bulindi-Budongo $MH=0.238$: McLennan & Plumptre 2012; this study= 0.255).

Species richness recorded in sample plots was similar between sites with 92 species recorded in plots in Waibira and 89 in plots in Kasongoire, a result contrary to the prediction that Kasongoire, as a human-impacted and heavily fragmented habitat, would have fewer species than the protected site in continuous forest. Regarding total predicted species richness, the Chao 2 and second-order Jackknife values both returned larger estimates of actual species richness for Kasongoire (161 and 157 respectively) than Waibira (118 and 131 respectively). While this is contradictory to Prediction 2, this makes sense considering the high number of plots where just one individual was found of a new species at Kasongoire: the way rarefaction works is to keep plotting higher estimates based on the rate new species are found within plots. This explains why the rarefaction curve did not reach an asymptote at Kasongoire and suggests that the majority of plots there generally contained fewer species than plots at Waibira, and that many species were rare. This may be expected in a human-impacted habitat where larger trees are rarer and where certain species may have been targeted for extraction. Hill and Curran (2001) found a strong relationship between forest size and the number of rare species, with larger forest blocks containing a much higher density of rare species. Habitat fragmentation will inevitably lead to a certain number of species becoming rare through forest loss in itself, but naturally rarer species and larger stems may be under the additional threat of being selectively targeted by loggers. For example, mahoganies were rare at Kasongoire (*Khaya* spp.), as well as the species *Cordia milenii*, and will likely be logged when or even before they reach maturity since they are extremely valuable (see Section 3.4.4 below for further discussion on this).

Budongo has the highest species diversity of any forest within the Albertine Rift (Plumptre et al. 2003, 2007); therefore results from this study where species richness estimates for Kasongore surpassed those for Waibira may still seem surprising. McLennan and Plumptre (2012) report overall species richness at Budongo to be much higher than this study, finding 150 species. One reason for this difference will be due to sample size: results from McLennan and Plumptre (2012) are based on a sample of 5581 stems from a forest-wide survey, compared to 1484 stems in this study. However, it is likely true that within the Waibira chimpanzee community home range the forest is a relatively uniform habitat as compared to Budongo Forest as a whole. The forested area of Budongo Forest Reserve covers a vast 482 km² and includes a variety of habitat types. Over ten percent of the habitat within the Waibira home range was *Cynometra* forest, which is expected to be naturally less species-rich, since this late successional stage forest will be dominated by *Cynometra alexandrii* (Eggeling 1947).

Colonising species not found in other interior forest types will also increase the number of new species in plots at Kasongore, compared to Waibira. Since the shape of the forest at Kasongore is long and narrow with a forest width of only around 200 m, the large edge area likely influences species composition. Tree density at the forest edge may sometimes be higher than in interior forest since disturbance creates ideal conditions for colonising species (see Murcia 1995 for a review), although forest fragmentation as a rule is known to result in tree species loss (Hill & Curran 2001; Laurance et al. 2002; Oliveira et al. 2004).

Additionally, there was more variety in habitat types at Kasongore than Waibira which may in part explain more new species being found as sampling effort increased at Kasongore. As happened at Bulindi, as additional plots were established in forest patches further from the chimpanzees' core range, the number of new species increased (McLennan 2010). For McLennan (2010) this was because these plots were in a new habitat type (primarily forest-grassland ecotone). Similarly, in Kasongore, the majority of plots were in mixed and swamp forest, habitat types which comprised the majority of the overall habitat, with later plots established in forest patches much further away from the chimpanzees' core range. For this reason, savannah-woodland areas were hardly sampled: only three plots were established in this habitat type because chimpanzees were not followed there and these areas were separated from the forest by villages, although some patches were within the main forest block and therefore fell within the sampling area. The forest edge at Kasongore is at a slightly higher altitude since the riverine forest gently slopes towards the stream, meaning that species recorded at the edge may also

include those found in savannah-woodland habitats. Outside of the forest boundary savannah-woodland habitat is common, primarily on the hill and in areas surrounding the road. Species found in savannah-woodland are often different to those in the riverine forest as they have adapted to a drier environment, so it is unsurprising to discover additional species in this habitat. In Kasongoire these include species such as *Vitex doniana*, *Annona senegalensis* and *Combretum molle*. At Bulindi, McLennan (2010) also found an increase in the number of species as savannah-woodland was included in additional plots. However, at Kasongoire new species were also recorded in plots in mixed and swamp forest, which helps to explain why the graph fails to reach an asymptote by the full 91 plots: of the 40 species which were found in just one plot, 11 of these were in the additional plots.

At Kasongoire, estimated total species richness was found to be much higher than in neighbouring Bulindi where McLennan (2010) reported an expected species richness of 91 and 103 from the Chao 2 and second-order Jackknife respectively. Bulindi has incurred a high level of recent forest loss (McLennan & Plumptre 2012) and situationally shares a lot in common with Kasongoire in that forest fragments there are privately owned and surrounded by agriculture. It is of concern that if forest area keeps declining at Kasongoire, it is likely that rarer trees will continue to be lost, which will reduce species richness and diversity in this habitat as well as the loss of potential food sources for chimpanzees.

The Shannon-Weaver Diversity Index at Waibira was higher than that found at Kasongoire, as expected (Prediction 3). Since species richness was found to be similar between sites but slightly higher at Kasongoire, this suggests a higher level of evenness in forest composition at Waibira, possibly due to the super-abundance of *Phoenix reclinata* at Kasongoire. Both sites were found to have lower recorded species diversity than reported at Bulindi and Budongo (McLennan & Plumptre 2012). In Sulawesi, Riley (2007) also found higher species diversity in the disturbed site as compared to minimally altered forest, although the disturbed habitat contained a lower density of key food species.

Moraceae was the third most important family in Kasongoire behind Arecaceae (comprised solely of *P. reclinata*) and Euphorbiaceae, and was the sixth most important family in Waibira. At Bulindi, Moraceae had the highest density of any family, in part due to the high density of *Trilepisium madagascariensis*, as well as, but to a lesser degree, *Antiaris toxicaria*. It is interesting that while *T. madagascariensis* was present at Kasongoire, it was found in just 6% of plots, as compared with

60% at Bulindi. Comparing with McLennan and Plumptre's (2012) findings, while there is a pattern of similarity in forest composition overall between Kasongoire and Bulindi forests, the closer proximity of Kasongoire to Budongo as compared to Bulindi may have an influence on forest composition, increasing the similarity between the two sites.

Interestingly, species richness within Moraceae was much higher in the fragmented (16 species) than continuous forest (nine species), and of the top 20 most important species, five at Kasongoire were in the Moraceae family compared with just two at Waibira. Similarly, in Kibale National Park, a study showed Moraceae density to be highest at the most disturbed of the three chimpanzee research sites there (Bortolamiol et al. 2014). However, while this would seem to suggest that Kasongoire may have high quality feeding species for chimpanzees, it is worth noting that the overall basal area for this family was almost equal at both sites, yet Moraceae stem density was almost double at Kasongoire. This means that there are significantly more (and potentially double) the number of large stems (and therefore fruit-bearing trees) in the Moraceae family within the Waibira chimpanzee home range.

3.4.3 Phenology

In this study, Waibira followed the trend from Bulindi and Sonso (McLennan 2013; Fawcett 2000; Twheyo & Babweteera 2007) in that fruit of chimpanzee feeding trees peaked during the drier months, January and February, and was scarce during wetter months. At Kasongoire, this pattern was harder to distinguish as a result of the strong influence of *Phoenix reclinata*. However, when *P. reclinata* is excluded, Kasongoire also showed a peak in fruiting of observed species during February, in the dry season.

McLennan (2013) notes that for many fig species (with the exception of *Ficus sur*), only large trees, measuring more than 30 cm DBH, produce fruit. Overall Moraceae density was slightly higher at Kasongoire as was found at Bulindi compared to Budongo (McLennan & Plumptre 2012), yet basal area was higher at Waibira suggesting that the overall amount of available fruit may be greater at Waibira. Despite this, the data indicate that fruit availability was relatively high in the unprotected forest at Kasongoire but appeared to be relatively low during the seven month monitoring period at Waibira (outside of *Cynometra* season). However, with only seven months of available data at Waibira rather than an annual cycle and with a low sample of observed chimpanzee feeding species monitored, it is important to interpret these results with caution.

The high density and importance value of *C. alexandrii* in Waibira shows how dominant this species is in Budongo Forest, in accordance with previous surveys (Eggeling 1947; Paterson 1991), despite having been specifically targeted by arboricide treatment in the 1950s and 1960s (Plumptre 1996). The majority of stems were found in mixed forest, indicating that perhaps that some parts of forest are maturing to a later successional stage: Eggeling (1947) describes the successional sequence to pass from colonising forest to mixed forest to *Cynometra*-dominated forest. Mixed forest in Waibira in particular was extremely species rich, containing 93% of sampled species. While the arboricide treatments increased the area of mixed forest and in turn the species richness and density of fruit species including *Ficus* spp. (Plumptre 1996; Tweheyo & Lye 2003), chimpanzees also feed heavily on *C. alexandrii* when it fruits (Hunt & McGrew 2002; Newton-Fisher 1999). If some areas of the forest within the Waibira chimpanzee home range are becoming increasingly dominated by *Cynometra* forest, it is possible in the future that there will be even higher high food availability in the months when *C. alexandrii* is ripe, but at other times of the year other fruit may become scarce.

In a review of over 100 studies providing phenological data in primate research, van Schaik and Pfannes (2005) found that fruiting seasonality could not be predicted by rainfall or sunshine, whereas leaf flushing and flowering were. Other studies in similar forests in Uganda show fruiting peaks occur during drier months: in a study reporting phenology data over 73 months in Budongo, Tweheyo and Babweteera (2007) found that the average quantity of fruit was higher during drier months, although fewer trees produced fruit. However, they also reported a positive relationship between the number of tree species producing fruit and rainfall, suggesting that predicting periods of fruit scarcity is not clear cut. More than one study in the neighbouring Sonso home range in Budongo Forest has found the dry season to be a period of lower fruit abundance (Newton-Fisher 1999; Tweheyo & Lye 2003). Similarly, a recent study comparing flowering and fruiting cycles across long-term sites across the African tropics found fruiting to peak equally in both wet and dry seasons (Adamescu et al. 2018).

Previous studies have found considerable inter-annual variations in fruit production, with some tree species known to produce fruits only every two years, or sometimes longer (Chapman et al. 1997, 1999, 2005). It is possible that the duration of my study saw a particularly lean period for Waibira chimpanzees, although the short length of phenology monitoring in this study means that it is difficult to make any solid interpretations on this. Trees in East African forests show a high level of diversity in fruiting cycles, including sub-annual, annual and supra-annual (Adamescu et al.

2018), as can also be seen in the forests at both Waibira and Kasongoire (Table 3.8). However, with 50% of monitored trees exhibiting an annual fruiting cycle in this study (that is, they commonly produce fruit predictably on a seasonal basis once per year), it is strange that the phenology results at Waibira were low. Additionally, fruits were barely recorded from some species that were expected to fruit continuously at Waibira; namely, *Celtis durandii*, recorded previously to produce fruits year-round in both Budongo and Kibale forests (Chapman et al. 1999; O'Driscoll Worman & Chapman 2005; Tweheyo & Babweteera 2007) produced ripe fruits during only one month of this study. This species was fed on extensively by chimpanzees during the pilot phase of this study but not once during the main data collection period, implying the genuine absence of fruit for this important chimpanzee feeding tree. With no complementary data on environmental factors such as rainfall or temperature, it is not possible to elucidate the possible reasons for the low phenology scores at Waibira, although elements of study design and data collection will have impacted the results to a certain degree.

3.4.4 Study limitations

The low sample size of phenology trees was a problem in this study, particularly at Waibira: only seven species which were observed being fed on by chimpanzees were monitored. Chimpanzees were observed feeding on ripe fruit from 17 species (Chapter 4) highlighting that additional species could have been monitored. As a result, the data likely do not reflect the true level of food availability for Waibira chimpanzees. As mentioned above, there were many low and zero values for ripe fruit scores even for chimpanzee feeding trees, suggesting that overall fruit availability may have simply been low in this habitat during the study period, although monthly surveys (rather than bi-weekly) can miss ripe fruit events. Phenology data at Waibira were not available for the first few months of the study due to logistical issues which will have an impact on the overall results since phenology data on important chimpanzee feeding trees, such as *Cordia milenii*, were missed entirely. Phenology data from the neighbouring Sonso home range were not used as it was considered that too much potential for inter-individual variation in fruiting among species might lead to errors in the data (e.g. Chapman et al. 1999). Janmaat et al. (2016) also report that a species could return a high fruit availability index score in one area, while being absent or scarce in the neighbouring area.

3.4.5 Implications of forest loss for chimpanzees

From published and anecdotal evidence and through personal observation during the study, some fundamental differences exist between the habitats within the Sonso and Waibira chimpanzees' ranges. The Sonso community is situated in and around the location of the old saw mill, the centre of which was previously cleared for the mill itself as well as staff quarters, some of which is now the current BCFS research station. A large proportion of the previously cleared area is now dominated by dense scrubby vegetation, most notably *Lantana camara*, and invasive shrub, and *Broussonetia papyrifera*, an exotic tree originally planted for paper pulp. These species are widespread in the core range area of Sonso chimpanzees, but were expected to be absent or rare within the Waibira home range.

The high density of trees at Waibira, along with the large basal area, suggests that despite decades of selective logging in Budongo forest, the forest has recovered to a certain degree. In the same way as in Kibale, forest with a history of low logging intensity had a much more similar vegetation structure to that of highly logged forest, where there was significantly less canopy closure and three times fewer trees measuring over 50 cm in DBH (Sekercioglu 2002). While overall stem density was much lower at Waibira, basal area was significantly higher. This highlights the impact that recent forest loss and targeting of larger individuals has had on forest structure at Kasongore and also shows that, despite extensive timber extraction at Budongo over the best part of 50 years, forests can regain biomass once left untouched. Further encroachment of the forest and selective logging at Kasongore will only exacerbate the loss of large stems. Unfortunately, small-scale deforestation in unprotected forests is often legal since most forest fragments are privately owned. Even in the case of an illegal logging incident (i.e. without the landowner's permission, or within 30 m of a water source - a stream or swamp in the case of Kasongore) there is extremely little law enforcement. Additionally, the enforcement in place (if effective) would be retrospective and likely not prevent the logging from taking place, meaning the damage to the forest composition is already done.

The fruit of *Cordia* spp. (and *Cordia millenii* in particular) is an important fruit species for chimpanzees and its regeneration relies primarily, or perhaps even solely, on seed dispersal by chimpanzees (Babweteera 2009; Reynolds 2005). In Waibira, only five *C. millenii* stems were found in plots, but a few additional large specimens measuring over 100 cm DBH were known chimpanzee feeding trees and did not fall within the sample plots. Conversely, only one stem of *C. millenii* was found in the core range of the Kasongore community. Although it was not yet mature

enough to bear fruit, it was cut down during the course of the study, as was also the case at Bulindi during the course of McLennan & Plumptre's study (2012). Similarly, two individual stems of *Cordia africana* were found in Kasongoire, and a large individual had been cut down in an active pit-sawing site at the commencement of the main study period. While these species were originally common in the area (*C. millenii* more in old-growth forest and *C. africana* around rivers and streams: G. Erickson, 2015, pers. comm.), unfortunately they are a commonly sought after timber species in the area currently. The species is preferred for boat building over that of other species since the wood is durable in water and Lake Albert is close by (Kityo & Plumptre 1997; Reynolds 2005). During this study loggers were discovered in the middle of the night felling *C. millenii* within 500 metres of BCFS camp and arrested (pers. obs.).

Ficus mucoso was not recorded in Kasongoire, with the last known specimen felled during the pilot study (November 2014). At Bulindi 12 stems were monitored for phenology and five stems were recorded in plots, although only one mature stem remains today (M. McLennan, 2017, pers. comm.). At Waibira four individuals were found in plots with only one large stem, but at least three other large specimens (DBH >150 cm) were known in the home range. *F. mucoso* is a known important feeding tree for chimpanzees as a food resource (Newton-Fisher et al. 2000; Watts et al. 2012a) and as an emergent tree with a wide crown diameter which can support large party sizes (Tweheyo & Lye 2003). This species may go two or three years without fruiting (Tweheyo & Lye 2003), but two of the known trees in the Waibira home range did produce ripe fruit during the study, so this does not explain the low fruit availability.

Ficus exasperata, *Morus mesozygia*, *Pseudospondias microcarpa* and *Strychnos mitis* were found in low densities in plots at Waibira. These trees tended to be clumped in the same patch and only found in one or two known areas of the chimpanzees' home range. While these species may have been found in low densities in this habitat, they are important chimpanzee feeding trees (McLennan 2013; Mitani et al. 2002). Guava trees (*Psidium guajava*) were observed at both sites but not recorded in plots at Kasongoire. These trees have become naturalised throughout large parts of Africa (Richardson 1998) and can be found in varying densities in patches of the forest. In Waibira, they had colonised the edge of old roads that ran through the forest for the old sawmill or roads that had been cut for tourism. At Bulindi, this exotic species was one of the chimpanzees' most important feeding species (McLennan 2013).

While Kasongoire may exhibit a high level of plant species diversity for a human-impacted and degraded habitat, Lindborg and Eriksson (2004) warn that there may be a 50 to 100 year time lag between habitat loss and the loss of plant species diversity. Therefore, it will be vital in Kasongoire and other similarly human-impacted forest habitats not just to halt or minimise any further forest loss but to invest in forest monitoring and reforestation projects. With the surrounding matrix consisting purely of crops, much of which is intense commercial monoculture plantation, the remaining forest is likely to experience strong negative edge effects and natural regeneration is unlikely without human intervention and management (Laurance et al. 2002). Since rare trees were uncommon at Kasongoire, the outlook for forest regeneration is not very positive: it is probable that large, less common species will become locally extinct as a result of future deforestation and low recruitment rates for older, large-seeded trees following habitat loss (Vellend 2003). Additionally, rare species may be out-competed by pioneer species following forest loss: Laurance et al. (2006) found that the density of early successional species tripled in forest fragments at around 15 years following the fragmentation event. Recent and ongoing deforestation at Kasongoire could therefore lead to further changes in forest composition in the coming decades, including the expansion of ecotone forest. Further to this, the fire-resistant invasive shrub, *Lantana camara*, which is persistent in this area, is often found pioneering edge zones and out-competing tree species.

CHAPTER FOUR

DIETARY FLEXIBILITY OF CHIMPANZEES IN A HUMAN-IMPACTED HABITAT AND A PROTECTED FOREST



Plate 17 (on previous page): A subadult male (BLY) foraging on the pith of mature sugarcane in the open gap between the forest edge and sugarcane plantation.

4.1 INTRODUCTION

In Chapter 3, I demonstrated that tree species composition was very different between the forests at Kasongoire and Waibira. This, along with exposure to cultivated areas, suggests that the diets of chimpanzees at each site are expected to show a certain level of variation. Particularly where animals persist in human-impacted habitats, it is imperative to document their diets and feeding strategies, since the loss of important food sources may have detrimental effects on the health and survival of a population.

Increasingly, studies have examined the impact of habitat fragmentation on feeding ecology, since anthropogenic changes to the habitat will have an impact on the availability of preferred feeding resources (Bessa et al. 2015; Donati et al. 2011; Hockings et al. 2009; McLennan 2013; Riley 2007). Animals will have to adapt their feeding strategy to incorporate alternative foods (wild or cultivated) in order to fulfil their energetic and nutritional requirements, including during periods of wild food scarcity. Feeding behaviour is therefore an important aspect of an animals' socio-ecological profile, since this will directly influence time budgets and ranging, and animals may have to enter risky anthropogenic habitats if their feeding strategy involves accessing human-grown foods. Ultimately, understanding how forest fragmentation affects species in different sites can help to tailor conservation strategies to ensure their survival.

Here I describe the feeding behaviour of chimpanzees in the Kasongoire and Waibira communities, focussing on the contribution of different food species and assess the influence of fruit availability on the level of dietary diversity. At Kasongoire, where chimpanzees have access to crops, including year-round access to sugarcane, the influence of foraging on this large-scale monoculture crop is examined.

4.1.1 Feeding strategies

Habitats in human-modified landscapes that have been deforested will likely have a reduced number and variety of potential feeding resources available for wild animals (Arroyo-Rodriguez & Mandujano 2006; Hill & Curran 2001; Fischer & Lindenmayer 2007; Turner 1996). As a result, habitats in human-modified landscapes may be regarded as lower quality than more pristine forest (Arroyo-Rodriguez & Mandujano 2006), although anthropogenic disturbance does not necessarily result in a lower quality habitat (Chapter 3). Human-impacted habitats may also

provide feeding resources (i.e. crops) which are unavailable to animals in a non-impacted forest setting.

Where anthropogenic resources are available, species across the Order Mammalia are known to incorporate human cultivars into diets (e.g. roe deer (*Capreolus capreolus*): Putman 1986; bush pigs (*Potamochoerus porcus*) and pourcupines (*Hystrix cristata*): Hill 1997; Naughton-Treves et al. 1998; Tweheyo et al. 2005; African elephants (*Loxodonta africana*): Jackson et al. 2008; Osborn 2004; Asian elephants (*Elephas maximus*): Kumar et al. 2017; Sukumar 1990) or exploit human resources such as garbage (e.g. Florida black bears (*Ursus americanus floridanus*): Noel & Pienaar 2017; yellow baboons (*Papio cynocephalus*): Altmann & Muruthi 1988; raccoons (*Procyon lotor*): Prange et al. 2004; wolves (*Canis lupus*): Meriggi & Lovari 1996). Many primate species are known to exhibit some level of dietary flexibility, allowing them to diversify their diet and potentially exploit resources in human-modified landscapes (McLennan et al. 2017). For example, howler monkeys (*Alouatta* spp.) which are primarily folivores, have proven to be extremely flexible in their diet, allowing them to persist in forest fragments across the meso/south American continent (Chaves & Bicca-Marques 2013).

For species in human-impacted habitats, dietary flexibility may be crucial for survival. Seasonal differences in fruit availability will determine behavioural and often physical responses in primates, among other taxa (Hemingway & Bynum 2005; Robbins & Hohmann 2006). However, when fewer preferred foods are available, due to either forest loss, natural periods of fruit scarcity, or both, species will need to adapt their foraging strategies, either expanding their range to locate preferred foods, or diversifying their diet, often consuming a higher breadth of foods of lower nutritional quality (Altmann 1998; Harrison & Marshall 2011; Lambert 2007; Marshall & Wrangham 2007; Schoener 1971).

Primates in human-impacted habitats such as forest fragments have sometimes been reported to exhibit lower dietary diversity than those in more pristine habitats (Irwin 2008; Ménard et al. 2014; Riley 2007). Collared lemurs (*Eulemur collaris*) in fragments exhibited slightly higher dietary diversity than those in more intact forest, although they spent less time feeding on preferred fruits (Donati et al. 2011). Similarly, Dunn et al. (2010) found that mantled howler monkeys (*Alouatta palliata mexicana*) in a small forest fragment fed on significantly larger variety of species and from smaller trees than those inhabiting a large fragment, and their feeding effort greatly increased during periods of fruit scarcity. Interestingly, even specialised primates have

been found to exhibit dietary flexibility: Bale monkeys (*Chlorocebus djamdjamensis*), which are specialised bamboo consumers endemic to the Ethiopian highlands, were found to respond to lower habitat quality and food availability in fragmented forest by diversifying their diets (Mekonnen et al 2018). Diademed sifakas (*Propithecus diadema*) in forest fragments fed more on fallback foods compared to those in continuous forest, which fed on rare fruit trees throughout a large home range (Irwin 2008). In all of these studies, authors found that human-impacted habitats were of lower quality with reduced species richness than their less-affected counterparts. Similarly, vervet monkeys (*Chlorocebus pygerythrus*) in heavily human-modified landscape in Uganda survived through using specific areas intensely and relying on large fruiting trees (Chapman et al. 2016).

The feeding strategy used by a species will depend on a number of inter-playing factors, including a species' dietary preferences and level of dietary specialisation, which foods are available and their nutritional content (McLennan & Ganzhorn 2017). The degree of risk involved to access the food will likely also play a role for species in human-impacted habitats (see Chapter 7). Sometimes wild food may be available yet human resources are preferred (Hockings et al. 2009; Naughton-Treves et al. 1998; Saj et al. 1999).

4.1.2 Chimpanzee diets

Chimpanzees are ripe fruit specialists (Wrangham 1977), although they exhibit diverse omnivorous diets incorporating flowers, leaves, pith, seeds, meat, insects, bark and honey into their dietary repertoires to different degrees across sites (Basabose 2002; Bessa et al. 2015; Carvalho et al. 2015; Dutton & Chapman 2015; Hockings et al. 2009; McGrew et al. 1988; McLennan 2013; Morgan & Sanz 2006; Newton-Fisher 1999; Nishida & Uehara 1983; Potts et al. 2011; Wrangham et al. 1998). The density of fleshy fruit trees has been found to predict the density of chimpanzee nests, showing that chimpanzees favour high quality habitats with fruit trees (Balcomb et al. 2000). During periods of wild fruit scarcity chimpanzees usually diversify their diet (Fawcett 2000; Watts et al. 2012b), ingesting non-preferred available foods or fallback foods (Harrison & Marshall 2011) or expanding their range to find preferred foods (Fawcett 2000).

Figs (*Ficus* spp.) fruit asynchronously and their availability is often year-round (Tweheyo & Lye 2003) and can be a key food for chimpanzees across their range. Harrison and Marshall (2011) make the case that some fig species can be defined as primary fallback foods for chimpanzees due to the consistent proportion found in the diet throughout the year. Fallback foods are food

sources that are usually available year-round or for extended periods, lower in nutritional quality than preferred foods and their consumption will show an inverse relationship to preferred foods (Marshall & Wrangham 2007; Marshall et al. 2009). Other studies have found figs to be a staple food rather than a fallback, since their consumption by chimpanzees was not inversely related to overall or preferred fruit availability (Bessa et al. 2015; Newton-Fisher 1999; Watts et al. 2012a). Since chimpanzees are omnivorous and known to exhibit a high degree of dietary flexibility, during lean periods they will likely consume a higher proportion of leaves, piths and bark as fallback foods, in addition to available fruits (Basabose 2002; Hladik 1977; McLennan 2013; Pruetz 2006; Wrangham et al. 1998). For example, Bulindi chimpanzees consumed significantly more leaves and pith during the low fruit season, showing the importance of non-fruit items as fallback foods (McLennan 2013).

Certain fig species (e.g. *Ficus mucuso*) may have individual trees which are large enough to support large feeding parties of chimpanzees (50 or more individuals at Ngogo: Watts et al. 2012a) and may be fed on heavily when fruits are available, making them a highly preferred and important food. Preferred foods can be defined as a food that is consumed in accordance with its increasing availability (Marshall & Wrangham 2007) while an important food can be classified as a food that is consumed in high proportions, either throughout the year or at certain times. McLennan (2013) defines an important food specifically as one that is present in over 10% of feeding samples over the year, or in at least 50% of samples during one or more months.

Where forest composition has been altered after human disturbance, chimpanzees may increasingly need to rely on fallback or less preferred foods, especially during periods of wild fruit scarcity. In Gishwati, chimpanzees consumed more terrestrial piths and bark than did those in similar montane habitats in less disturbed forests, suggesting that where humans have altered forest composition, chimpanzees may rely increasingly on less preferred foods (Chancellor et al. 2012). Additionally, figs have been found to act as fallback foods (Bulindi: McLennan 2013) or possible fallback foods (Gishwati: Chancellor et al. 2012) for chimpanzees inhabiting forest fragments, and were important, but not preferred, foods in both sites.

It may be difficult or impossible for chimpanzees in anthropogenic landscapes to expand their range in response to fruit scarcity: either suitable habitat simply does not exist, or animals have to traverse risky anthropogenic habitat to access food species. Therefore, it may be expected for chimpanzees in human-influenced landscapes to diversify their diet, including foraging on crops.

In all known cases where chimpanzees inhabit human-modified landscapes, they incorporate crops into their diet (Hockings & McLennan 2012). For primates in anthropogenic habitats, certain crops may be preferred feeding items (Bicca-Marques & Calegario-Marques 1994; Hockings et al. 2009; McLennan 2013). However, crops also have the potential to act as seasonal fallback foods, especially those that are available for extended periods (Hockings et al. 2009, 2010; McLennan 2013).

Inter-community variations in crop foraging preferences have been found at different sites across chimpanzees' range, with some chimpanzee communities ignoring available crops when available (Hockings & McLennan 2012; McLennan & Hockings 2014). However, some crops, primarily fruit crops high in simple sugars such as mango, banana and papaya, are consumed by chimpanzees wherever they are available (McLennan & Hockings 2014). Whether a crop will constitute a fallback food or not will depend on its availability and level of preference and the interactions with available wild foods.

4.1.3 Sex differences in diet composition

Across mammalian taxa, males and females may show differences in dietary composition (Clutton-Brock 1977). This will usually vary according to the level of sexual dimorphism in the species (Key & Ross 1999), with the larger sex consuming either a higher quantity of the same foods as the smaller sex, or other food items to fulfil its energetic requirements (Clutton-Brock et al. 1982). In species without considerable differences in body weight, females will likely require a higher intake of metabolisable energy than males to meet their reproductive requirements (Gittleman & Thompson 1988; Wade & Schneider 1992) and are predicted to be energy-maximisers, spending more time foraging and exerting less energy (in travel time or distance) than males (Schoener 1971). Males are expected to be time-minimisers, spending less time feeding, allowing for more of their activity budget to be spent engaging in social behaviours. In elephants, males are more likely to forage on crops than females (Chiyo et al. 2011a), and also will consume more during a crop-foraging bout (Sukumar 1991). This difference in feeding behaviour in elephants may be explained by males' dietary need to consume large quantities of foods to maximise their body size and condition in order to increase their reproductive chances with females (Stokke & du Toit 2000). This can be especially relevant when foraging on high energy crops: males which engage in risky crop-foraging may even be sexually selected for (Chiyo et al. 2011b).

In primates, some studies have found females to spend more time foraging and feeding than males (e.g. squirrel monkeys (*Saimiri oerstedii*), Boinski 1988; white-faced capuchins (*Cebus capuchinus*), Rose 1994), where others have found the reverse (e.g. green monkeys (*Cercopithecus sabaues*), Harrison 1983). During a period of fruit scarcity, female orang-utans (*Pongo pygmaeus wurmbii*), spent less time feeding and had a lower caloric intake than males, although higher urinary ketones shows that this came at a high metabolic cost for females (Knott 1998).

In a human-impacted landscape, male chimpanzees at Bossou in Guinea were more likely to forage on cultivated foods than females (Hockings et al. 2009). Increased risk perception may affect female chimpanzees' decisions in leaving the forest or when foraging in the village-garden matrix (Priston et al. 2012; Strum 2010; Wallace & Hill 2012), potentially leaving females to forage predominantly, or solely, on wild foods. If males and females in anthropogenic habitats have dramatically different diets, then this will likely impact their socio-ecology. For example, if males reach their energy requirements faster through exploiting cultivated foods, they might have altered time budgets, potentially freeing up time to socialise more and increase resting, whereas females might continue to forage for wild foods (investigated in Chapter 5). This may be particularly evident during periods of wild fruit scarcity (Hockings et al. 2012b).

4.1.4 Comparison with neighbouring sites

To build hypotheses and draw comparisons, it is useful to refer to the dietary data available from the Sonso and Bulindi chimpanzee communities since these are Waibira and Kasongoire chimpanzees' neighbouring communities, respectively. However, it is worth noting that there are considerable differences between communities: while Waibira and Sonso are neighbouring communities within Budongo Forest, the Sonso community range is much more human-impacted than that of the Waibira community because it surrounds the old Budongo sawmill site and shares a boundary with a village and agricultural land at the forest edge. Much of this habitat is characterised by logged forest and scrub, where the open areas are dominated by the invasive shrub *Lantana camara*, which forms large dense thickets in disturbed areas, and *Brousonettia papyrifera* an exotic tree species planted originally for paper pulp. Sonso chimpanzees rest almost daily (Kosheleff & Anderson 2009) under *L. camara* and spend more time feeding on *B. papyrifera* than any other species (on both leaves and flowers; Tweheyo et al. 2004). This scrubby logged habitat is rare in the Waibira home range and *B. papyrifera* is entirely absent, meaning that considerable differences are to be expected even between neighbouring communities. Similarly,

while Bulindi is comparable in habitat type and degradation to Kasongoire, there are differences in both floristic composition and anthropogenic land use types and intensities (McLennan & Plumptre 2012).

Forest composition at Kasongoire is dramatically different to that at Waibira (Chapter 3, Section 3.4.1). Therefore it was expected that the diets of chimpanzees in each community would show differences. Since Kasongoire is riverine forest, compared to semi-moist deciduous forest found in Budongo forest, even if Kasongoire chimpanzees had a 'pristine' forest, there would be considerable differences in their diet to Waibira chimpanzee solely due to the different type of habitat. This is reinforced by the low level of species overlap found between the two habitats.

However, certain similarities will be expected: Sonso chimpanzees' were reported to spend almost half their entire feeding time consuming just five species, all of which were in the Moraceae family (Tweheyo et al. 2004), demonstrating the high importance of ripe fruits, and figs in particular. Similarly in Bulindi, fig seeds were found in almost 90% of faeces (McLennan 2013) showing their dominance in the diet, although they were not classified as preferred foods, i.e. their representation in faeces did not increase with increasing availability. Some species found in both habitats will likely be important feeding species for both communities, particularly those belonging to the Moraceae family, including *Ficus* spp., *Antiaris toxicaria* and *Morus mesozygia* (Tweheyo et al. 2004).

4.1.5 Chapter aims

The aims of this chapter are:

1. To describe the diets of Waibira and Kasongoire chimpanzees.
2. To compare differences in dietary composition and feeding strategies of chimpanzees in continuous versus human-influenced landscapes.
3. Investigate sex differences in dietary composition, with a particular focus on chimpanzees in Kasongoire human-impacted habitat.
4. Assess whether dietary diversity changes as result of wild fruit availability.

4.1.6 Hypotheses and predictions

Table 4.1 outline the hypotheses and predictions tested in this chapter.

Table 4.1: Hypotheses and predictions relating to chimpanzee feeding strategies at Waibira and Kasongoire, and the framework for testing them.

Hypothesis	Prediction	Analysis
<i>Animals in anthropogenic habitats will have to exhibit high dietary flexibility to survive.</i>	1. Dietary diversity will be higher at Kasongoire than Waibira.	1. I calculate monthly dietary diversity using the Shannon Weaver Diversity Index and a Mann Whitney U test to determine whether chimpanzee diets at Kasongoire are significantly greater than at Waibira.
<i>Chimpanzee diets will not vary considerably from those reported at other sites across their range.</i>	2. Fruits from the Moraceae family will dominate chimpanzee diets at both sites. 3. Time spent feeding on ripe fruits will account for the majority of feeding observations at both sites; 4. Time spent feeding on all other food parts will not differ significantly.	2. I calculate the proportion of overall diets comprised by fruits from the Moraceae family. 3. I calculate the proportional time spent consuming ripe fruits per month at each site to determine whether ripe fruit accounted for the highest contribution to chimpanzee diets. 4. I calculate the proportional contributions of different plant parts to the diet per month and use Mann Whitney U tests to determine whether time spent feeding on different food parts varied significantly.
<i>Chimpanzee feeding strategies will reflect the availability of food in the forest.</i>	5. Time spent feeding on ripe fruits will increase as the ripe fruit availability increases; 6. Dietary diversity will increase as ripe fruit availability decreases.	5. I calculate the time spent feeding on ripe fruit per species and use a Spearman's Rank correlation to determine whether there is a significant positive correlation with the monthly FAI score of the same species. 6. I use a Spearman's Rank correlation to determine whether there is a significant negative correlation between the monthly H' score for dietary diversity and the FAI score for that month.
<i>Where animals have access to crops, their feeding strategy will incorporate these as fallback foods; some crops may be preferred foods.</i>	7. Chimpanzees at Kasongoire will spend more time feeding on sugarcane as wild fruit availability decreases.	7. I calculate the time spent feeding on sugarcane and use a Spearman's Rank correlation to determine whether there is a significant negative correlation with the monthly FAI score.

Where animals feed on crops, males will consume more crops than females since they are less risk averse.	8. Kasongoire males will spend more feeding time than females consuming sugarcane; 9. Kasongoire females will exhibit higher dietary diversity than males: at Waibira dietary diversity is expected to be similar between males and females.	8. I calculate the monthly contribution of sugarcane to male and female chimpanzee diets at Kasongoire and use a Mann Whitney U test to determine whether males spent significantly longer time consuming sugarcane than females. 9. I calculate diversity H' scores for male and female diets overall at both sites and assess which sex within and between sites showed higher dietary diversity.
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4.2 METHODS

4.2.1 Data collection

I collected feeding data during 15 minute instantaneous scan samples, recording the species and plant part fed on by chimpanzees. If at least one adult in the party was recorded as feeding during a scan, the feeding species was recorded as well as the part consumed. Feeding was recorded for males and females separately. If individuals were feeding on more than one species or part, the species and feeding item consumed by the majority of the party was recorded, as per Watts et al. (2012a). A food item represents a plant part from a certain species: i.e. more than one plant part may be consumed from the same species. Different plant parts from the same species constitute different food items.

Gilby et al. (2010) found that scan sampling was an adequate equivalent to focal sampling for recording feeding data, although they state that information may be lost by failing to record species consumed infrequently. In this study I collected feeding data by recording the diet of the majority of individuals in the party, as opposed to continuous focal sampling of one individual. This means that rarer feeding items may have been missed as individuals may not have fed on an item during the moment of the scan. However, new species that were observed being fed on were recorded through *ad libitum* sampling, and feeding traces were also recorded when not following the group. Therefore I present here the main contributions to chimpanzee diets in Kasongoire and Waibira.

When calculating the proportional contribution of each species and part to the diet of the community as a whole (including males and females), the species consumed by the majority of individuals was used, in accordance with the original method of collecting the feeding item consumed by the majority of the party. For example, if males and females consumed a different feeding item on one scan sample, the item fed on by most individuals in the whole party was used in the analysis.

Feeding data were collected using scan samples rather than continuous focal sampling, meaning feeding time *per se* was not recorded (in minutes, for example). Therefore the term ‘feeding time’ is presented in the results as the proportion of sample points where chimpanzees were feeding. Data from scan samples were used in the analysis, and feeding items consumed during other times through *ad libitum* observations were added to the species inventory. *Ad libitum* observations did not contribute to results on the proportional dietary contributions of each species to chimpanzee feeding time but were used to complete the list of species consumed at each site.

Feeding data from party scans in this study allow for comparison in dietary composition and diversity from wild food species only, since chimpanzees were not followed into villagers’ crop gardens. As sugarcane feeding by chimpanzees is tolerated by Kinyara Sugarworks Ltd., data on the contribution of sugarcane to chimpanzee diets at Kasongoire were collected.

4.2.2 Data analysis

The observed feeding time on each species and plant part was calculated for each community over the study period using data from scan samples, where I collected information on how many individuals were recorded as feeding and the species and part eaten. These calculations were then made again for males and females. Monthly means of the contribution of each species to each community’s diets were then calculated. Dietary diversity for each community over the study period and per month was measured using the Shannon-Weaver Diversity Index. This was calculated from the equation:

$$H' = -\sum p_i \ln p_i$$

where p_i is the proportion of time spent feeding on the i th species in the diet (Shannon & Weaver 1963). Species contributions to diet were broken down by part for diversity scores, since this reflected nutritional diversity and fruit availability (e.g. observed feeding time for young leaves and ripe fruit of the same species would contribute separately diversity scores).

The data failed the assumptions of normality even after transformation, consequently non-parametric tests were used. For analyses assessing the relationship of dietary composition and diversity with fruit availability, scores from the monthly fruit availability index (FAI) were used (Chapter 3). I used a Mann-Whitney U test to assess differences in monthly dietary diversity scores between Waibira and Kasongoire (Prediction 1). For differences in plant part consumed, both between Kasongoire and Waibira chimpanzees overall and between males and females within sites, I used Mann-Whitney U tests comparing the monthly totals for each plant part (Predictions 4 & 9). To test whether fruit consumption was associated with fruit availability, I used a Spearman's rank correlation, comparing monthly FAI scores for each species with the observed monthly feeding time for the ripe fruit of that species (Prediction 5). At Waibira, chimpanzees consumed seeds from *Cynometra alexandrii* which were combined in the analysis for time spent feeding on ripe fruit species consumed since this constituted a major part of the diet. I used a Spearman's rank correlation test to determine whether there was an association between dietary diversity and fruit availability, using monthly dietary diversity scores and corresponding monthly FAI scores (Prediction 6). A Spearman's rank test was used to determine whether there was a correlation between fruit availability and sugarcane consumption at Kasongoire, using the monthly average proportion of records chimpanzees spent feeding on sugarcane and corresponding monthly FAI score (Prediction 7). Lastly, I used a Mann Whitney U test to assess whether there was a difference between the monthly contribution of sugarcane to male and female diets at Kasongoire.

4.3 RESULTS

4.3.1 Chimpanzee diets at Waibira and Kasongoire

A total of 1563 feeding records were analysed. This included 505 whole party scans over 10 months at Waibira (391 male and 354 female feeding data points) and 1057 whole party scans over 13 months at Kasongoire (767 male and 645 female feeding data points). Waibira chimpanzees were recorded to consume a total of 36 different food items from at least 31 species belonging to 15 families and Kasongoire chimpanzees consumed 58 food items from at least 43 species belonging to 19 families. The Shannon-Weaver diversity index (H') for chimpanzees' diets gave an overall value of 2.82 at Waibira and 2.63 at Kasongoire, but varied across the months of the study (Table 4.2). Contrary to Prediction 1, no significant difference was found in monthly diversity scores between the two communities ($U=58$, $N=23$, $p=0.664$). All species and plant parts

fed on by adult male and female chimpanzees at both sites and their proportional contribution to chimpanzee diets (in observed feeding time) are presented in Table 4.3.

Table 4.2: Shannon Diversity H' scores of chimpanzee diets per month (nd=no data).

Month	Waibira	Kasongoire
July_15	0.78	1.02
August	0.98	0.80
September	1.30	1.24
October	1.45	0.92
November	1.09	0.80
December	0.64	1.99
February	1.80	1.88
January	nd	2.03
March	1.78	1.97
April	1.80	1.74
May	0.77	1.56
June	nd	1.87
July_16	nd	1.75

Regarding shared species, there was considerable variation between the diets of chimpanzees in each community, reflecting the differences in forest composition. A low level of dietary species overlap was found, with fruit from only eight species being consumed at both sites. Additionally, in agreement with Prediction 2, six of these belonged to the Moraceae family. Honey was also consumed at both sites.

4.3.2 Contribution of different food parts to chimpanzee diets

Ripe fruits dominated chimpanzee diets at both sites, supporting Prediction 3 (see below for further information on each community). The plant parts consumed varied between sites (Figure 4.1): Kasongoire chimpanzees consumed fewer fruits, leaves and seeds and more pith and flowers than did chimpanzees at Waibira. Pith constituted a significantly higher proportion of the diets of chimpanzees in Kasongoire than at Waibira ($U=130$, $N=23$ months [Waibira= 10, Kasongoire=13], $p<0.001$); no other plant parts were found in statistically different proportions between sites, showing overall support for Prediction 4 (RF: $U=54$, $p=0.522$; UF: $U=59.5$, $p=0.738$; ML: $U=67.5$, $p=0.879$; YL: $U=40.5$, $p=0.131$; FL: $U=95$, $p=0.067$; ME: $U=75$, $p=0.563$; IN: $U=43$, $p=0.186$; HY: $U=67.5$, $p=0.879$).

Table 4.3: Species consumed and percentage of feeding time (proportion of records) by adult chimpanzees at Waibira and Kasongore.

Species	Family	Part eaten ¹	Data ²	Sp. Type ³	% Male	% Female	% Total	Status ⁴
Waibira								
<i>Antiaris toxicaria</i>	Moraceae	RF	S	T	2.81	3.95	3.17	P
<i>Balsamocitrus dawei</i>	Rutaceae	RF	S	T	2.30	0.00	1.78	
<i>Celtis mildbraedii</i>	Ulmaceae	YL	S	T	9.72	9.32	11.29	I
<i>Celtis wightii</i>	Ulmaceae	YL	S	T	3.84	1.41	3.17	
<i>Celtis zenkeri</i>	Ulmaceae	YL	S	T	0.51	0.00	0.40	
<i>Cordia millenii</i>	Boraginaceae	RF	S	T	7.67	9.32	8.91	I
<i>Cynometra alexandri</i>	L. - Caesalpinioideae	SD	S	T	0.51	1.13	0.79	P
<i>Desplatsia dewevrei</i>	Tiliaceae	RF	S	T	1.28	0.00	0.99	
<i>Dialium excelsium</i>	L. - Caesalpinioideae	RF	S	T	11.00	10.17	8.91	I, P
<i>Erythrophleum suaveolens</i>	L. - Caesalpinioideae	SD	S	T	0.26	0.00	0.20	
<i>Ficus exasperata</i>	Moraceae	RF	S	T	11.76	6.78	9.70	P
<i>Ficus mucoso</i>	Moraceae	RF	S	T	17.39	25.71	19.80	I, P
<i>Ficus natalensis</i>	Moraceae	RF	S	T	3.07	2.54	2.38	
<i>Ficus saussureana</i>	Moraceae	RF	S	T	1.02	1.13	0.79	
<i>Ficus sur</i>	Moraceae	RF	S	T	4.35	5.65	4.75	
<i>Ficus variifolia</i>	Moraceae	RF	S	T	0.00	0.85	0.59	
		YL	S		2.05	1.13	1.58	
Honey		HY	S	O	0.77	1.13	0.79	
<i>Mammea africana (traces)</i>	Calophyllaceae	RF	A	T				
<i>Mildbraediodendron excelsum</i>	L. - Caesalpinioideae	RF	S	T	2.30	1.69	1.78	
<i>Morus mesozygia</i>	Moraceae	RF	S	T	0.00	1.13	0.79	
<i>Myrianthus holstii</i>	Moraceae	RF	S	T	0.00	0.85	0.59	
<i>Pseudospondias microcarpa</i>	Anacardiaceae	RF	A	T				
<i>Sterculia dawei</i>	Sterculiaceae	UF	S	T	1.79	2.54	1.78	
<i>Strychnos mitis</i>	Loganiaceae	RF	S	T	0.77	0.56	0.59	
Terrestrial piths	Various	PI	S	S, G	0.26	0.00	0.20	
<i>Platyserium elephantotis</i>	Unknown	ML	S	E	0.77	1.13	0.79	

Unknown tree sp.1	Unknown	X	S	T	1.28	0.85	0.99	
Unknown tree spp.	Various	UF	S	T	0.26	0.00	0.20	
		YL			0.26	0.00	0.20	
Unknown climber sp.1	Unknown climber	RF	S	L	4.60	5.93	4.95	I, P
		UF			0.26	0.00	0.20	
Unknown climber spp.	Various	RF	S	L	1.53	0.00	1.19	
		UF			3.84	2.82	2.97	
		YL			1.79	1.98	2.57	
Unseen	Various	X	S	Var	0.00	0.28	0.20	
Kasongoire								
<i>Acacia spp.</i>	L. - Mimosoideae	SD	S	T	0.94	0.78	0.87	
<i>Acanthus pubescens</i>	Acanthaceae	PI	S	S	0.40	0.31	0.48	
<i>Alaphia lowdoides</i>	Apocynaceae	RF	S	L	1.21	1.26	1.36	
<i>Albizia sp.</i>	L. - Mimosoideae	SD	S	T	0.13	0.16	0.10	P
<i>Aningeria altissima</i>	Sapotaceae	RF	S	T	4.32	8.48	6.30	P
<i>Antiaris toxicaria</i>	Moraceae	RF	S	T	3.78	3.45	3.20	P
		YL	S		0.27	1.26	0.87	
		FL	S		4.05	5.81	4.07	P
Ants	Unknown	IN	S	O	0.27	0.00	0.19	
<i>Blighia unijugata</i>	Sapindaceae	YL	S	T	0.54	0.31	0.39	
<i>Colobus guereza occidentalis</i>	Cercopithecidae	ME	S	O	1.75	2.04	1.65	
<i>Cola gigantea</i>	Sterculiaceae	RF	A	T				
<i>Cyperus papyrus</i>	Cyperaceae	PI	S	G	0.27	0.94	0.68	F
<i>Ficus bubu</i>	Moraceae	RF	S	T	0.27	0.31	0.29	
		UF	S		0.00	0.16	0.10	
<i>Ficus exasperata</i>	Moraceae	RF	S	T	0.40	1.57	1.07	
<i>Ficus natalensis</i>	Moraceae	RF	S	T	2.16	2.04	1.75	
<i>Ficus ovata</i>	Moraceae	RF	S	T	0.27	0.78	0.48	
<i>Ficus sansibarica</i>	Moraceae	RF	S	T	0.67	1.10	0.68	
<i>Ficus saussureana</i>	Moraceae	RF	S	T	2.70	2.67	2.33	
		UF	S		0.27	0.47	0.29	

		ML	S		0.00	0.16	0.10	
		YL	S		0.40	0.31	0.39	
<i>Ficus sur</i>	Moraceae	RF	S	T	1.75	1.57	1.75	S
		UF	S		0.00	0.31	0.19	
<i>Ficus vallis-choudae</i>	Moraceae	RF	S	T	2.70	4.24	3.10	F
		UF	S		0.40	1.41	0.97	
		YL	S		1.35	3.30	2.62	F
Honey		HO	S	O	0.13	0.16	0.19	
<i>Lantana camara</i>	Verbenaceae	YL	S	S	0.13	0.00	0.10	
<i>Macaranga schweinfurthii</i>	Euphorbiaceae	PI	S	T	0.00	0.47	0.29	
<i>Maesopsis eminii</i>	Rhamnaceae	RF	A	T				
<i>Morus mesozygia</i>	Moraceae	RF	S	T	7.83	10.36	8.83	P
		UF	S		0.27	0.16	0.29	
<i>Myrianthus holstii</i>	Moraceae	RF	S	T	0.27	0.31	0.29	
<i>Parkia filicoidea</i>	L. - Mimosoideae	RF	S	T	1.48	3.30	2.33	P
<i>Pennisetum purpureum</i>	Poaceae	PI	A	G				
<i>Phoenix reclinata</i>	Arecaceae	RF	S	T	2.16	4.71	3.69	I, S
<i>Pseudospondias microcarpa</i>	Anacardiaceae	RF	S	T	6.34	9.42	8.44	S
		ML	S		0.27	0.16	0.29	
		YL	S		0.00	0.31	0.19	
<i>Pycnanthus angolensis</i>	Myristicaceae	RF	S	T	0.40	0.16	0.29	
<i>Saccarum officinarum</i>	Poaceae	PI	S	G	43.59	17.27	30.46	I, S
<i>Sterculia dawei</i>	Sterculiaceae	RF	S	T	0.54	0.16	0.10	
<i>Syzygium guineense</i>	Myrtaceae	RF	S	T	1.21	1.41	1.55	
Terrestrial piths	Various	PI	S	S, G	0.13	0.47	0.39	
Unknown climber spp.	Various	YL	S	L	1.89	1.88	2.52	
		PI	S		0.00	0.16	0.10	
		SD	S		0.13	0.00	0.10	
Unknown tree sp.2	Unknown	RF	S		0.13	0.63	0.39	
Unknown tree sp.3	Unknown	UF	S	T	0.00	0.47	0.29	
Unknown tree sp.4	Unknown	YL	S	T	0.13	0.16	0.10	

Unknown tree sp.5	Unknown	FL	S	T	0.13	0.00	0.10
Unknown tree spp.	Various	ML	S	T	0.00	0.16	0.10
		YL	S		0.54	1.57	1.16
		FL	S		0.00	0.31	0.10
Unseen	Various	X	S	Var	0.81	0.47	0.97
<i>Vernonia amangdelena</i>	Vernonieae	YL	A	S			
<i>Zanha golungensis</i>	Sapindaceae	RF	S	T	0.13	0.16	0.10

¹RF=Ripe fruit; UF=Unripe fruit; ML=Mature leaves; YL=Young leaves; FL=Flowers; PI=Pith; ME=Meat; IN=Insects; SD=Seeds; HY=Honey; X=Unknown.

²S=Scan sample; A=Ad libitum data.

³T=Tree; L=Liana; S=Shrub; E=Epiphyte; G=Grass; O=Other; Var=Various.

⁴Status: I=Important; P=Preferred; S=Staple; F=Fallback. See Section 4.1.2 for definitions.

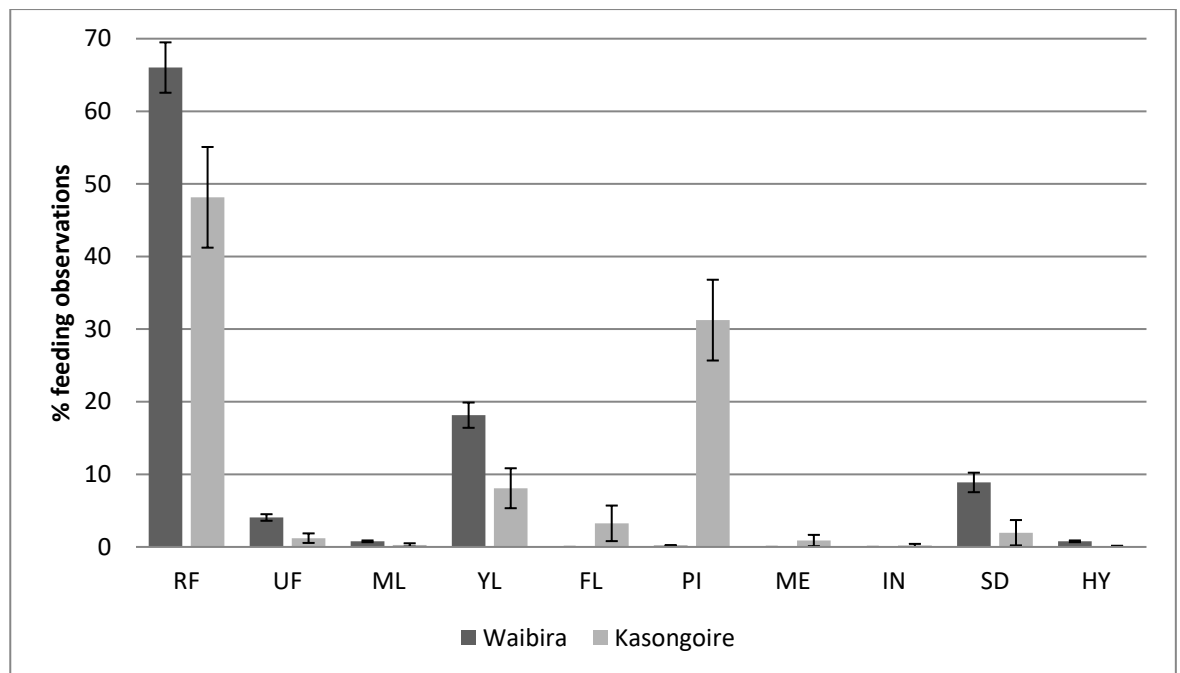


Figure 4.1: Average time ($\pm$ SE) spent feeding on different food items at Waibira and Kasongoire. RF=Ripe fruit; UF=Unripe fruit; ML=Mature leaves; YL=Young leaves; FL=Flowers; PI=Pith; ME=Meat; IN=Insects; SD=Seeds; HY=Honey.

The proportion of observed feeding time consuming fruit per month was significantly positively correlated to the amount of fruit available for that species (monthly FAI score) both at Waibira ($r_s=0.340$, $N=36$ [6 months FAI data for 6 species observed fed on], $p=0.043$) and Kasongoire ($r_s=0.535$, $N=192$ [12 months FAI data for 16 species observed fed on], $p<0.001$), supporting Prediction 5. Contrary to Prediction 6, no association was found between monthly fruit availability and chimpanzee dietary diversity scores at Kasongoire ($r_s=0.007$, $N=12$ months, $p=0.983$); phenology data at Waibira were too limited to statistically assess a correlation between fruit availability. See Appendix 8 for details of the monthly contributions of species to chimpanzee diets.

Waibira

The majority of the chimpanzees' diet at Waibira comprised ripe fruits: ripe fruits accounted for 66% ($\pm$ SE 3.46) of observed feeding records although unripe fruits were consumed occasionally (5.2% of feeding time for males and 3.3% for females) (Figure 4.2). Waibira males and females did not exhibit any significant differences in dietary composition of plant items ($N=20$ months [10 male, 10 female], RF: $U=45.5$, $p=0.733$; UF: $U=47$, $p=0.766$; ML: $U=49.5$, $p=0.942$; YL: $U=39$, $p=0.399$; PI: $U=45$, $p=0.371$; SD: $U=43.5$, $p=0.579$; HY: $U=49.5$, $p=0.942$). Male diets exhibited slightly larger diversity than females, with an H' index of 2.81 as compared to 2.61, respectively, in contrast to Prediction 9.

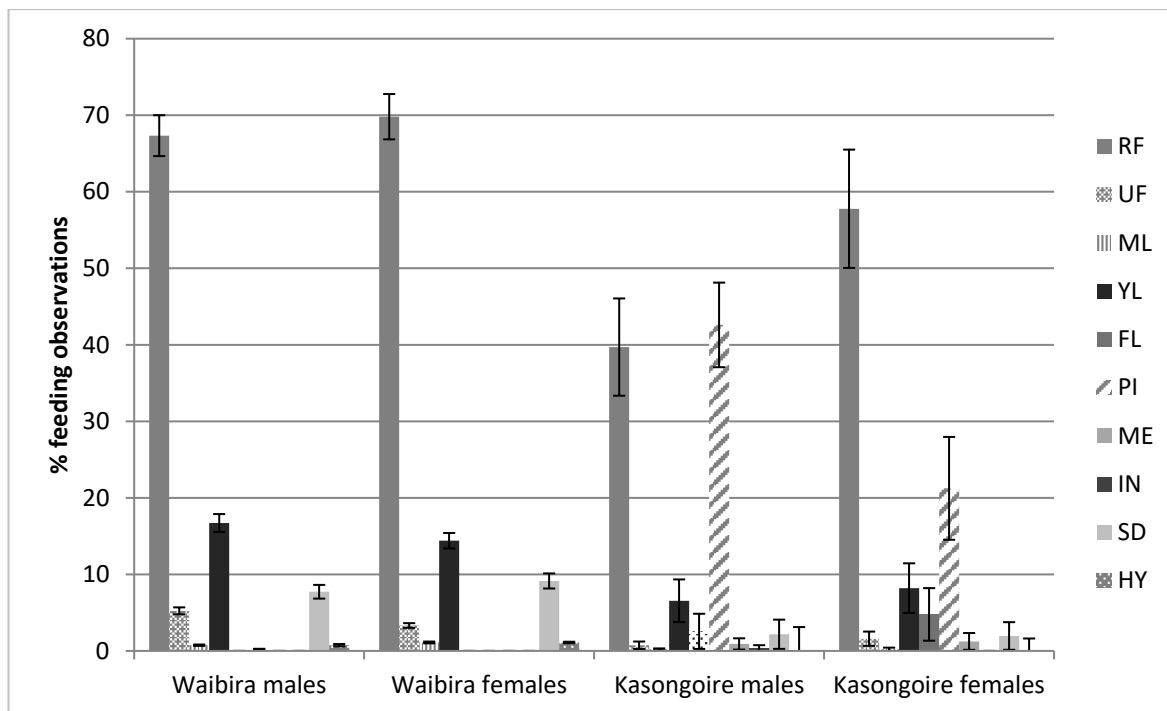


Figure 4.2: Average proportion of feeding time ($\pm$ SE) spent consuming different food parts by males and females at Waibira and Kasongoire. RF=Ripe fruit; UF=Unripe fruit; ML=Mature leaves; YL=Young leaves; FL=Flowers; PI=Pith; ME=Meat; IN=Insects; SD=Seeds; HY=Honey.

Trees belonging to nine different species within the Moraceae family accounted for 45.1% of all feeding time, showing strong evidence to uphold Prediction 2. With the one exception of *Ficus varifolia* for which only young leaves were consumed (1.4% of all Moraceae feeding time), chimpanzees fed exclusively on ripe fruit in this family. One species, *Ficus mucoso*, which had the largest basal area of any tree within the Waibira home range (Chapter 3), accounted for 19.8% of all feeding time by the community overall and was consumed in only November and April.

Young leaves were consumed for 14.8% and 13.6% of male and female overall observed feeding time, and mature leaves 0.8% and 1.1% respectively. Multiple species of leaf were consumed, including tree, liana and epiphytic species. *Celtis* spp. (Ulmaceae) dominated leaf ingestion (young leaves exclusively were consumed from this family), accounting for 11.4% of all feeding time and were fed on over 7 out of the 10 months where feeding was recorded. Young leaves of unidentified lianas contributed 6.7% of total observed feeding time. Males were recorded feeding on terrestrial herbaceous vegetation (THV) on just one occasion. Flowers and insects were not observed consumed by the community over the study period, and no hunting was observed. Seeds comprised a large portion of Waibira chimpanzees' diet from November to January (Figure 4.3): a single record of feeding on *Erythrophleum suaveolens* seeds was collected, with *Cynometra alexandrii* accounting for all other seed consumption.

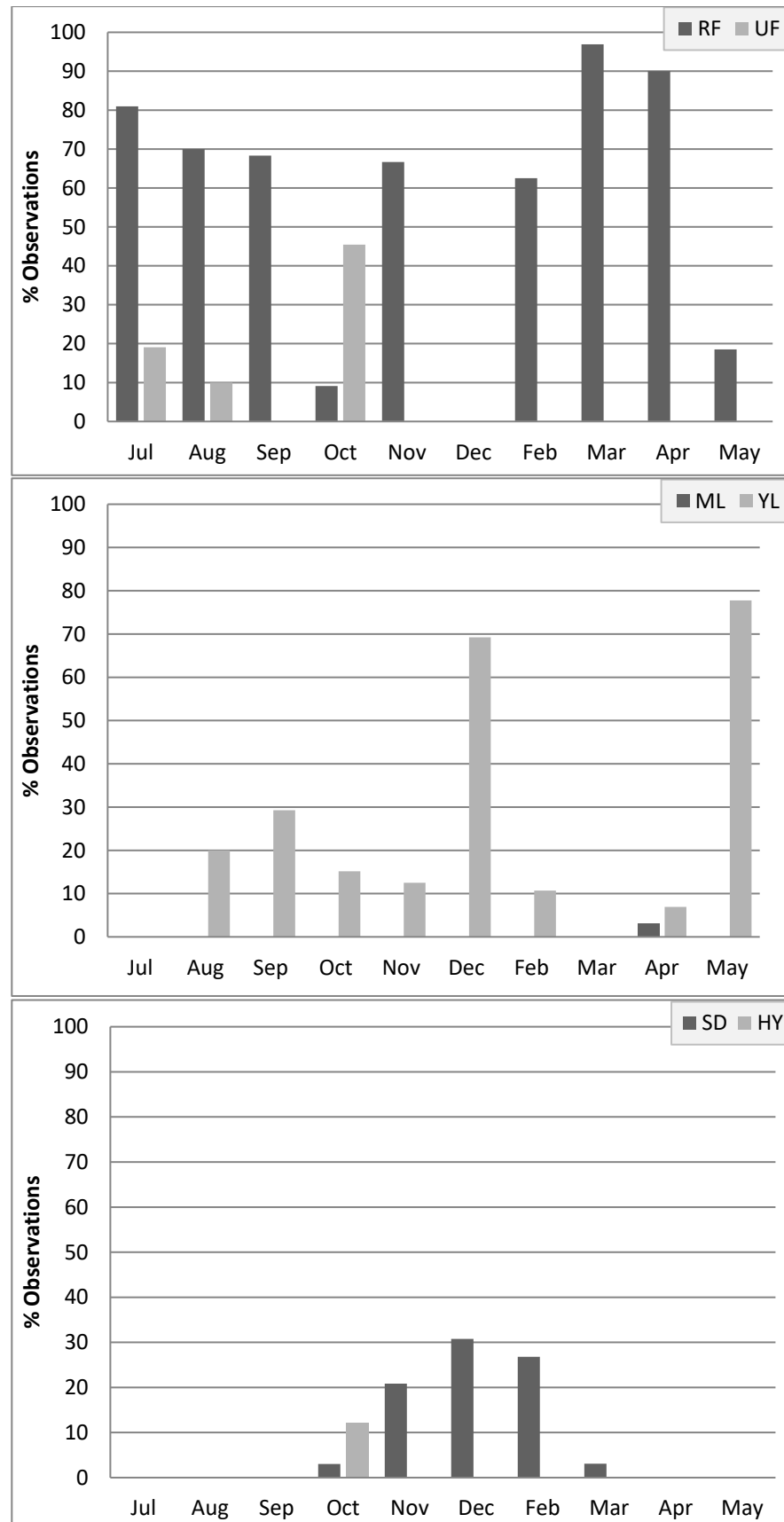


Figure 4.3: Average monthly proportion of feeding time spent consuming the most commonly eaten food parts by adult chimpanzees at Waibira. RF=Ripe fruit; UF=Unripe fruit; ML=Mature leaves; YL=Young leaves; SD=Seeds; HY=Honey.

Non-plant foods

Waibira chimpanzees were observed consuming honey on one occasion during October, accounting for just 0.7% of their total feeding time. No other non-plant parts were observed being consumed during this study.

Kasongoire

Kasongoire chimpanzees consumed more ripe fruit than any other part overall comprising an average of 48.2% ($\pm$ SE 6.9) of feeding observations, showing that chimpanzees in this human-modified habitat also show a preference for ripe fruits (Figure 4.4). Species from the family Moraceae were consumed over other wild species accounting for 32.9% of feeding time from 11 different species. Mainly ripe fruits were consumed from this family, although all parts were consumed, with the exception of bark. No single species in the Moraceae family accounted for over 10% of the community's feeding time at Kasongoire: the species chimpanzees were observed feeding on the longest was *Morus mesozygia*, accounting for 6.9% and 9.9% of male and female feeding time, respectively.

Males consumed significantly more pith than females (N=26 months [13 male, 13 female], U=35, $p=0.011$), but there were no significant differences in other food items consumed (RF: U=52, $p=0.96$; UF: U=81, $p=0.808$; ML: U=79, $p=0.611$; YL: U=80.5, $p=0.835$; FL: U=67.5, $p=0.32$; IN: U=78, $p=0.317$; SD: U=78, $p=0.628$; HY: U=84, $p=0.956$).

Young leaves accounted for 5.7% and 9% of male and female feeding time, respectively, and were consumed from at least 11 species and primarily from *Ficus vallis-choudae* (2.6% of overall feeding time) and unidentified species of trees and lianas. Pith accounted for an average of 32% of the observed feeding time (44.3% for males and 19.7% for females). Sugarcane (*Saccharum officinarum*) accounted for the majority of pith in the diet: other piths were occasionally ingested, including that from *Acanthus pubescens* and *Cyperus papyrus*, although these accounted for less than 1% of feeding time. Flowers were only consumed during 3 months and constituted 4% of total feeding time. In January, flowers comprised around a third of chimpanzee feeding time, when flowers of *Antiaris toxicaria* were fed on in large parties.

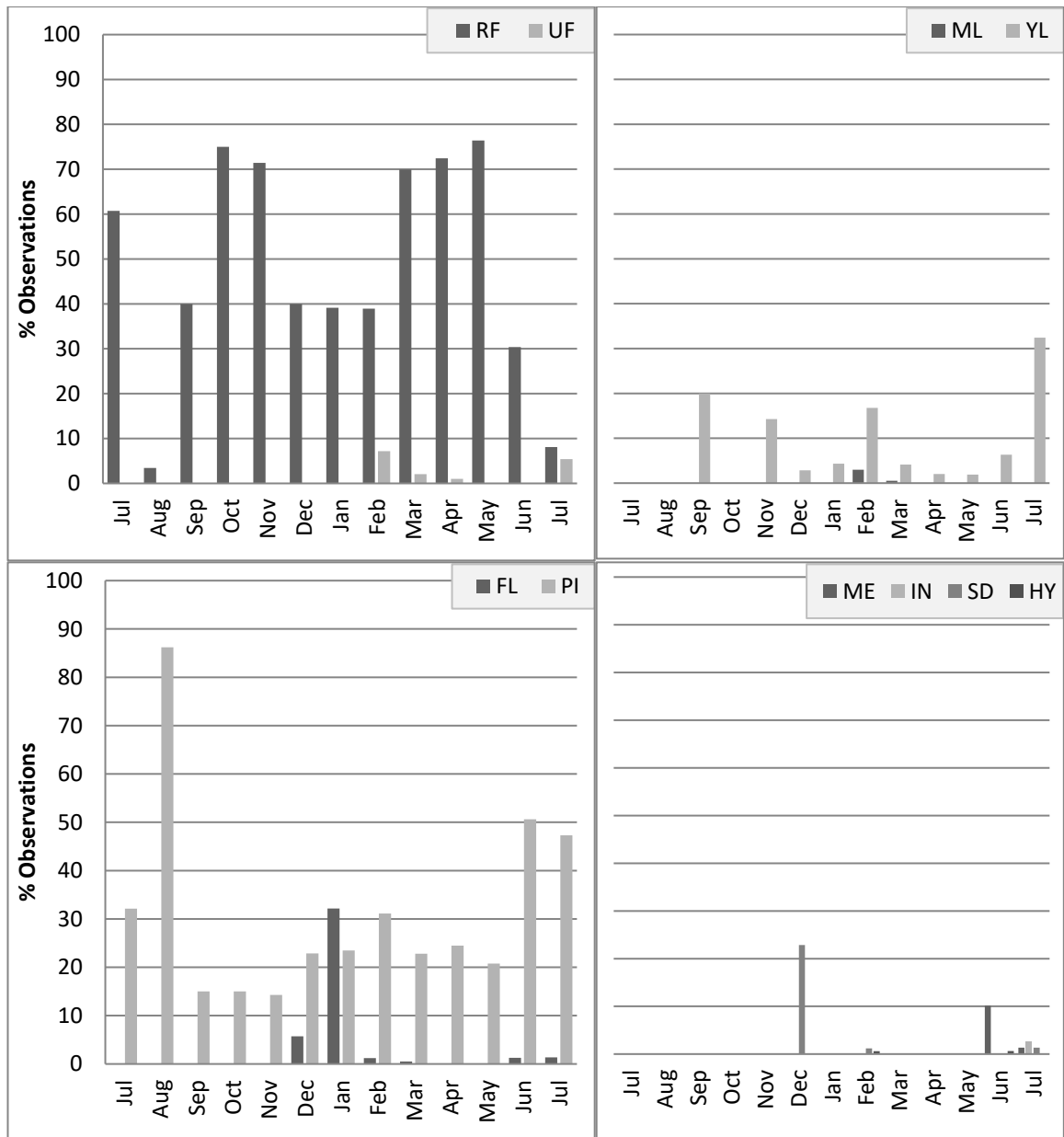


Figure 4.4: Average monthly proportion of feeding time spent consuming different food parts by adult chimpanzees at Kasongoire. RF=Ripe fruit; UF=Unripe fruit; ML=Mature leaves; YL=Young leaves; FL=Flowers; PI=Pith; ME=Meat; IN=Insects; SD=Seeds; HY=Honey.

Influence of consuming sugarcane on Kasongoire chimpanzee diets

Sugarcane accounted for the highest proportion of any one species in the diet. As an average from the whole community, Kasongoire chimpanzees spent 30% of their total feeding time consuming sugarcane. Contrary to Prediction 7, no correlation was found between sugarcane consumption and the fruit availability index at Kasongoire ($r_s = -0.467$, $N=12$ [months with corresponding FAI data], $p=0.118$; Figure 4.5).

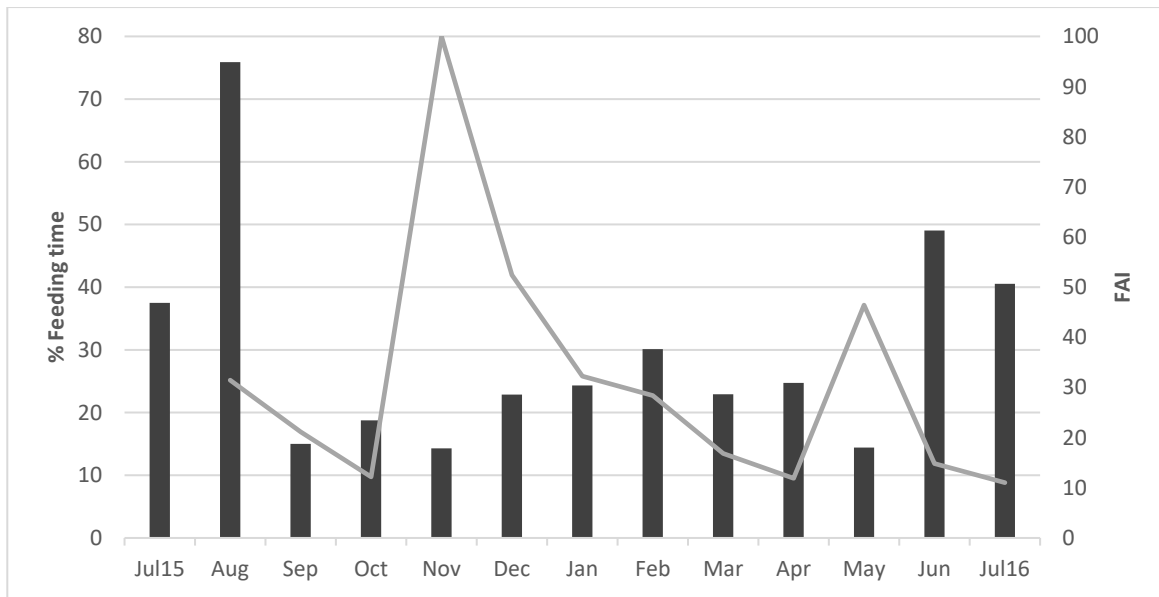


Figure 4.5: Kasongoire chimpanzees' consumption of sugarcane each month (bars) and wild fruit availability (line).

Sugarcane was the only species consumed every month during the study and there was high monthly variation, with sugarcane accounting for between 14.4% (May) and 75.9% (August) of monthly feeding time (Figure 4.5). When fruit availability was at its highest sugarcane still comprised over 10% of the overall diet, showing that sugarcane is a preferred food for Kasongoire chimpanzees overall. Males spent 43.1% of their overall feeding time on sugarcane, and females spent 17.1%, supporting the expectation that males would spend significantly more time foraging on sugarcane than females (Prediction 8; N=26 months [13=male, 13=female], U=17, $p<0.001$).

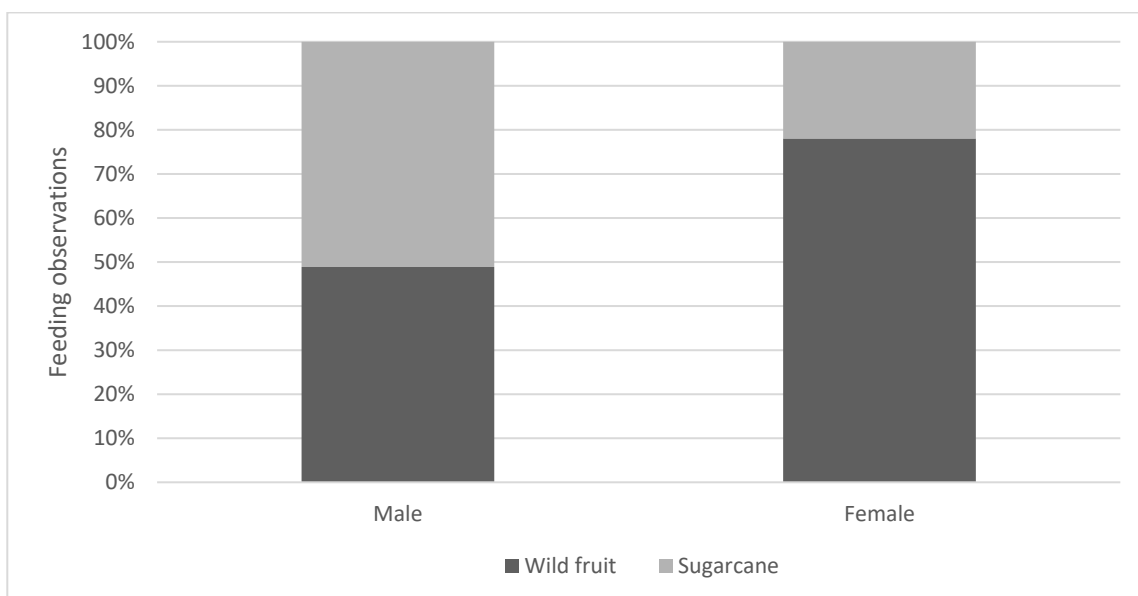


Figure 4.6: Proportion of feeding time spent on wild fruits versus sugarcane for males and females at Kasongoire.

Males spent more time consuming sugarcane than wild fruit (total feeding time: sugarcane=43.1%, wild fruits=41.3%; Figure 4.6). Female chimpanzees at Kasongoire exhibited greater dietary diversity than males: the Shannon-Weaver H' index was 2.84 for females as compared to 2.27 for males. This corroborates with Prediction 9, showing that with fewer cultivated foods in the diet, females must increase their dietary diversity.

Although chimpanzees were not followed into crop gardens, from *ad libitum* data taken during chimpanzee follows, they were recorded as leaving the forest to enter crop gardens on 35% of observation days (45 of 127 days). Chimpanzees foraged on crops – both sugarcane and crops from villagers' crop gardens – on a minimum of 75 of 127 observation days, 59% of days when they were followed (Figure 4.7). When including data from feeding traces, from both *ad libitum* data (see Chapter 2) and mango feeding traces (see Chapter 7), chimpanzees were found to forage on crops on 106 days, although this sample includes days where chimpanzees were not followed for behavioural observations.

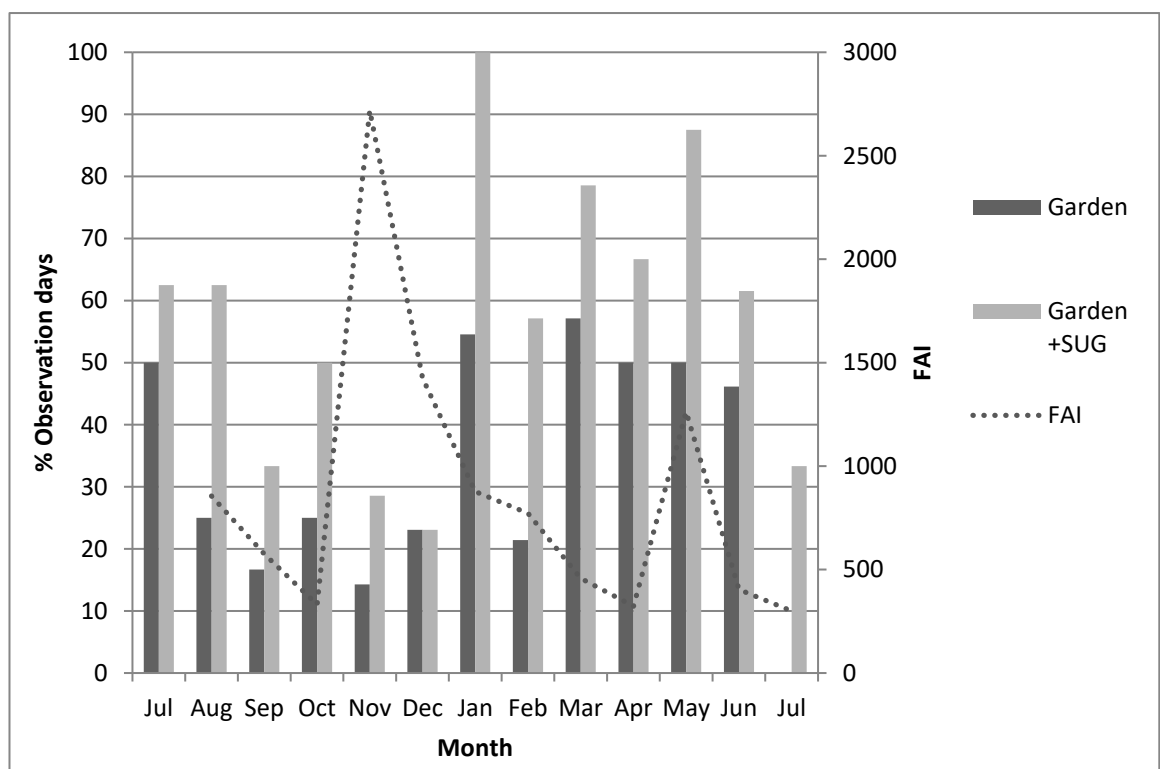


Figure 4.7: Proportion of observation days per month where chimpanzees were recorded as foraging on crops, in villagers' gardens (Garden) and all crops (Garden+SUG), against wild fruit availability.

Non-plant foods

Kasongoire chimpanzees were observed consuming honey from stingless bees (*Meliponula* sp.), accounting for 0.19% overall feeding time. Chimpanzees were once observed apparently using

stick tools to feed on insect prey, most likely ants. This suggests that Kasongoire chimpanzees exhibit a higher level of insectory than at Waibira, although this was not observed to be habitual. Black and white colobus monkeys (*Colobus guereza occidentalis*) were observed being successfully hunted and consumed on three occasions.

4.4 DISCUSSION

4.4.1 Overview of chimpanzee diets at Waibira and Kasongoire

Chimpanzees were predicted to exhibit higher dietary diversity at Kasongoire than at Waibira. Contrary to the findings of Ménard et al. (2014) and Riley (2007) who found primates in fragments to have lower dietary diversity than those in less disturbed forests, I predicted that chimpanzees in Kasongoire would show a high dietary diversity since the forest there was found to have higher tree species richness than Waibira (Chapter 3). However, statistically, no differences in diversity scores were found between communities, overall or monthly meaning that Prediction 1 was not supported. However, Waibira chimpanzee diets were slightly more diverse than those at Kasongoire as shown from the Shannon-Weaver H' Index. Although I was not able to record the contribution of crops from villagers' crops gardens, chimpanzees at Kasongoire incorporate anthropogenic food resources meaning that the dietary diversity scores are likely very even between the two communities. Tree species richness in Kasongoire was higher than in Waibira (Chapter 3), which was reflected in the higher species richness in the dietary composition of Kasongoire chimpanzees as compared with Waibira. Reflecting the low level of species overlap found in habitat sampling at both sites (Chapter 3; Appendix 7), dietary species overlap between Kasongoire and Waibira chimpanzees was low with only eight shared species in the chimpanzees' diets.

Fruits from the Moraceae family dominated the diets of chimpanzees at both sites, confirming Prediction 2, and showing that despite living in a fragmented forest, Kasongoire chimpanzees still exhibit similar dietary patterns to those in more intact forest, regarding wild foods at least. In the same way, consistent with chimpanzee communities elsewhere and as expected (Prediction 3), chimpanzees in both Waibira and Kasongoire consumed more ripe fruits than other plant parts (see Watts et al. 2012a for a comparison of plant part contributions to chimpanzee diets across long-term study sites). Overall, food items consumed (plant and non-plant parts) did not differ significantly, supporting Prediction 4. With the exception of pith (which was principally sugarcane), there was no significant variation in time chimpanzees spent consuming various food

items at each site. Ripe fruit availability and ripe fruit consumption were significantly correlated (Prediction 5), also corroborating with results from other sites (Carvalho et al. 2015; Piel et al. 2017; Watts et al. 2012a; cf Bessa et al. 2015). Ripe fruits comprised over 70% of Waibira chimpanzees' diets and consumption was relatively stable throughout the year (above 60% monthly contribution to the diet) with the exception of December when consumption of *Cynometra alexanderi* seeds peaked and May when only fruits from *Mildbraediodendron excelsum* were consumed. At Kasongoire, fruit consumption fluctuated from comprising more than 60% of feeding observations per month over half of the study period, then dropping to only 3% of feeding time in August when sugarcane comprised over 75% of the diet.

Chimpanzees were predicted to broaden their dietary diversity or forage more on crops during periods of fruit scarcity, particularly at Kasongoire since expanding their range is risky and there is simply less forest to expand to, since the landscape is highly fragmented. Yet, contrary to predictions (Prediction 6), dietary diversity did not increase during periods of wild fruit scarcity at Kasongoire. However, because Kasongoire chimpanzees were not followed into crop gardens it was not possible to record whether they utilised more crops during periods where fewer wild fruits were available. Due to limitations in the phenology data it was not possible to assess statistically whether dietary diversity increased when fruit availability decreased at Waibira. However, Waibira chimpanzees did appear to exhibit dietary flexibility in response to lower quantities of available fruit by increasing the proportion of young leaves in their diet, as did chimpanzees at Ngogo in Kibale National Park (Watts et al. 2012b).

4.4.2 Preferred and fallback foods

At Waibira, the largest single contributor to the diet was *Ficus mucuso*, comprising 20% of the chimpanzees' diets there and can be classed an important feeding species, similar to the contribution to the diets of Ngogo chimpanzees in Kibale National Park (18% contribution, Watts et al. 2012a). However, unlike in other sites where figs have been defined as staple or fallback foods, no species of fig was consumed for more than four months at Waibira and in half of the months of study no figs were observed to be consumed at all. *Ficus sur* accounted for 15% of Sonso chimpanzees' feeding time (Tweheyo et al. 2004), whereas it accounted for less than 5% of Waibira chimpanzees' observed feeding time despite fruit being available every month during this study. Therefore, while *F. mucuso* constituted an important part of Waibira chimpanzees' diets, figs overall could not be categorised as staple, fallback or important foods, since they were not observed consumed throughout the study period.

Conversely, at Kasongoire, fig consumption appeared to be spread throughout the year, with chimpanzees feeding on figs when other preferred foods were less readily available, rather than fluctuating with *Ficus* availability itself. Chimpanzees consumed *F. vallis-choudae* in 12 out of 13 months during the study and its consumption was inversely related to wild fruit availability, showing its value as an important and fallback food resource. *F. sur* was also fed on during more than half of the study months, although its consumption was not related to food availability or the consumption of preferred foods, meaning that it can be classified as a staple food for Kasongoire chimpanzees. Similar results have been found for chimpanzee fig consumption at other sites where figs constitute important fallback or staple foods (Bessa et al. 2015; Chancellor et al. 2012; McLennan 2013; Watts et al. 2012b). Additionally, *Phoenix reclinata* was consumed over 8 months of the study and although its consumption was not related to its availability or that of other fruits, its consumption was inversely associated with the consumption of preferred feeding items showing that it may act as a fallback food for Kasongoire chimpanzees. For non-fruit items, the pith of papyrus (*Cyperus papyrus*) was fed on only during wild fruit scarcity, suggesting that, although not consumed often, it may provide an abundant fallback resource in this habitat.

Young leaves were consumed more at Waibira than at Kasongoire, but this did not appear to reflect changes in fruit availability. At Kanyawara chimpanzees responded to fruit scarcity by feeding more on terrestrial piths, although leaf intake did not appear to increase (Wrangham et al. 1991), whereas neither chimpanzee community substantially incorporated wild terrestrial piths into their diet during this study. Terrestrial herbaceous vegetation (THV) accounted for an unexpectedly low proportion of Waibira chimpanzees' feeding time. For neighbouring Sonso chimpanzees, THV comprised 3.2% of total feeding time (Newton-Fisher 1999) compared with Waibira's 0.1%. At Kasongoire and Bulindi, THV similarly contributed to a small part of chimpanzee diets (McLennan 2013). The likely explanation for the low figure at Waibira is that rather than not consuming piths and leaves of THV, chimpanzees would often become lost or out of sight when on the ground especially during early afternoons when feeding on THV is more likely (Newton-Fisher 1999).

Waibira chimpanzees were not observed to consume flowers at all during this study, whereas neighbouring Sonso chimpanzees feed heavily on flowers of *Brousonetia papyrifera*, an exotic species which accounts for as much as 8.8% of chimpanzee feeding time during dietary studies there (Newton-Fisher 1999; Tweheyo et al. 2004). A simple explanation for this difference is that *B. papyrifera* is not found within the Waibira home range, although there may have been other

species which it would be expected for individuals to consume which were either not flowering during this study or which flowered during a time when other preferred foods were available. While it is possible that Waibira chimpanzees did incorporate some level of flowers into their diets as the observation sample size was low, other study sites have also reported a generally low level of flower consumption (Watts et al. 2012a), showing that this plant part does not ordinarily constitute an important component of chimpanzee diets. Interestingly, Kasongoire chimpanzees fed heavily on flowers of *Antiaris toxicaria*, whereas Waibira chimpanzees apparently ignored them completely, despite their availability.

4.4.3 Sugarcane consumption at Kasongoire

Kasongoire chimpanzees consumed sugarcane every month, with it contributing over 50% to their diets during one month and regularly contributing to over 20% of their diets overall (9 out of 13 months). Therefore, sugarcane can be considered both an important (the most important) and staple resource in the Kasongoire chimpanzees' dietary repertoire, and not a fallback food as I had predicted (Prediction 7). A recent study showed that for blond capuchins (*Sajapus flavius*), sugarcane contributed a similarly high proportion to primate diets as at Kasongoire: one- to three-quarters of annual diet (de Sousa Lins & Ferreira 2018). However, sugarcane in the capuchin diet was found to be inversely related to fruit availability and was therefore categorised as a staple fallback food. At Bossou, although some crops were consumed in relation to their availability regardless of wild fruit availability, chimpanzees increased their overall consumption of cultivated foods during periods of wild fruit scarcity: sugar fruits in particular were identified as fallback foods (Hockings et al. 2009). Plant parts other than fruit and leaves can also be fallbacks: chimpanzee in Kibale National Park fed on banana pith during periods of fruit scarcity (Naughton-Treves et al. 1998). Similarly, the bark of cultivated jackfruit (*Artocarpus heterophyllus*) and durian (*Durio zibethinus*) trees were found to be fallback foods for orangutans (Campbell-Smith et al. 2011).

The high level of sugarcane integrated into Kasongoire chimpanzees' diet suggests that Kasongoire chimpanzees may meet their metabolic needs quickly, despite this being a degraded habitat. Mango fruits (*Mangifera indica*) were also fed on heavily during the peak season, although time spent feeding on mangos could not be calculated in this study (see Chapter 7 for an assessment through indirect observation). Previous research has noted that chimpanzees have a taste for sweetness, and that calorie content can be a determining factor for food choice (Matsumoto-Oda & Hayashi 1999). It was not possible to understand how crops in general were

incorporated into Kasongore chimpanzee diets since they were not followed into crop gardens, although from direct observations and *ad libitum* data, chimpanzees were recorded as foraging on crops on over half of all observation days. It would be interesting to know whether Kasongore chimpanzees respond to periods of fruit scarcity by increasing crop consumption generally or eating a greater diversity of cultivated foods and if any crop species can be deemed as fallback foods. For example, chimpanzees at Gishwati consumed maize during the period of wild fruit scarcity, but not at other times, despite maize availability (Chancellor et al. 2012). Conversely, chimpanzees at Bossou in Guinea and Kibale National Park in Uganda consumed maize whenever it was available, regardless of wild fruit availability (Hockings et al. 2009; Naughton-Treves et al. 1998).

Being a large-scale monoculture crop, sugarcane is not only a high-energy resource but spatially hyper-abundant and available year-round. Therefore perhaps it is not surprising that Kasongore chimpanzees fed on it to the high extent reported, with no effect of wild fruit availability on the proportion of feeding observations consuming sugarcane. This shows that sugarcane has become fully integrated into chimpanzee diets at Kasongore and suggests that chimpanzees, and particularly males, are willing to leave the forest and enter a more exposed area where guards are often present in order to exploit this resource (see Chapter 6 for a further investigation into chimpanzee risk perception when leaving the forest).

No previous study has reported such a high level of consumption of a single crop by chimpanzees, although reliance on a single cultivated species has been recorded in other primates. In a few other cases have wild primates been reported to incorporate a high level of anthropogenic resources into their diet, including actively provisioned white-faced capuchins (*Cebus capuchinus*) in Costa Rica (McKinney 2011), which get around 60% of their diet from anthropogenic sources. Fruit and leaves of jackfruit (*Artocarpus heterophyllus*) accounted for over 65% of feeding time for purple-faced langurs (*Trachypithecus vetulus nestor*) in Sri Lanka, inhabiting a human-dominated habitat with no remaining forest (Moore et al. 2010). Lastly, in an extreme scenario, black howler monkeys (*Alouatta caraya*) inhabiting a gallery forest fragment set in an agricultural mosaic foraged heavily on exotic fruit species, and particularly on oranges (*Citrus sinensis*), which comprised almost 100% of their diet during wild fruit scarcity (Bicca-Marques & Calegario-Marques 1994).

Whilst foraging on a single crop has been documented for a number of different primate species in anthropogenic habitats, foraging heavily on a commercially important monoculture crop such as sugarcane has not been recorded to this extent for chimpanzees. This may have implications for land management strategies around sugarcane plantations where chimpanzees persist. The sugarcane grown around Kasongoire forest is managed by Kinyara Sugarworks Ltd. (KSWL) who tolerate foraging by chimpanzees, meaning that, in theory, loss of sugarcane by chimpanzee crop-foraging should not cause any negative human-chimpanzee interactions. However, although the sugarcane found around the forest in Kasongoire is grown directly by the company, elsewhere in the landscape outside Budongo Forest, it is commonly grown by outgrowers who sell their produce to KSWL (McLennan & Hill 2015; Reynolds 2005; Zommers et al. 2012). Outgrowers will likely be much less tolerant of crop losses since this will reduce their profit from a cash crop, which is a long-term investment (McLennan & Hill 2012).

4.4.4 Non-plant feeding items

At Waibira, hunting by chimpanzees was not observed during this study. A recently study showed that Budongo chimpanzees' hunting rate is likely influenced by human presence during the early habituation period (Hobaiter et al. 2017), which probably affected this study's results at both sites. The preliminary hunting data from Hobaiter et al. (2017) also showed that Waibira chimpanzees have a preference for duiker over primate prey, as opposed to the neighbouring Sonso community which primarily hunts for primates, in particular black and white colobus monkeys (*Colobus guezera occidentalis*). At Kasongoire, successful hunting was observed on three occasions, unsuccessful hunts observed twice and a further three carcasses found, certainly remains of recent chimpanzee hunts. *C. g. occidentalis* was the target species on every occasion. The difference in hunting rates between the two communities may be partially explained by the differences in protein intake. Kasongoire chimpanzees' near-avoidance of young leaves may suggest that they hunt and consume meat to fulfil a nutritional requirement for protein, whereas Waibira chimpanzees' higher consumption of young leaves may satisfy this requirement. It is also possible that prey species at Kasongoire may simply be easier to locate, considering the small size of the forest, although hunting by chimpanzees appears to be absent in neighbouring Bulindi (Cibot et al. 2017; McLennan 2010).

Chimpanzees at both Waibira and Kasongoire consumed honey, although rarely. Waibira chimpanzees were observed feeding on honey on one occasion, from bees from the *Apini* tribe (likely *Apis mellifera*), as the chimpanzees were constantly stung as they were feeding.

Chimpanzees fed in a large party (7-11 individuals) from a nest in the bottom of a standing tree and moved away when the honey was depleted. At Kasongoire, chimpanzees were observed feeding on honey from bees from the *Melaponini* tribe (stingless bees) on two occasions. Chimpanzees obtained the honey directly from nests in dead logs on the ground, either using hands or directly feeding with the mouth.

On two occasions, Kasongoire chimpanzees were observed apparently feeding on ants. In one instance individuals were observed preparing and using stick tools to disturb either ants or other insect prey (possibly grubs) between the bark and the branch of the tree. Waibira chimpanzees were not observed feeding on ants during the study, and only one case of ant-feeding has been observed there (Mugisha et al. 2016) where chimpanzees used leaves to dip into a driver ant swarm (*Dorylus* sp.). However, with such a low sample drawing inferences about levels of insectivory cannot be made. Certainly, Kasongoire chimpanzees were not witnessed to exhibit the high levels of insectivory that neighbouring Bulindi chimpanzees have shown, although levels of insectivory among chimpanzees that are not fully habituated are best determined through faecal analysis rather than direct observation (McLennan 2014).

Regarding the one confirmed occasion in Kasongoire where chimpanzees used stick tools when foraging on what appeared to be ants, a party of five females and their offspring (total 12 individuals) was feeding and grooming in a *Parkia filicoidea* tree including the adult female, SYL, and all three of her offspring, GER, STO and SAB. After all individuals had stopped feeding on the ripe fruits of *P. filicoidea*, most chimpanzees in the party were grooming. During this time SAB (male, ~3 years old) was seen with a stick ~10 cm long from which he had stripped the bark with his teeth. He was brushing it on the side of the tree branch, putting the stick in his mouth and drawing it away. He inserted the stick in between the bark and the wood of the tree branch, brought it out and put the stick in his mouth, inter-changing between inserting the stick and his finger. This was sustained for five minutes. His brother GER (male, ~11 years old) then joined him, broke off a stick ~15 cm long from the same tree, stripped it of the bark and proceeded to perform the same behaviour as SAB. He then brushed the branch of tree to disturb what appeared to be ants there, inserted the stick between the bark and the branch and put the stick back in his mouth. Similarly, he changed between inserting the stick and his finger. After sustaining this behaviour for six minutes, both stopped and SAB returned five minutes later and continued to use the stick for both foraging and play for a further 5 minutes. The actual ingestion of ants was not confirmed, and so the target may have been other insect prey.

Chimpanzees inhabiting Budongo Forest Reserve famously do not have any stick-tool use in their cultural repertoire (Gruber et al. 2009; Whiten et al. 1999), and chimpanzees in mid-western Uganda have small tool repertoires as compared with those in other eastern chimpanzee study sites or western chimpanzees (Whiten et al. 1999). For eastern chimpanzees, ant consumption with stick tools in long-term field sites has been reported in Tanzania at Gombe (Goodall 1964; McGrew 1974) and Mahale (McGrew & Collins 1985; Nishie 2011), but in Uganda only in Kalinzu (Hashimoto et al. 2000) and Bwindi (Stanford & Nkurunungi 2003). Chimpanzees in neighbouring riverine fragments in the Budongo-Bugoma corridor forests have been reported to use stick-tools to obtain honey on rare occasions at (Kasokwa: Wallis pers. comm., cited in Gruber et al. 2010). McLennan (2014) reports habitual insectivory in neighbouring Bulindi chimpanzees, primarily weaver ants and subterranean stingless bees' nests, the latter of which are obtained by stick tools (McLennan 2011). However, this behaviour was not seen at Kasongore, despite the close proximity of the two communities and ant consumption was observed only rarely. It is possible that chimpanzees at Kasongore may exhibit some low level of stick tool use, as they are geographically closer to chimpanzees at Bulindi to those in the forest block at Budongo. Further observations must be made to understand the level of insectivory and tool use at Kasongore.

On one occasion, Kasongore chimpanzees were observed handling the carcass of a dog, which on later inspection appeared to be semi-feral. Whether the chimpanzees hunted and directly killed the dog cannot be confirmed as it was not clearly witnessed, but vocalisations before the observation suggests that they did. However, the chimpanzees did not feed on the dead animal, instead appearing to inspect and play with it. Only adult males and females were observed interacting with the dead animal. Similar behaviour has been reported in chimpanzees at other sites, although rarely (Cibot et al. 2017; Hockings et al. 2012b), and usually by juvenile or subadult individuals.

Lastly, another rare observation was made at Kasongore during this study involving an owl (observation made by BKJ only – I was at Waibira). Two owls (species as yet confirmed) were regularly seen on an *Antiaris toxicaria* tree, a tree also popular with a group of *C. g. occidentalis*. Colobus monkeys had been previously witnessed harassing the owls in this tree, but on this occasion they killed one of the owls, without consuming it – an incident reported once before, by red colobus (*Procolobus tephrosceles*) in Kibale National Park (Goldberg et al. 2006). Kasongore chimpanzees were travelling on the forest edge at the same time of this incident, perhaps attracted to the area by the noise of the incident itself. One adult male, SCA, picked up the dead

owl from the ground, fed on it briefly and disposed of the remaining carcass as he travelled on. One previous report of chimpanzees feeding on an owl has been made by Carvalho et al. (2010), but this behaviour has been witnessed very rarely.

4.4.5 Study limitations

As described in Chapter 3, phenology surveys had not previously been conducted in the Waibira home range, meaning that the species monitored there were based on feeding information from neighbouring Sonso chimpanzees. However, the high incidence of ripe fruit in Waibira chimpanzees' diet when fruit availability was reported as scarce suggests that additional species could have been monitored to improve the data. For example, *Dialium excelsum* contributed to more than 10% of male and female diets overall, yet was not discovered at all in plots. Additionally, staff at BCFS had never previously identified this species as a feeding item so it was not included in phenology monitoring. However, with the exception of *D. exclesum*, no other fruit tree species that was not included in phenology surveys accounted for over 4% of the overall diet.

Without inter-annual data on fruit availability it is impossible to assess whether there was comparatively little ripe fruit during this study as compared with other times and years. At Waibira, because the number of observed chimpanzee feeding species that were monitored in phenology surveys was very limited, interpretations of the data on the effect of fruit availability on chimpanzee diets must be made with caution. However, some species monitored for phenology in this study either did not fruit at all or produced very little fruit: *Celtis durandii* is likely to be an important feeding species but produced no fruit during this study (it fruited during the pilot phase and was fed on extensively) and *Chrysophyllum albidum*, which is a masting species, did not experience a fruiting season. While these are only two species, the absence of their fruit may impact chimpanzee feeding strategies and time budgets since they are both known to be important feeding species for chimpanzees (Newton-Fisher 1999; Potts et al. 2011).

There was a much higher number of unknown species at Kasongore as compared with Waibira, largely due to difficulties with accessing and identifying feeding trees. At Kasongore, observations could not be made from standing in the ecotone forest since it was too scrubby and impenetrable. Therefore, it was often most practical to observe chimpanzees feeding and collect feeding data from outside the forest edge. This made observations often easier at Kasongore than at Waibira, although it was then difficult or impossible to collect a sample of the feeding item for later identification.

Time spent feeding on fruits is often over-represented as many fruiting trees are large and chimpanzees often repeatedly pant-hoot from them during times of fruit abundance. However, when feeding on other food items, particularly terrestrial herbaceous vegetation and piths, chimpanzees are silent on the ground and can easily be lost or unseen (Wrangham et al. 1991). Therefore, if chimpanzees are easier to locate and observe in large trees with abundant resources as compared to on the forest floor consuming rarer species, data will be slightly biased (Gilby et al. 2010). Where subjects are poorly habituated or observation difficult faecal analysis gives valuable data on diet (McGrew et al. 2009), but due to time constraints I was unable to include this method in this study. Additionally, since I was unable to identify several liana species from which chimpanzees consumed young leaves, dietary species richness will have been higher in both sites.

4.4.6 Balanced diets

In a study comparing the diets of chimpanzees at Gombe and in Gabon, Hladik (1977) concluded that the most important factor determining food selection, other than fruit availability, is nutrient intake. He suggests that other than seeking to maximise energy intake, chimpanzees seek specific nutritional qualities in different species. Ripe fruits are generally low in protein and high in sugars, whereas the reverse is found for young leaves (Lambert & Rothman 2015). Additionally, figs contain high levels of calcium, which contributes to making them an attractive nutritious resource (O'Brien et al. 1998). In this respect, chimpanzee diets in this study fit with that reported from other sites, as both chimpanzee communities' diet comprised principally of ripe fruits dominated by Moraceae species.

Leaves contain significantly higher levels of protein than fruits (Matsumoto-Oda & Hayashi 1999) and are often consumed in higher proportions during lean periods since they remain available during most, or all, of the year (Tweheyo & Babweteera 2007). In Kibale, chimpanzees in the Kanyawara community fed on leaves of only one species of mature tree and significantly increased pith consumption during periods of fruit scarcity (Wrangham et al. 1991). Nutritional analyses suggested that these piths contained high levels of fermentable fibre. Piths constituted an important part of Kanyawara chimpanzees' diet, yet at Waibira this plant part was virtually absent from the diet. At Kasongire, pith constituted a major part of the diet, although the majority of this was sugarcane rather than pithy stems of terrestrial herbaceous vegetation. The high proportion of young leaves consumed by Waibira chimpanzees compared to Kasongire chimpanzees may be reflective of the low fruit availability there. Further studies should assess

whether Waibira chimpanzees increase their level of frugivory accordingly in years and seasons with more available fruit.

Kasongoire chimpanzees were found to incorporate more species and food parts into their diets than did Waibira chimpanzees though, reflecting the higher tree species richness at that site. Similarly, Bourtoulini's Blue monkeys (*Cercopithecus mitis boutourlinii*) living in a forest fragment in Ethiopia were found to have a higher dietary species richness than those in continuous forest (Tesfaye et al. 2013). Higher does not necessarily mean better though: in the case of the blue monkeys, those living in the forest block fed heavily on high-quality figs whereas those in fragments spent a lot of their feeding time consuming bamboo, which is high in toxins.

Dela (2007) points out that while primates living commensally with humans may be able to exploit new cultivated resources, the physiological effects of incorporating fruit crops into their diets remains unknown. In Kasongoire, chimpanzees are consuming a considerable quantity of sugarcane in addition to wild foods, likely fulfilling their energetic requirements much faster than if feeding on wild foods alone. One negative factor to such a high level of sugarcane consumption will be a lack of nutrient balance in the diet. Sugarcane is high in soluble sugars and non-detergent fibre (although due to the 'wading' method of consuming sugarcane, chimpanzees do not ingest the fibrous pith), but lacking in protein (McLennan & Ganzhorn 2017). Crop-foraging black lemurs (*Eulemur macaco*) in an anthropogenic environment suffered from a nutritional imbalance, which ultimately may be affecting their population density (Simmen et al. 2007). For Kasongoire chimpanzees, foraging on crops may even provide a benefit for fecundity, as has been reported for baboons foraging on human foods (Strum 2010) and potentially for chimpanzees at neighbouring Bulindi (M. McLennan, 2016, pers. comm.). However, the long-term nutritional implications of this high level of sugarcane consumption are unknown.

In Kasongoire, the chimpanzees are clearly able to supplement their diet with an abundant cultivated resource. Dunn et al. (2010) note that in particularly lean years, primates inhabiting forest fragments may struggle to find adequate resources. Although this study did not find a distinct period where there was very little wild fruit available in Kasongoire, it is unknown what the chimpanzees' feeding strategy would be during a lean year. Like other primate species in heavily human-influenced landscapes, it is not clear whether they would survive in the long-term without supplementing their diet with anthropogenic resources (Bicca-Marques & Calegario-Marques 1994; McLennan 2013).

CHAPTER FIVE

THE EFFECTS OF LIVING IN A HUMAN-INFLUENCED HABITAT ON THE ACTIVITY BUDGETS OF CHIMPANZEES



Plate 18 (on previous page): Kasongoire chimpanzees grooming in the open gap between the forest edge and sugarcane plantation.

5.1 INTRODUCTION

Forest dependent species must either adapt or perish in the face of habitat changes, whether those changes are natural or induced by human beings (Estrada et al. 2017). Human-driven habitat alterations will directly affect forest composition, and therefore food availability for wildlife. As seen in Chapter 3, anthropogenic activities can impact floral composition within the forest, as well as presenting novel foraging opportunities outside the forest boundary. This will most likely result in specific responses by animals, such as modified feeding (Chapter 5) and ranging behaviour, as the distribution and availability of the natural resources changes and opportunities arise to exploit new resources. Measuring changes in activity budgets is a method commonly used to investigate and understand how animals respond to habitat and resource differences and risky situations (Dunbar 1988), including those driven by human activities.

In this chapter I examine activity budgets in the two chimpanzee communities, to investigate chimpanzee socio-ecological responses to living in a human-influenced habitat. Understanding these variations in behaviour and ecology will provide information about how animals adapt to living in human-influenced habitats and offer insights for their long-term survival prospects.

5.1.1 Activity budgets: trade-offs for survival

Optimality models consider the costs and benefits to animals in foraging decisions, taking into account the trade-offs in energy expenditure when food is abundant or not (Dunbar 2002; Stephens & Krebs 1986). Optimality theories suggest that animals will respond to reduced preferred food availability either by increasing their feeding time to incorporate less nutritious, less preferred foods or fallback foods, or increasing their travel time to search for less abundant higher energy foods (Stephens & Krebs 1986). The effect of species' foraging strategies will directly affect overall activity budgets: once animals have fulfilled their metabolic needs, they free up more time for other activities which may improve overall fitness (Dunbar & Shultz 2007; Leonard & Robertson 1997; Silk 2007). Dietary flexibility will be an important factor contributing to overall energetics and therefore impacting the fulfilment of an animal's metabolic needs (Harrison & Marshall 2011). Species which exhibit less dietary flexibility may have to travel further to find food at the expense of other activities during periods of preferred food scarcity.

Gorillas (*Gorilla* spp.) decrease their day range and change their diet to incorporate lower quality foods during periods of wild fruit scarcity (Yamagiwa & Mwanza 1994), although western lowland

gorillas (*Gorilla gorilla gorilla*) may expand their range to find preferred fruits as they are more frugivorous than other gorilla species (Masi et al. 2009; Yamagiwa & Mwanza 1994). Similarly, orangutans in peat-swamp forests (e.g. Sebangau and Tuanan, Borneo; Suaq, Sumatra) exhibit very different foraging strategies to those in mixed-dipterocarp forests (Morrogh-Bernard et al. 2009). Peat-swamp forests display significantly less seasonal variation in fruit availability than masting dipterocarp forests, where orangutans respond to periods of fruit scarcity by drastically reducing their feeding time, balancing this with increased time resting, decreased travel and overall reduced active day length. Japanese macaques (*Macaca fuscata*) decreased feeding time and spent more time travelling when feeding on higher quality foods, with those in a poorer quality environment spending a much higher proportion of time feeding (Agetsuma & Nakagawa 1998).

The physical availability of food resources will be affected by human disturbance in human-impacted habitats since forest composition will have been altered, but seasonal changes in resource abundance will likely affect species' activity budgets in all habitats. In a review by Oates (1987), more frugivorous species were reported to increase foraging time during periods of fruit scarcity, as opposed to more folivorous species which spent more time resting. While chimpanzees are an omnivorous and flexible species, they show a distinct preference for ripe fruits (Wrangham 1977), suggesting that they will likely increase their foraging efforts in response to fruit scarcity, which will impact their activity patterns.

Tai chimpanzees respond to food scarcity by spending more time feeding but in smaller parties and on lower quality food items, as well as reducing overall community daily ranging (Doran 1997). Sonso chimpanzees in Budongo were found to spend less time resting and travelling during periods of fruit scarcity (Fawcett 2000), although another study at the same site did not find any effect of seasonal changes on activity patterns (Bates 2005).

5.1.2 Habitat quality

Habitat quality can be measured in terms of the nutritional quality, abundance and spatio-temporal distribution of food resources. Each of these factors will influence primate activity patterns. From the literature on primate activity budgets and foraging strategies it can be predicted that access to high energy foods will likely result in a reduction in time spent feeding and travelling and an increase in time spent resting and perhaps socialising. However, when developing hypotheses about the impact of human activities on the activity patterns and diet of

Kasongoire chimpanzees as compared with the Waibira community, it is important to first consider: what makes a “better” quality habitat?

Habitat quality in this context is defined by Marshall (2010, p. 9) as: *“The most widely used index of habitat quality is the population density that a habitat can support at carrying capacity; high quality habitats support high population densities and low quality habitats support low population densities (Begon et al. 1996; Krebs 2001). Thus, habitat quality (i.e., habitat-specific population density) should be a function of the net energy available to support primate biomass, or the balance between habitat-specific energy availability and habitat-specific costs (Caldecott 1980; Iwamoto and Dunbar 1983).”*

Within a forest-only setting (as opposed to human-influenced habitat), measures of important tree density and food abundance define the “better” habitat, as Marshall (2010) describes. Factoring in human disturbance, this then develops into a comparison of protected versus unprotected, continuous versus fragmented, and rural versus urban habitats. Habitats which have high levels of human activities could reasonably be initially dismissed as “worse” quality habitats, assuming that proximity to humans and human-driven habitat loss and disturbances would negatively impact most species of flora and fauna. Additionally, the size of the habitat is constrained (Chancellor et al. 2012). However, the costs of potentially lower food availability as a result of the loss of wild food species may be over-ridden by the benefits of available human foods, including crops (Hockings & McLennan 2012), provisioning through tourism (McKinney 2015; Saj et al. 1999) or food waste (Altmann & Muruthi 1988). McLennan (2013) states that Bulindi, which is similar to Kasongoire in both forest structure and degree and type of human disturbance, is not a food-impooverished habitat for chimpanzees.

5.1.3 Effect of human foods on behaviour

Differences and changes in energy intake will directly affect activity budgets, as driven by habitat quality and seasonal fluctuations in food availability. Cultivated foods which can be easily accessible provide alternative resources that are often energy-rich, high in simple sugars and easily digested carbohydrates (Hockings et al. 2009; McLennan & Ganzhorn 2017). These will likely be valuable to primates, particularly during periods of wild food scarcity.

Chimpanzees are known to feed on a range of cultivated foods (Bessa et al. 2015; Bryson-Morrison et al. 2016; Hockings & McLennan 2012; McLennan 2013; McLennan & Ganzhorn 2017;

Naughton-Treves et al. 1998). Indeed, the higher the degree of exposure a chimpanzee community has to crops, the more likely it is they will feed on them (Hockings & McLennan 2012). Where chimpanzees inhabit highly fragmented landscapes in proximity to agriculture, crops are likely to be an integrated part of their diet (Hockings et al. 2009; McLennan 2013). Therefore, if cultivars are available during periods of wild fruit scarcity it is likely they will influence the activity budgets of chimpanzees in human-impacted habitats.

Primates which forage on human food have often been reported to spend more time resting and less time travelling than their counterparts without access to anthropogenic foods. Semi-provisioned barbary macaques (*Macaca sylvanus*) which had access to human food through tourists spent less time feeding and travelling, and more time resting and engaging in aggressive behaviours (El Alami et al. 2012). Savannah baboons (*Papio cynocephalus*) foraging on garbage were reported to spend a dramatically lower proportion of time feeding and higher proportion resting than wild-feeding groups (Altmann & Muruthi 1988). Similarly, Strum (2010) found that olive baboons (*Papio anubis*) consuming crops fed less, rested more and socialised more than those who did not. Campbell-Smith et al. (2011) also found that crop-foraging Sumatran orangutans (*Pongo abelii*) inhabiting an isolated agro-forest habitat fed less and rested more than all other studied orangutan populations. Alternatively, Hockings et al. (2012b) found that chimpanzees (*Pan troglodytes verus*) spent more time feeding, travelling and socialising and less time resting on days when cultivated foods were consumed.

Primates show some variations in their socio-ecological responses to living in human-impacted habitats. However, overall it seems that primates affected by humans often respond by exhibiting decreased feeding time and increasing resting time, as mentioned above. In a forest setting without (or with minimal) human disturbance, this is how primates are expected to respond when inhabiting “better” habitats (such as those with higher feeding species densities) (Iwamoto & Dunbar 1983). Anthropogenic habitats encompass a diverse array of habitats, so this needs to be taken into account when examining the ways that wildlife responds to humans and their activities. However, whether in an urban environment, through provisioning by tourists or as a result of human encroachment into forested habitat, proximity to humans may result in a higher availability of food resources, meaning that anthropogenic habitats may be more similar to “better” quality forested habitats in certain instances.

An additional factor which may influence chimpanzee activity patterns is the risk posed by humans themselves: animals in proximity to humans may have to alter their behaviour to deal with potential risks in the habitat (Hockings et al. 2012b; see also Chapters 6 and 7). Chimpanzees in human-impacted habitats may be fearful of human contact, especially where hunted or directly persecuted (Hicks et al. 2012, 2013) and avoidance of certain areas or of humans themselves may influence travel patterns and time spent travelling. Lion-tailed macaques (*Macaca silenus*) in close proximity to humans increased their time travelling and spent less time resting than those in protected areas as a result of frequent human presence in the forest (Menon & Poirier 1996). However, some chimpanzee populations living in close proximity to humans may not avoid anthropogenic areas (Bortolamiol et al. 2016; McLennan 2008), although perhaps this is a result of very little remaining habitat. Where human pressure is high, chimpanzees may forage on crops at specific times to avoid the risks of entering crop gardens when they are guarded. For example, chimpanzees at Sebitoli in Kibale National Park, Uganda, are known to forage on crops at night perhaps to avoid detection (Krief et al. 2014).

5.1.4 Chapter aims

In this chapter I examine the socio-ecological responses of chimpanzees in a human-influenced environment through a direct comparison of activity budgets between those inhabiting a low-impact habitat (Waibira) and those in a high-impact habitat (Kasongoire). Specific questions addressed here are:

- Do chimpanzees in Waibira and Kasongoire show differences in their overall activity budgets?
- Are there inter- and intra-community sex differences in activity budgets?
- Are there seasonal differences in activity budgets within each community?
- Does access to human cultivars influence chimpanzee activity budgets at Kasongoire?

5.1.5 Hypotheses and predictions

Table 5.1 outlines the hypotheses and predictions tested in this chapter, relating to the research questions listed in section 5.1.4.

Table 5.1: Hypotheses and predictions relating to chimpanzee activity budgets at Waibira and Kasongoire, and the framework for testing them.

Hypothesis	Prediction	Analysis
Primates incorporating high-energy crops into their diets will exhibit altered activity budgets as compared to those with no access to crops.	1. Kasongoire chimpanzees will spend less time feeding, more time resting and less time travelling than Waibira chimpanzees; 2. At Kasongoire, males will spend less time feeding and more time resting than females; 3. Waibira males and females will not show significant differences in activity budget; 4. Kasongoire females will not show significantly different activity budgets to those at Waibira.	1. I calculate the time spent engaged in each activity per day and use Mann Whitney U tests to determine significant differences in each activity between communities. 2, 3 & 4. I calculate time spent in each activity for males and females per day and use Mann Whitney U tests to determine significant differences in each activity between sexes within and between communities.
When preferred foods are scarce, animals will have to show flexibility in their time budgets	5. When ripe fruit availability is low, chimpanzees will spend more time feeding and less time resting and travelling as compared to when fruit availability is high.	5. I compare daily time spent in each activity against FAI scores, categorised as “low”, “medium” and “high” based on categorisations previously made for FAI scores (Chapters 3 & 4) using a Mann Whitney U test for Waibira data (2 FAI categories) and Kruskal Wallis for Kasongoire data (3 FAI categories).
Chimpanzees will show altered activity budgets on days when crops are consumed as compared to days when they are not consumed.	6. Kasongoire chimpanzees will travel less and rest, groom and engage in other behaviours more on days when sugarcane is consumed.	6. I calculate daily time spent in each activity use Mann Whitney U tests to assess whether activity budgets changed as a function of whether sugarcane was consumed or not consumed.

5.2 METHODS

5.2.1 Data collection

Chimpanzee activity and feeding behaviour are typically recorded using continuous focal sampling (Doran 1997; Hockings et al. 2012b). However, following a focal individual for a day was not generally possible in this study because chimpanzees were out of sight when in thick vegetation.

An alternative sampling method was required that would be equally effective at recording the data needed to answer the research questions.

Instantaneous group scan sampling is a suitable alternative to focal sampling. Fragaszy et al. (1992) suggest that group scan sampling is well-suited to profiling activity budgets, particularly when not all individuals in a party are known or visible. However, Amato et al. (2013) found that instantaneous group scans over-estimated travelling and under-estimated feeding, whereas Gilby et al. (2010) found that group scans slightly over-estimated feeding, particularly for males. What is most important to note is that these studies unanimously found that overall focal and scan sampling data sets were highly correlated and thus scan sampling is a more than adequate choice of methods if focal sampling is not possible.

The activity of all individuals in the party was recorded during every 15 minute scan using the ethogram (Table 5.2, based on Nishida et al. 1999). State and event behaviours were recorded and behaviour codes used for the overall activity budget comparisons. For example, if an aggressive interaction (event) was occurring during the scan, then this would be recorded as 'Other' (state).

Table 5.2: Ethogram of chimpanzee activities taken during 15 minute scan samples.

Behaviour categories	Description
Feed (F) [Sugarcane feeding (S)]	The ingestion of any food stuffs, including drinking. Time spent moving within the same tree to access the same food (foraging) was included, if the individual had previously been feeding and continued to feed. Chimpanzee feeding on sugarcane (S) was recorded in Kasongoire for analyses involving effects of sugarcane on activity but was classed as feeding (F) for comparison of overall activity between chimpanzee communities, since Waibira chimpanzees did not have access to sugarcane.
Rest (R)	Inactive periods with no other activity; sitting or lying on the ground or in a tree or nest.
Travel (T)	Moving with intent to change location: including quadrupedal walking on the ground or in a tree, clambering between trees, climbing trees and bipedal walking.
Groom (G)	Grooming with another individual(s) or self-grooming.
Other (O)	All other activities, including nest-building (N), hunting (H), vocalising (V), and non-grooming social behaviours and events: playing (P), aggression (A) (initiator or recipient).
Unseen (X)	Individual known to be in party but unable to confirm activity. Usually passive (resting, self-grooming) but unable to distinguish through vegetation. Also used when individual was counted in the party but unseen.

In the Waibira chimpanzee home range, large clusters of lianas would sometimes obstruct observations. At Kasongoire, papyrus swamps were dominated by 2-3 m high *Cyperus papyrus* often making these areas impenetrable to the observer; edge habitat was dominated by thick scrubby vegetation, namely the invasive shrub *Lantana camara* and also *Acanthus pubescens*. These habitats were often favoured by chimpanzees for resting in during the hottest hours. When chimpanzees spent periods of time in these dense habitat types I was usually able to stay with the animals but was often out of visual contact with many, or sometimes all, of the party. In these instances chimpanzee activity was marked as “unseen”.

Data were collected by AO (July 2015-July 2016), BKJ (November-July) and MR (July-September) at Kasongoire and by AO only at Waibira. Inter-observer reliability tests were conducted every three months to ensure consistency between observations.

5.2.2 Data analysis

The proportion of time the chimpanzees spent in each activity was calculated for each day by summing the records for each activity and dividing by the total number of records. This was repeated with the proportion of time per day spent on each activity calculated for males and females. Days with fewer than five scans and more than 50 percent of records marked as “unseen” were eliminated from the analysis. Fruit availability was categorised into “high” (FAI>1000), “medium” (FAI=500-999) and “low” (FAI<500), based on the results of this study (Chapter 3).

In Kasongoire, whether sugarcane had been fed on that day was added after summarising the data: sugarcane feeding was recorded under a separate code in the field but was included in “feeding” for the comparative analysis with Waibira. However, because further analyses within Kasongoire alone assess the impact of sugar-feeding days on chimpanzee activity patterns, the proportion of time spent in each activity was calculated to make a separate data set for Kasongoire representing time spent feeding on sugarcane and wild foods.

Normality tests were performed on the activity data for both communities (data were strongly positively skewed) and remained non-normal after transformation. Therefore, I used non-parametric statistics to analyse the data. I used chimpanzee activities from the ethogram (Feed, Rest, Travel, Groom, Other) as response variables and performed Mann Whitney U tests to assess whether there were significant differences in chimpanzee activity budgets between Kasongoire

and Waibira communities (Prediction 1), as well as between males and females within and between sites (Predictions 2, 3 & 4). At Waibira, there were two categories of fruit availability (low and medium) since no data were collected during the period of high fruit availability (January); at Kasongoire there were three (low, medium and high). Therefore, I used a Mann-Whitney U test to assess the influence of fruit availability on activity budgets at Waibira and a Kruskal-Wallis test was used with the Kasongoire data since there were three categories (Prediction 5). Lastly, I used a Mann Whitney U test to assess whether consuming sugarcane affected chimpanzee activities at Kasongoire, sorting the data into days when sugarcane was and was not consumed (Prediction 6). Post-hoc Dunn's test revealed differences between categories, with adjusted p-values using a Bonferroni correction.

5.3 RESULTS

Chimpanzee behavioural data were collected from July 2015 to May 2016 at Waibira, and between July 2015 and July 2016 at Kasongoire. Chimpanzees were followed on 161 days, generating 829 hours of observation data. After removing days with fewer than 5 scans and/or $\geq 50\%$ records marked as unseen, 8.1% of all scans were eliminated, leaving a 3052 scans and 15,990 records included in the final analyses (see Table 5.3 for sampling effort and total number of scans and records collected and analysed).

Table 5.3: Sampling effort at Waibira and Kasongoire.

	Total collected			Analysed*		
	Days	Scans	Records	Days	Scans	Records
Waibira						
All parties	36	817	3341	33	791	3265
Male only	34	748	2022	30	727	1954
Female only	32	776	1271	31	772	1267
Kasongoire						
All parties	125	2499	14,361	102	2261	12,725
Male only	118	2426	8660	97	2174	7550
Female only	114	2406	5273	97	2197	4828

*Scans and records remaining for analysis after removing days with < 5 scans and/or $\geq 50\%$ records marked as "unseen"

Waibira chimpanzees spent a mean of 55.1% ($\pm$ SE 3.4) of their daily percentage time recorded feeding, 16.1% ($\pm$ SE 2.5) resting, 10.16% ($\pm$ SE 1.6) travelling, 6.7% ($\pm$ SE 1.2) grooming and 2.5% ($\pm$ SE 0.3) engaged in other activities. Chimpanzees were recorded as unseen in 11.3% ($\pm$ SE 1.7) of all records (Figure 5.1).

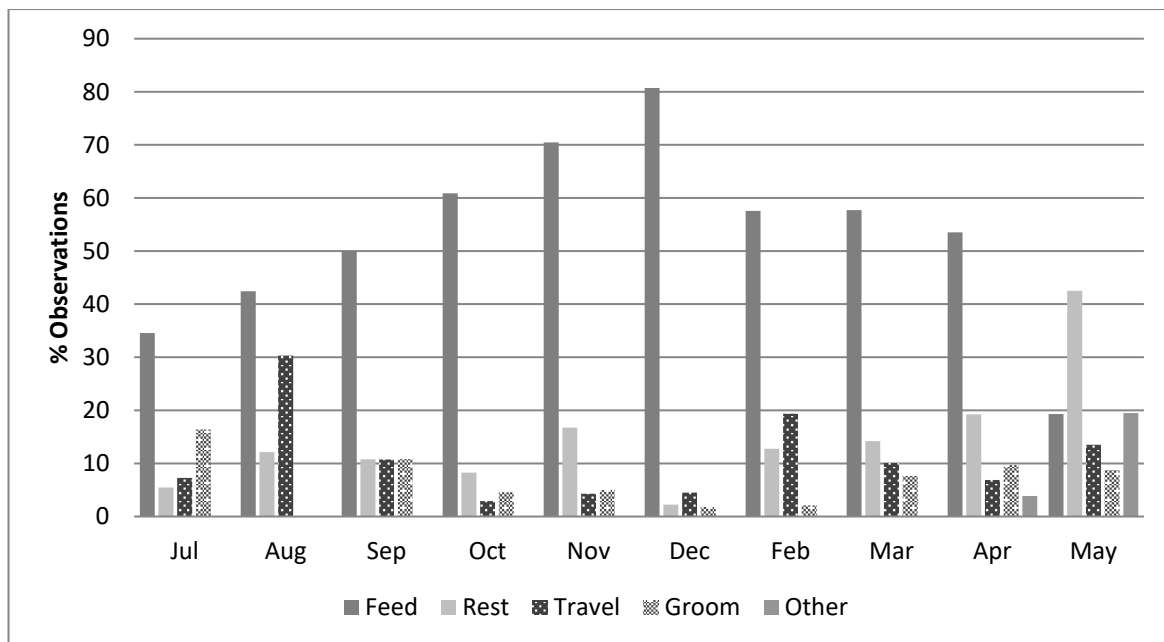


Figure 5.1: Monthly variation in Waibira chimpanzees' activity budget.

At Kasongoire, chimpanzees spent 28.4% ($\pm$ SE 1.5) of their daily time feeding, 29.5% ($\pm$ SE 1.5) resting, 7.8% ($\pm$ SE 0.8) travelling, 9.5% ($\pm$ SE 0.8) grooming and 0.9% ($\pm$ SE 0.2) in other activities (Figure 5.2). A mean of 23.8% ($\pm$ SE 1.1) of all records were marked as 'unseen'. Kasongoire chimpanzees spent 17.5% ($\pm$ SE 1.3) of their total activity budgets feeding on wild foods and 10.9% ($\pm$ SE 1.5) feeding on sugarcane.

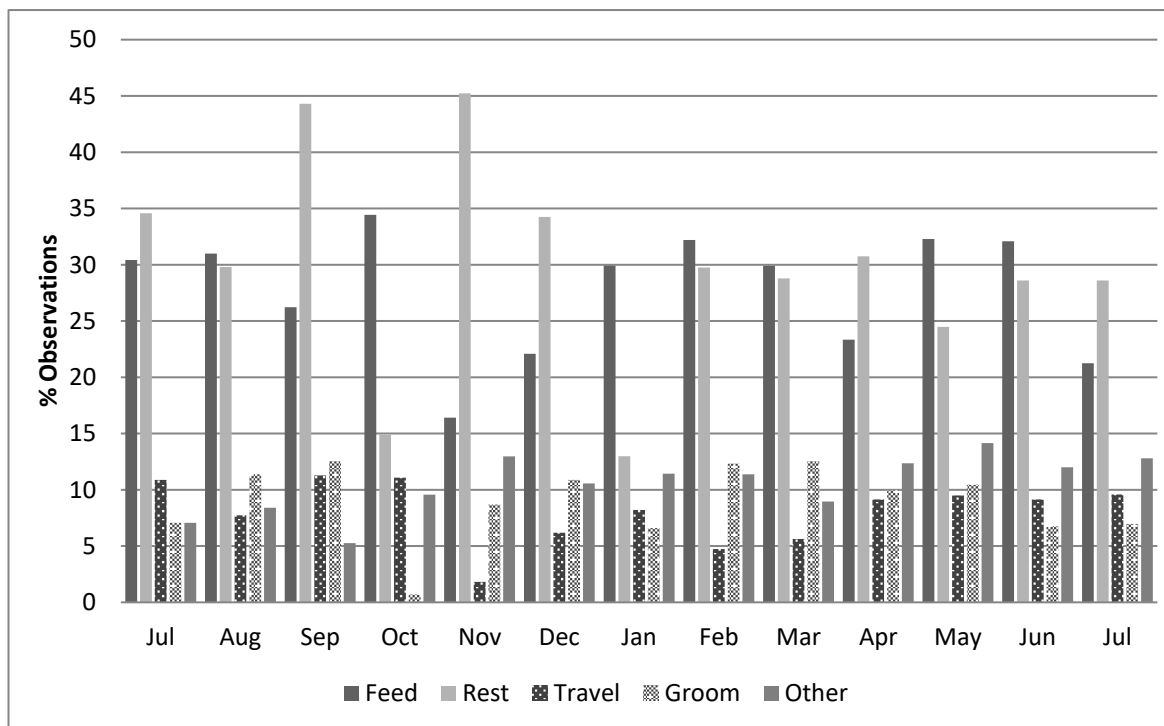


Figure 5.2: Monthly variation in Kasongoire chimpanzees' activity budget.

5.3.2 Activity budget comparison by site

Mann-Whitney tests showed significant differences between chimpanzee daily activity patterns at each site (Figure 5.3). As expected (Prediction 1), Kasongoire chimpanzees spent less time feeding ($U=2911$, $N=135$ [Waibira: 33 days, Kasongoire: 102 days], $p<0.001$), and more time resting ($U=728.5$, $p<0.001$) and grooming ($U=1259$, $p=0.03$) than did Waibira chimpanzees. There were no significant differences in time spent travelling ($U=1999$, $p=0.105$) or engaging in social behaviours ($U=1496.5$, $p=0.255$) between the two communities. Kasongoire chimpanzees were recorded as “unseen” significantly more often than chimpanzees at Waibira ($U=636$, $p<0.001$).

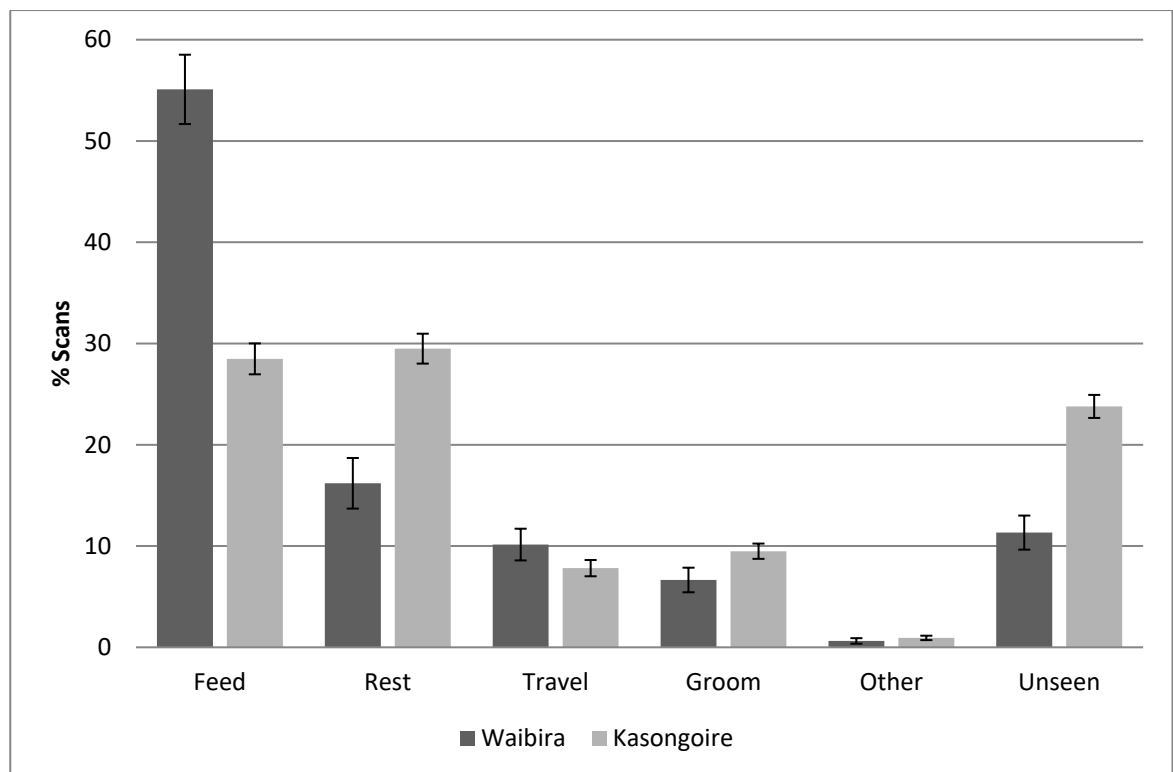


Figure 5.3: Activity budget profiles of chimpanzees at Waibira and Kasongoire during the overall study period showing mean values ($\pm$ SE) across the study period.

5.3.3 Influence of sex on activity budgets

Kasongoire males spent less time engaging in ‘other’ behaviours than Kasongoire females ($U=3756.5$, $N=194$ [males=97 days, females=97 days], $p=0.001$; Figure 5.4). No other activities were significantly different between sexes within Kasongoire chimpanzees (feed: $U=4555.5$, $p=0.703$; rest: $U=4581$, $p=0.752$; travel: $U=4723.5$, $p=0.961$; groom: $U=4593$, $p=0.755$), contradicting the expectation that males and females at Kasongoire would show significant differences in their activity budgets as a result of males foraging heavily on sugarcane (Prediction 2). Waibira males and females showed no significant differences in activity budget profiles ($N=62$

[males=32 days, females=30 days], feed: $U=512.5$, $p=0.652$; rest: $U=458$, $p=0.751$; travel: $U=366$, $p=0.106$; groom: $U=526$, $p=0.514$; other: $U=436$, $p=0.347$), supporting Prediction 3.

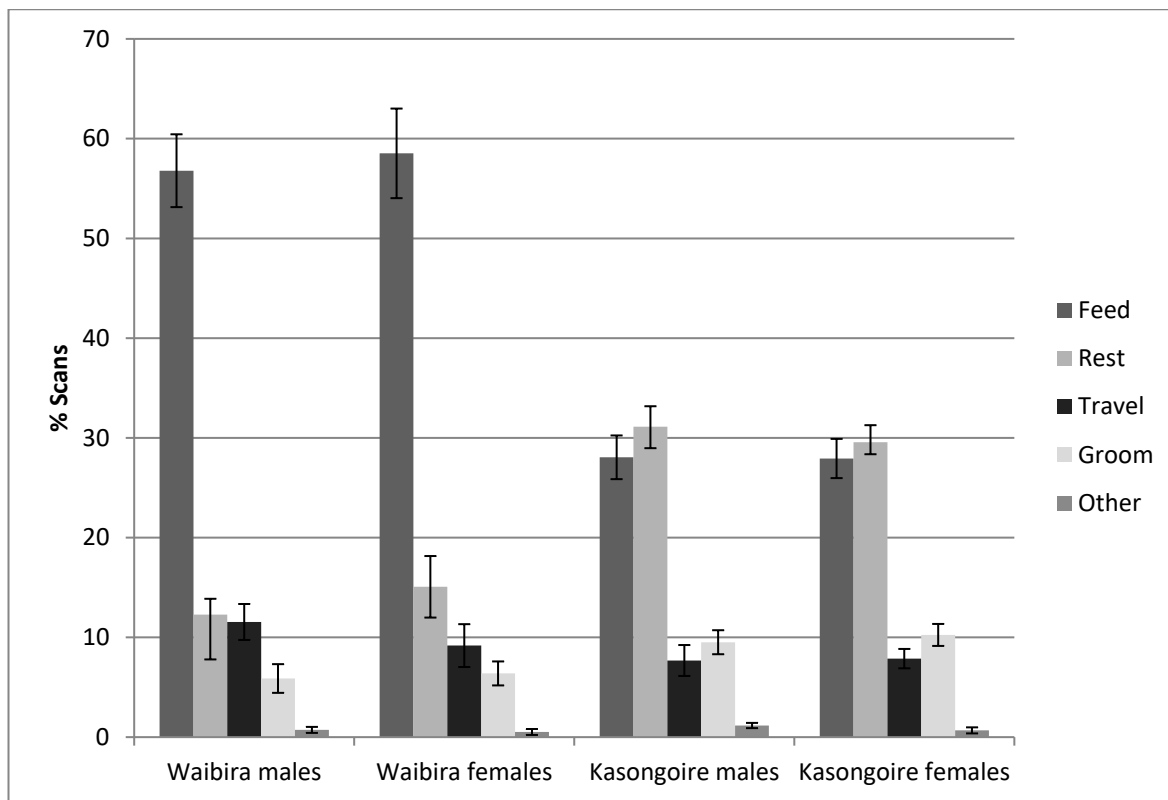


Figure 5.4: Activity profiles of males and females in Waibira and Kasongoire, showing mean values ($\pm$ SE) across the study period.

Kasongoire males spent significantly less time feeding than did Waibira males ($U=433$, $N=12$ [Waibira=30 days, Kasongoire=97 days, $p<0.001$], more time resting ($U=2405$, $p<0.001$), less time travelling ($U=1008.5$, $p=0.010$) and more time grooming ($U=1885.5$, $p=0.014$): there was no difference in time spent engaging in other behaviours ($U=1587.5$, $p=0.357$). Kasongoire females spent significantly less time feeding ($U=466.5$, $N=128$ [Waibira=31 days, Kasongoire=97 days], $p<0.001$) and more time resting ($U=2298$, $p<0.001$) than Waibira females, meaning that Prediction 4 was unsupported. Unlike males, there were no differences in females' time spent travelling ($U=1399.5$, $p=0.558$) or grooming ($U=1788$, $p=0.11$) and no differences were found in time engaged in other behaviours ($U=1492.5$, $p=0.915$).

5.3.4 Effect of fruit availability on activity budgets

Waibira chimpanzees spent less time resting and grooming and more time travelling during the period of higher fruit availability, although due to the low sample of phenology data this was not statistically tested (Figure 5.5a). At Kasongoire, fruit availability did not influence chimpanzee

activity budgets overall, contrary to Prediction 5 (N=95 [95 days of records with corresponding phenology data], feed: $H(2)=1.356$, $p=0.508$; rest: $H(2)=2.846$, $p=0.241$; travel: $H(2)=3.057$, $p=0.217$; groom: $H(2)=0.3$, $p=0.861$; other: $H(2)=2.347$, $p=0.309$; Figure 5.5b).

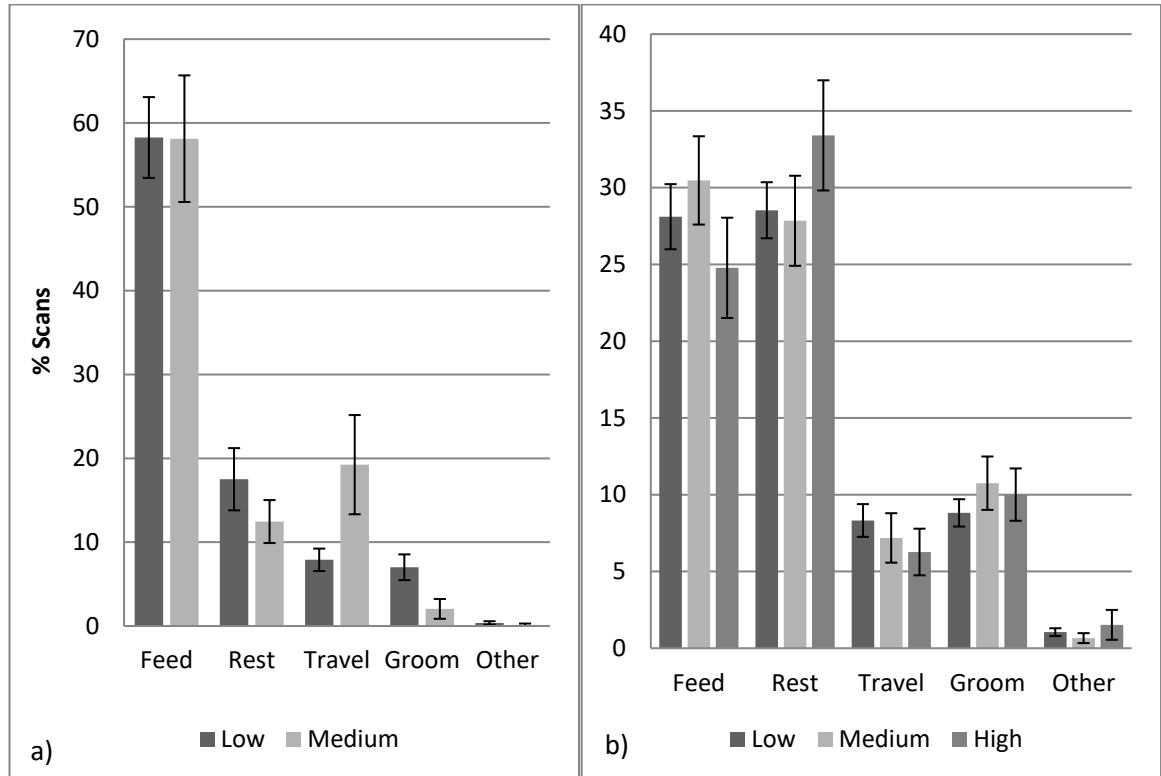


Figure 5.5: Effect of fruit availability on the activity budget profiles for (a) Waibira and (b) Kasongoire chimpanzees, showing average values ($\pm$ SE) across periods of different wild fruit availability.

5.3.5 Influence of sugarcane consumption

Kasongoire chimpanzees spent more time feeding ($U=846.5$, $N=102$ days, $p=0.004$) and travelling ($U=802.5$, $N=102$, $p=0.001$) on days when sugarcane was consumed ($n=58$). On days when only wild foods were consumed ($n=44$) chimpanzees spent significantly more time resting ($U=1925$, $p<0.001$) and grooming ($U=1774.5$, $p=0.001$), contrary to Prediction 6. However, in support of Prediction 6, chimpanzees did spend more time engaging in other behaviours ($U=887$, $p=0.002$) on days when sugarcane was consumed (Figure 5.6).

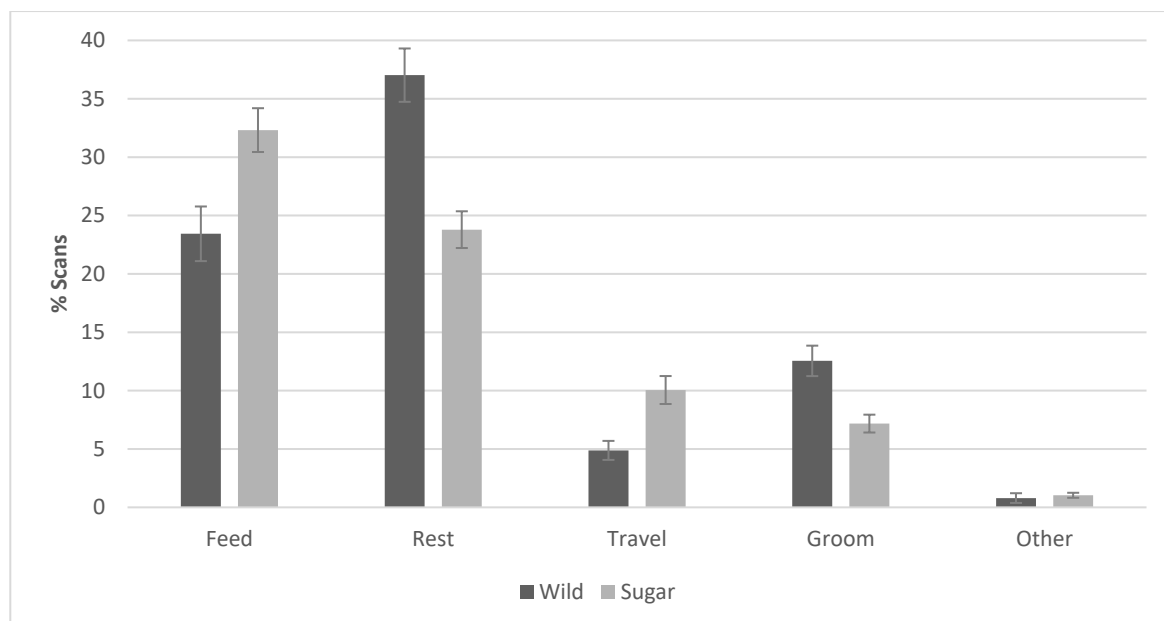


Figure 5.6: Mean percent ($\pm$ SE) of daily activity budgets for Kasongoire chimpanzees on days when sugarcane was consumed as compared with days when only wild foods were consumed.

5.4 DISCUSSION

5.4.1 Chimpanzee activity budgets

The results from this study show that chimpanzees at Kasongoire adjust their activity budgets in response to living in a human-influenced habitat. As expected (Prediction 1), chimpanzees at Kasongoire spent significantly less time feeding, more time resting and less time travelling than did chimpanzees at Waibira, as is the case for most other studied primates in human-influenced habitats (Altmann & Muruthi 1988; Campbell-Smith et al. 2011; El Alami et al. 2012; Strum 2010). I hypothesised that this comparatively higher amount of time spent resting and lower time feeding would be driven in large part by the availability of cultivated foods. In the case of Kasongoire chimpanzees the only cultivated food I was able to record them feeding on was sugarcane and so I expected that they would rest more and feed less on days when sugarcane was consumed. However, chimpanzees at Kasongoire seem to exhibit this pattern on days when only wild food was consumed, meaning that sugarcane consumption was not necessarily the cause of this behaviour: on days when Kasongoire chimpanzees fed on wild foods only, they fed for a significantly shorter amount of time than when sugarcane was consumed. One possibility explaining this is that the chimpanzees adopt a strategy of optimising caloric intake when choosing to forage on sugarcane, although there will be other aspects of nutritional requirements involved in their foraging habits (see Section 4.4.6, Chapter 4). It has already been established

that despite human-driven forest loss the habitat at Kasongoire is not food impoverished (Chapter 3), implying that wild foods still provide a substantial amount of energy and nutrients, as is the case with neighbouring Bulindi chimpanzees (McLennan & Ganzhorn 2017). Further analyses using first order autoregression could shed light on whether the effect of consuming sugarcane the day before predicted Kasongoire chimpanzee activity budgets the following day.

The fact that Kasongoire chimpanzees spent less time feeding and more resting suggests that they meet their metabolic needs faster than those at Waibira. Saj et al. (1999) reported that vervet monkeys (*Chlorocebus aethiops pygerythrus*) with access to high-quality and predictably available human food sources spent almost twice as much time engaging in resting than feeding, attributing this to dramatically increased foraging efficiency and acquisition of energetic needs. While not so pronounced (Kasongoire chimpanzees spent only slightly more time resting than feeding overall), it is certainly likely that they experience much greater foraging efficiency than Waibira chimpanzees when feeding on a hyper-abundant and spatially clumped high-energy resource such as sugarcane.

However, time spent feeding may have been over-represented at Waibira. This is due to often initially finding chimpanzees in feeding trees within the home range, rather than through other methods, such as following vocalisations or opportunistic encounters. Since the Waibira chimpanzees' home range is large, the likelihood of encountering chimpanzees opportunistically was low when searching in the morning or when we lost the chimpanzees. Similarly, due to the undulating topography, locating chimpanzees by listening to their vocalisations was often difficult as hills acted as a barrier to the sound carrying in certain areas. Therefore, the most effective technique for locating chimpanzees at Waibira was by checking known feeding trees, where a large fruiting *Ficus* sp. could support over 30 individuals.

Travelling was likely under-represented at both sites due to difficulties in terrain, although this may have been more pronounced in the forest habitats at Kasongoire. Chimpanzees would often travel larger distances at the forest edge in the gap between the forest and the sugarcane plantations, meaning that any potential bias from under-recording chimpanzees travelling in the forest interior would have been balanced by successful recording in the edge. However, time spent travelling within the village-garden matrix will have been completely missed since chimpanzees were not followed into crop gardens. Hockings et al. (2012b) provide the only study focusing on activity patterns where chimpanzees were followed to crop gardens. They found that

on crop-feeding days chimpanzees at Bossou increased their travel time, presumably to access cultivars.

Sex differences

Male primates have often been reported to forage on crops more than females (Hockings et al. 2012b; Strum 2010; Wallace & Hill 2012), with some exceptions (e.g. Sumatran orangutans, *Pongo abelii*: Cambell-Smith et al. 2011). Therefore, males and female chimpanzees at Kasongoire were predicted to exhibit differences in their activity patterns as a result of higher crop consumption by males, particularly sugarcane (Prediction 2). However, against predictions, no differences in time spent feeding, resting or travelling were found between the sexes at Kasongoire.

At Waibira, males and female chimpanzees also did not differ in their activity patterns, in line with Prediction 3. Tying in with the overall comparative results between communities, males at Kasongoire spent significantly less time feeding than males at Waibira and more time resting, likely explained by the high proportion of their overall feeding time engaged in consuming sugarcane. Waibira males spent significantly more time travelling than did males at Kasongoire, which could be explained by optimal foraging theories, i.e. they needed to spend more time travelling to access foods. Additionally, Kasongoire males appear to have no need for border patrolling, since they share no obvious territorial borders with other chimpanzees communities. In contrast, Waibira males have to maintain the borders of a much larger overall home range against neighbouring chimpanzee communities (Mitani & Watts 2005). Although this is not a daily activity, it will likely have an impact on overall activity patterns, particularly time spent travelling.

It was expected that females at Kasongoire, with their lower consumption of crops, as compared with males, would exhibit no significant differences in their activity patterns than females at Waibira (Prediction 4). However, females at Kasongoire spent significantly less time feeding and more time resting than females at Waibira, reflecting the same pattern found for males. This suggests females with access to crops may still meet their metabolic needs more efficiently than those in more in-tact habitats with a predominantly wild food diet, despite the fact that they incorporated sugarcane into their diet to a much lesser degree than males.

Influence of wild fruit availability on activity budgets

When ripe fruit availability was high I expected chimpanzees to spend less time feeding and more time resting and travelling (Prediction 5), as was found for chimpanzees in Tai (Doran 1997) and in one study at Sonso (Fawcett 2000). However, contrary to what I expected, at Kasongoire fruit

availability did not affect chimpanzee activity budgets. At Waibira, the small phenology data set meant that it was not possible to analyse the influence of wild fruit availability on chimpanzee activity statistically. However, it is evident that chimpanzees spent less time resting and more time travelling when fruit was more abundant. When wild foods were most abundant (February) chimpanzees spent almost 50% of their feeding time foraging on just two species which were spatially clumped in the north eastern side of their territory (seeds of *Cynometra alexanderi* and ripe fruits of *Strychnos mitis*). Why the chimpanzees were found to travel more when their feeding resources appeared geographically clustered could be potentially explained by the location and availability of water during this period. Waibira chimpanzees travel to specific water sources in the dry season when temperatures are hotter. This meant that although they primarily concentrated their foraging efforts in a specific area, they regularly travelled some distance to and from the water sources. Therefore, instead of resting more during the period of wild food abundance to save energy, chimpanzee time budgets were impacted by their need to access water.

Kosheleff and Anderson (2009) found that chimpanzee activity budgets were impacted by temperature in the sun and the level of sun exposure at Sonso, particularly in the human-impacted site of the old sawmill, where chimpanzees spend large portions of the day resting under *Lantana camara*. They found that increased temperature and exposure resulted in a significantly higher degree of terrestriality and increased time spent resting, corroborating results from Bossou (Takemoto 2004). As a result of edge effects and more broken and open canopies due to logging (Laurance et al. 2011) at Kasongore, chimpanzees there are more exposed to the sun than those at Waibira. Therefore, it is very likely that in addition to cultivated food availability affecting feeding patterns, time spent resting was similarly strongly affected by temperature in the sun and sun exposure. If Kasongore chimpanzees are affected by sun temperature, it would also have been expected to see peaks in travelling during the cooler parts of the day, as has been recorded in chimpanzees in Fongoli, a much hotter and more arid environment than most forest populations experience (Pruetz & Bertolani 2007). However, Kasongore chimpanzee travel time did not vary throughout the day at all, although travel distances seemed, through personal observation, to be much greater during the morning and evening periods. At Kasongore the highest proportion of “unseen” records were collected between 10:00-15:45, when chimpanzees increase their time taking cover from the sun and resting. The thick vegetation in the swamp and edge habitats was preferred by chimpanzees to spend much of their inactive period during the hottest part of the day, explaining the higher proportion of “unseen” records during these parts of

the day. Given that the proportion of time recorded as “unseen” was significantly higher in Kasongoire than at Waibira, it can be assumed that the proportion of time resting and grooming were under-represented in Kasongoire. Therefore, the difference between resting and grooming between Kasongoire and Waibira communities might be even more pronounced.

5.4.2 Comparisons with chimpanzee communities across Africa

Although resting was likely under-represented at Waibira, the values reported in this study are still higher than those found for chimpanzees in similar forest in Uganda, in Kibale National Park (Kanyawara and Ngogo, Table 5.4). From studies of the neighbouring Sonso community, chimpanzees at Budongo are reported to spend around 53% of their daily activity budget feeding (Fawcett 2000), also suggesting the results from this study may not be so distorted.

Table 5.4: Summary of activity budgets from this study and comparisons to other chimpanzee study sites. Feeding, resting, travelling and social/other are expressed as proportions of daily time budget spent in each activity.

Study community	Country	Author/s	Disturb. ranking ¹	Feed	Rest	Travel	Social /Other
Waibira	Uganda	<i>This study</i>	7 ²	55.1	16.1	10.2	9.1
Kasongoire	Uganda	<i>This study</i>	13+ ³	28.4	29.5	9.5	10.4
Bossou	Guinea	<i>Hockings et al. 2012b</i>	13	22.5	52.4	19.5	5.6
Conkouati-Douli	DRC	<i>Renaud et al. 2013</i>	n.d.	51.5	26.5	14.9	2.5
Gombe	Tanzania	<i>Wrangham 1977</i>	8	55.6	23.5	14	2.6
Goualougo	Congo	<i>Sanz 2004</i>	4	22.1	50.8	12.8	14.3
Fongoli	Senegal	<i>Pruetz & Bertolani 2009</i>	12	24.5	63	11.5	-
Kanyawara	Uganda	<i>Potts et al. 2011</i>	10 ⁴	44	11	45	0
Mahale	Tanzania	<i>Huffman 1990</i>	5	29.7	38.6	19.5	12
Sonso	Uganda	<i>Fawcett 2000</i>	10	52.8	25	7.5	14.3
Ngogo	Uganda	<i>Potts et al. 2011</i>	10 ⁴	47	14	34	5
Tai	Ivory	<i>Doran 1997</i>	6	43	39	12	6
Tai	Coast	<i>Boesch & Boesch-Achermann 2000</i>	6	54	22	22	Incl. in resting

¹ Disturbance ranking, as assessed by Hockings et al. (2015a) based on 4 categories: elimination of predators, hunting pressure, harassment from humans and site disturbance. 0 denotes no disturbance, although the minimum score was 4. The maximum was Bossou with 13.

² If the score is the same as Budongo it would be 10 (Hockings et al. 2015a). However, it is likely this score measures the Sonso habitat around the previous sawmill site. Waibira will therefore have a lower score than Sonso: based on personal observations of the four categories I have scored it at 7.

³ Only long-term field studies were ranked in Hockings et al. (2015a), meaning that fragment communities such as Bulindi were not included. These would certainly have a higher score than long-term field sites.

⁴ Kanyawara and Ngogo are both chimpanzee communities within Kibale National Park. The score for disturbance in Hockings et al. (2015a) is reported for Kibale, although the two sites are impacted by humans to differing degrees: Ngogo is relatively undisturbed compared to Kanyawara. See Appendix 1 for revised further information about disturbances at these sites.

As highlighted in Table 5.4, chimpanzees across study sites exhibit a high level of variation in their activity budgets: there is no apparent pattern seen in chimpanzee activity patterns across the spectrum of sites of varying degrees of disturbance. The proportion of time spent feeding by chimpanzees at Kasongoire is certainly below the average from several other studies, although Bossou chimpanzees' time spent feeding was even lower (Hockings et al. 2012b). Considering that unseen behaviours recorded at Kasongoire were largely during times of days when chimpanzees were resting and grooming, resting and social/other behaviours are under-represented. Therefore, activity patterns of chimpanzees at Kasongoire more closely reflected results from both less disturbed sites including Goualougo (Sanz 2004) and Mahale (Huffman 1990), and the disturbed sites at Bossou (Hockings et al. 2012b) and Fongoli (Pruetz & Bertolani 2009), where chimpanzees spent less time feeding than resting.

5.4.3 Impacts on survival

At Kasongoire, like many other fragmented sites, chimpanzees have access to cultivated resources outside the forest, but without the abundant and spatially clumped resource of sugarcane, their activity patterns and responses to disturbance would likely look a lot different. The responses and survival prospects of an animal therefore rely on the nature of the disturbance and human-influenced habitat. Black howler monkeys (*Alouatta caraya*) in Brazil would not survive or would survive only in very low densities if it was not for the availability of exotic species, primarily orange, *Citrus sinensis*, which is described by the authors as a staple food for these primates (Bicca-Marques & Calegario-Marques 1994). Bearded saki monkeys (*Chiropotes satanas chiropotes*) in small fragment forests in the central Amazon showed a large degree of behavioural and dietary flexibility, feeding on food items that conspecifics in continuous forest ignored (Boyle & Smith 2010; Boyle et al. 2012). However, the authors predict that this foraging strategy is unlikely to be viable in the longer term without habitat connectivity (Boyle et al. 2012) and show that disturbance has already had a deleterious effect on low reproductive rates (Boyle & Smith 2010).

As well as the nature of disturbance, the habituation of animals to that disturbance is also a factor to take into account when considering their responses on a broader scale. In a review of the impact of logging on mammals in Borneo, Meijaard and Sheil (2008) broadly classified animals

into those that were “tolerant” and “intolerant” of logging. However, even within the same species, different responses can be seen based on the history and type of contact with humans, which will affect the same species’ behavioural responses differently. In jackass penguins (*Spheniscus demersus*), individuals in a group which was habituated to human disturbance were more relaxed (laying down resting) compared with the undisturbed group which showed much more pronounced agitation and vigilance when humans approached (van Heezik & Seddon 1990), showing that animals can become habituated to disturbances. In chimpanzees, avoidance (e.g. Bili chimpanzees, Hicks et al. 2012, 2013) or non-avoidance (e.g. Sebitoli chimpanzees, Bortolamiol et al. 2016) of humans will impact travel distances and time spent travelling, which will in turn affect overall energetics and activity budgets.

Orangutans have been reported to leave an area of active disturbance but return once the disturbance has stopped (Ancrenaz et al. 2010) showing a level of intolerance towards logging and implying that during the period of logging animals travelled further. However, orangutans can sometimes persist in landscapes with high levels of human activities, such as oil palm (Ancrenaz et al. 2015; Spehar & Rayadin 2017) and acacia plantations (Meijaard et al. 2010) and agroforest mosaics (Campbell-Smith et al. 2011). Russon et al. (2015) found that feeding and activity patterns of orangutans in Mentoko, East Kalimantan, had returned to normal levels twelve years after a major habitat perturbation. Their study showed that the diet and activity patterns of orangutans adjusted multiple times over the course of the forest’s recovery from major forest fires, and highlighted three important factors that influence primate behaviour in disturbed or damaged habitats: the damage and recovery type, the spatial scale of the damage and the recovery time scale.

At Kasongore, chimpanzees’ habitat has been encroached over a matter of decades: the forest was logged intensively in the 1970s and again in the 1990s when Kinyara Sugarworks Ltd cleared much of the remaining forest to make a large part of the landscape available to grow sugarcane. Most long-term studies of chimpanzees have initially been set up in supposedly “pristine” environments, and although many of these have been encroached (e.g. see Hockings et al. 2015a for a rating of long-term studies’ human disturbance rating), the literature from these field sites often still focuses on “pure” biology questions, ignoring or glossing over the impacts of humans (Hockings et al. 2015a). It would be interesting to see a long-term behavioural study on chimpanzees facing direct logging, from the stage of a low disturbance environment to fragmentation. It would be extremely difficult to conduct such a study on habituated

chimpanzees, especially since researcher presence usually has a positive effect on decreasing human activities (Campera et al. 2017; Laurance et al. 2013). However, in the area to the south of Kasongoire and Bulindi, Bugoma Forest Reserve is under increasing pressure from loggers and chimpanzees there are currently in the process of being habituated, offering a unique opportunity to study chimpanzees presently experiencing high levels of habitat disturbance.

Chimpanzees have proved to be highly flexible, even in the event of a high degree of human influence and disturbance on the landscape (Hockings et al. 2015b). In Kasongoire there appears to be enough wild food to sustain chimpanzees, in addition to cultivated foods. Even in Bulindi, which is disturbed to a higher degree than Kasongoire, McLennan (2013) describes the habitat “in no way food impoverished”, and chimpanzees continue to survive there. McLennan and Plumptre (2012) found that human-impacted sites may even support a higher density of important feeding trees. This is significant in the case of Kasongoire chimpanzees and how we understand chimpanzee behaviour and survival potential and raises the question: what do we consider a “bad” habitat? Although Kasongoire chimpanzees are able to adapt their activity budgets to persist in this human-impacted habitat, presumably there is a limit to how much habitat modification they will be able to tolerate. As long as animals have access to resources in anthropogenic habitats, whether wild, cultivated, provisioned or in urban landscapes, they may be able to survive. The key determinant to long-term persistence is human tolerance: a “bad” habitat in this context is therefore one in which animals exploiting human foods are persecuted for doing so.



CHAPTER SIX

**STEPPING ON DANGEROUS GROUND: CHIMPANZEE PARTY
RESPONSES WHEN LEAVING THE FOREST**



Plate 19 (on previous page): An all-female party travelling with their infants in the open gap between the forest edge and sugarcane plantation

6.1 INTRODUCTION

Leaving the forest is potentially risky since animals may face direct hostility or aggression from humans. Chimpanzees are a behaviourally flexible species which exhibit a high degree of fluidity in their level of fission-fusion dynamics. In a recent analysis comparing the grouping dynamics of three primate species with fission-fusion social systems – chimpanzees (*P. t. schweinfurthii*), spider monkeys (*A. geoffroyi*) and geladas (*Theropithecus gelada*) – chimpanzees were found to exhibit the highest degree of temporal variation in party composition (Ramos-Fernandez et al. 2018), highlighting the constantly shifting nature of chimpanzee party composition. Since party membership is highly fluid in chimpanzee communities, both spatially and temporally, it is likely that they would show responses in their party grouping patterns when leaving the forest.

Investigating responses to risk has been a focus of many studies, but primarily from the point of view of predation risk rather than human influences (Bleicher 2017). Studies investigating species' responses to the "Landscape of Fear" have often focused on levels of vigilance of prey species and prey-predator habitat use over space and time (Iribarren & Kotler 2012; Laundré et al. 2001, 2010; Thaker et al. 2011). In Kasongore, although humans can and do enter the forest, the risk of human interactions is much higher outside the forest boundary where chimpanzees could potentially encounter cane guards, in addition to people at the water points and on the road. This makes the spatial element of risk quite clear cut, and since chimpanzees at Kasongore spent over 40 percent of their feeding time consuming sugarcane, in addition to other crops not recorded, their use of the habitat outside the forest is a very regular occurrence (Chapter 4). This warrants further investigation into chimpanzee social responses to potential risks: exploring animal responses when in the anthropogenic matrix may help shape mitigation strategies for conflicts between humans and wildlife. Understanding changes in chimpanzee party dynamics will give further insights into their perceptions of risk in a human-influenced habitat.

In this chapter I investigate chimpanzee responses to the risk of leaving the forest habitat, comparing party dynamics of chimpanzees when engaged in different activities within and outside the forest. Factors investigated include party size and cohesiveness (the distance between the two furthest individuals in a party) and the relative composition of males and females. The information provided in this analysis will contribute to the literature on chimpanzee flexibility in risky environments and increase our knowledge of primate responses to anthropogenic landscapes.

6.1.1 Group dynamics: an overview

For group-living animals, there are numerous costs and benefits of associating with other individuals. Animals in groups must compete for resources and mating opportunities, but could benefit from reduced predation risk, building social alliances and defending territories. Costs and benefits will differ for males and females, since the primary competition between males is for access to mates (Clutton-Brock 1989; Kappeler 1999) and between females it is access to food (Sterck et al. 1997). Dunbar (1996) provides a model predicting that group size is determined by three major factors. Firstly, animals living in groups must be able to manage their time budgets, requiring group size to be balanced by feeding competition with intra-specifics in order to fulfil their basic energetic requirements. Second, animals must maintain a minimum group size that reduces predation risk which is sustainable with the reproductive rate of the group. Lastly, there is a cognitive component, determined by the neocortex size of the animal, which means that the group size must be small enough to allow them to maintain social stability within the group.

6.1.2 Party size

Predation risk

Many species form larger groups in order to counter predation risk (Alexander 1974; Anderson 1986; Dunbar 1988). Increased group size can potentially allow for individuals within the group to decrease time spent being vigilant, such as scanning and monitoring their surroundings (Beauchamp 2015). In addition to the benefit of reduced individual vigilance, larger groups create a dilution effect if a predation event occurs, whereby mortality affects only a small proportion of the group (Roberts 1996).

In diurnal primates, one of the benefits of living in groups is to allow for the detection of predators and reduction of predation rate (van Schaik 1983). Lehmann et al. (2007) found species that experience high levels of predation pressure form groups that are larger than expected, and in a study reviewing the responses of 39 species of Cercopithecoid primate groups, Hill and Lee (1998) found that high predation risk resulted in larger group sizes. Similarly, some species form polyspecific associations in response to predation risk (Terborgh 1990), as has been reported in red colobus (*Procolobus pennantii*) and red-tailed guenons (*Cercopithecus ascanius*) (Chapman & Chapman 2000), and white-bellied spider monkeys (*Ateles belzebuth*) and red howler monkeys (*Alouatta seniculus*) (Link et al. 2011), again highlighting this relationship between predation risk and primate group size. Other studies have shown no relationship between predation risk and

group size (Treves & Chapman 1996), and one study found group size decreased with higher predation rate (Isbell 1994). This presumably is a response to detectability: a larger group will be more visible than a smaller group or a lone animal. Primates generally do not exhibit lower levels of vigilance as a function of larger group sizes (Treves 2000), likely as a result of increased vigilance due to conspecific threats in larger parties.

Anthropogenic risk

When considering the size of a primate group or party in relation to risk, studies to date have almost exclusively focused on predation risk rather than the risks involved when entering an anthropogenic area. This literature helps to build an idea of how primates respond to potential risk and shows that predation risk almost unanimously results in larger group sizes, yet there is something inherently different to the risk faced by chimpanzees from humans when leaving the forest. The risk of injury or death from a human, particularly to a semi-terrestrial primate species with a higher body mass, will differ from that of a raptor to an arboreal monkey, for example. However, human presence can be considered similar to a predation risk in specific contexts (Frid & Dill 2002). Chimpanzees are a protected species and are not generally actively hunted for meat in Uganda (Babweteera et al. 2012). Nevertheless, humans are known to occasionally kill or persecute chimpanzees in this region, often in response to crop losses and in retaliation to chimpanzee attacks on people (McLennan 2008; McLennan et al. 2012; McLennan & Hockings 2016; Reynolds 2005).

Kasongire chimpanzees spent most of the observed time outside the forest foraging on sugarcane, which is theoretically tolerated by Kinyara Sugarworks Ltd. (KSWL), the company which grows and processes the sugarcane. Cane guards patrol the area for other crop-foraging animals, namely baboons, in order to chase them away. Baboons are sometimes killed by cane guards and hung up like scarecrows to deter other baboons from foraging on crops (Plate 7, Chapter 2). I did not collect specific data on how cane guards behaved towards chimpanzees when not in my presence. Therefore, it was impossible to know exactly how cane guards responded to chimpanzee presence or sugarcane foraging. However, cane guards were reported to chase chimpanzees away, meaning that chimpanzees would likely show behavioural or social adaptations as result.

Comparisons of the influence of risk from natural predators and humans are worthwhile. For chimpanzees in Taï Forest, leopards are the top cause of predation mortality (Boesch 1991); in

human-influenced landscapes humans appear to be the leading cause of mortality. While there is no specific data on this, the growing literature on chimpanzees in anthropogenic habitats is increasingly reporting fatalities (Hockings & Humle 2009) through direct attacks (Grossman cited in Pusey et al. 2007; Reynolds 2005), snares and mantraps (McLennan et al. 2012; Reynolds 2005), poaching (Boesch & Boesch-Achermann 2000; Pusey et al. 2007) and road accidents (McLennan & Asiimwe 2016), in addition to fatalities through respiratory diseases (Boesch 2008; Pusey et al. 2008; Scully et al. 2018).

In the few studies that have analysed the impact of anthropogenic risk on primate group or party size, it seems that entering risky habitats, such as crops or roads, does have an impact on party size. Buton macaques (*Macaca ochreata brunnescens*) formed larger groups when foraging on crops further from the forest boundary and the larger the group, the longer time they spent in crop-foraging forays (Priston et al. 2012). Sakura (1994) found that Bossou chimpanzees formed larger parties when crossing a major road, with smaller parties waiting for other individuals or parties to assemble before crossing. Hockings et al. (2012b) found that chimpanzee parties were slightly larger on days when they foraged on crops compared to days when they fed only on wild foods, although only in the presence of a maximally swollen female. Conversely, Warren (2009) found that baboon parties entering crop fields had a significantly reduced party size, likely to avoid detection by farmers. Similarly, Wallace and Hill (2012) found the majority of crop-foraging parties involved three or fewer individuals.

Other factors

Risk will be an important factor in shaping party dynamics. However, there are other important factors that need to be considered that will also affect party dynamics, principally the availability of food resources and the presence of sexually receptive females. Feeding competition and predation risk are also predictors of group size in primates (Janson & Goldsmith 1995), which will have a direct influence on chimpanzee grouping.

The ecological constraints model proposes that the abundance and distribution of food determines the upper limit of the number of individuals in a group: limited resources cannot support an unlimited number of animals (Chapman & Chapman 2000). In primates, the ecological constraints model has been upheld for some species, but not others. Howler (*Alouatta palliata*) and spider monkeys (*Ateles geoffroyi*) in Costa Rica were found in smaller subgroups when food resources were found at low density and spatially clumped, whereas capuchins (*Cebus capuchinus*) did not alter their grouping dynamics in response to changes in food density and

distribution (Chapman 1990). In Kibale National Park, Uganda, group sizes of red colobus monkeys (*Procolobus pennantii*) and red-tailed guenons (*Cercopithecus ascanius*) increased with food density, also upholding the ecological constraints model (Chapman & Chapman 2000).

Chimpanzees exhibit a fission-fusion social structure whereby individuals within the community associate with others temporally forming subgroups, or parties, which vary in size and sex composition (Goodall 1968; Nishida 1968; Symington 1990). It has been proposed that chimpanzees adopt a fission-fusion social system as a way of dealing with the ecological constraint of limited food availability, breaking into smaller parties to reduce competition (Lehmann et al. 2007). Due to the nature of chimpanzee social organisation, where group size and composition changes throughout the day, it is expected that chimpanzees will respond flexibly to changes in habitat and risk.

Overall, party sizes in chimpanzees increase with a higher availability of food, although not always to habitat-wide measures of abundance. For example, Sonso chimpanzees were found to form larger parties when feeding on larger patches of fruit, but there were no associations found between party size and overall measures of fruit abundance (Newton-Fisher et al. 2000). Similarly, Anderson et al. (2002) found the only measure of food availability to influence party size was the abundance of food within patches. The density and distribution of fruit was found to influence both chimpanzee and spider monkey party sizes positively, although for chimpanzees neither factor alone (density or distribution) explained this increase (Chapman et al. 1995). Other studies have found that food availability had only a partial influence on determining chimpanzee party size (Boesch 1996; Hashimoto et al. 2003; Isabirye-Basuta 1988; Matsumoto-Oda et al. 1998).

It is important to consider that a forest has a limited availability of resources, fluctuating monthly in patch size, density and the total quantity of fruit. Sugarcane availability at Kasongoire is different however: availability changes in terms of location and the amount of hectares that are mature (it is grown cyclically in hectare blocks), but overall it is a hyper-abundant and widely distributed resource. When food is spatially clumped, primates are expected to form larger parties (Chapman et al. 1995; Wrangham 2000). The joint effect of foraging outside the forest boundary and on an abundant resource will therefore presumably result in larger party sizes.

Chimpanzee party size is known to increase when there are cycling females with maximally swollen anogenital swellings (Anderson et al. 2002; Hockings et al. 2012b; Matsumoto-Oda et al.

1998; Mitani et al. 2002; Nishida 1979; Sakura 1994). The presence of swollen females has been reported to have as important an effect, if not larger, than the influence of food availability on chimpanzee party size (Anderson et al. 2002; Mitani et al. 2002). The activity of the party may also influence party size: travelling parties can be smaller than resting or feeding parties (Anderson et al. 2002; Boesch 1996).

6.1.3 Party spread

With increasing predation risk, group-living animals are likely to respond by tightening group cohesion, decreasing party spread and the distance between individuals (Hamilton 1971; van Schaik & van Noordwijk 1989). Similarly, party cohesion will likely increase when there is an abundant resource since inter-individual feeding competition is reduced (Schreier & Swedell 2012). Information on the influence of risk on party cohesion is limited, but it would be likely that individuals stay closer together in groups in areas with high predation risk. In the one study that examined the effect of entering crop fields on party cohesion, Hockings et al. (2012b) found that Bossou chimpanzees reduced arboreal party spread on days when they foraged on cultivated and abandoned fruit trees compared to wild foods.

There are interacting factors that must be considered when analysing data on party cohesion. Most importantly, party size and party spread will be correlated (Smith et al. 2005): a very large party cannot fit into the same circumference of spread as one or two individuals. It would also be expected for parties engaging in different activities to exhibit different levels of group cohesion, irrespective of risk. For example, a feeding party can only spread as far as the feeding resource will permit; grooming primates in a resting party will be in contact; and all individuals in a travelling party would be travelling together in a clear unit, which by definition requires a certain level of cohesion.

6.1.4 Party composition

With increasing predation risk, the ratio of males increases (Anderson 1989; Hill & Lee 1998; Stanford 1998). Female primates may show a higher level of risk aversion, but males have sometimes been found to be more vigilant (van Schaik & Hörstermann 1994; van Schaik and van Noordwijk 1989). In capuchin monkeys (*Cebus spp.*), males spend a significantly higher proportion of time being vigilant than do females and both adult and subadult males are more likely to mob a predator (van Schaik & van Noordwijk 1989). Similarly, male vervet monkeys (*Cercopithecus aethiops*) spend more time being vigilant than females, climbing to the top of trees to scan for

attacks from raptors (Baldellou & Henzi 1992). Therefore, males can be assumed to take on the burden of predation risk, defending conspecifics from potential attack.

Chimpanzees engage in border patrols, where individual animals risk confrontation, injury or death with conspecifics in neighbouring communities (Wilson & Wrangham 2003). Chimpanzees form all-male or male-dominated, large parties when going on border patrols to reduce the risk of aggression from a neighbouring community (Mitani & Watts 2005). This suggests that even within a non-human-influenced environment, males are the sex which takes on most of the risky activities and increasing party size is a strategy to defend against the threat of aggression.

At Kibale, chimpanzee parties that visited crops contained more males than parties in the core home range (Wilson et al. 2007). Adult male chimpanzees have been found to forage on crops more than females (Hockings et al. 2007; Wallace & Hill 2012) signifying their overall higher willingness to enter risky anthropogenic habitats. Female chimpanzees in Sebitoli, Uganda, even foraged on crops at night perhaps to avoid detection by humans (Krief et al. 2014). In Kasongore, males and females exhibit differences in their time spent consuming sugarcane (Chapter 4). With a large proportion of time spent consuming sugarcane outside the forest, this would likely influence grouping patterns for both sexes. In an environment where there is the potential risk of an aggressive encounter with humans, it is therefore expected that parties outside the forest will contain a higher male to female ratio.

Although female chimpanzees may be more risk averse, male chimpanzees still show behavioural responses to anthropogenic risk. At Kibale, Uganda, male chimpanzees reduced their rate of pant-hoot vocalisations when in crops compared to other parts of their home range, most likely to avoid detection (Wilson et al. 2007). Adult males at Bossou exhibited signs of anxiety when foraging on crops, as shown by increased rates of rough self-scratching, a self-directed behaviour, when in the presence of local people (Hockings et al. 2007). This suggests that even chimpanzees which are not hunted and have been living alongside humans and cultivation for a long period of time show responses to risk outside of the forest.

6.1.5 Chapter aims

In this chapter I investigate how degree of risk impacts chimpanzee grouping patterns to better understand chimpanzee behavioural flexibility in an anthropogenic landscape and their perception of risk. In particular, I investigate whether Kasongore chimpanzees respond to

entering the edge habitat by adjusting their grouping patterns, including party size, party spread and party composition (ratio of independent males in a party).

6.1.6 Hypotheses and predictions

Table 6.1: Hypotheses and predictions relating to ecological and risk factors predicting chimpanzee party size at Kasongoire and the framework for testing them.

Hypothesis	Predictions	Analysis
Chimpanzees will respond flexibly to anthropogenic risks by altering their grouping patterns	1. Party size will increase: a. When chimpanzees are outside the forest as compared to within the forest; b. In the presence of swollen females; c. During periods of high wild fruit availability; 2. Party cohesion will increase: a. When chimpanzees are outside the forest as compared to inside it; b. When chimpanzees are resting; c. During periods of high wild fruit availability. 3. The ratio of males to females will increase: a. When chimpanzees are outside the forest as compared to inside it; b. In the presence of swollen females; c. During periods of low wild fruit availability.	I use a generalised linear mixed model to determine whether party size, spread and the ratio of males increase as a function of: a) being inside the forest vs outside; b) the presence of at least one maximally swollen female (absent, present); c) the overall activity of the party (feeding, resting, travelling) and d) wild fruit availability (low, medium, high).

6.2 METHODS

6.2.1 Data collection

When chimpanzees were being followed, I recorded the identity of all individuals present and their activity via instantaneous scan sampling every 15 minutes, as described in Chapter 2 (Altmann 1974; Chapman et al. 1995). Party spread (measure of party cohesion) was recorded during each scan as the distance between the two individuals furthest from each other in a group. The swelling size was recorded daily for all females observed using a scale of 0 (no swelling) to 4

(maximally swollen) (Hockings et al. 2012b). The presence of a maximally swollen female was determined for each scan (present: 1; absent: 0). Habitat type was also recorded every 15 minutes using the classifications outlined in Chapter 3. If the party was spread over an ecotone of two habitats, the habitat type occupied by the majority of individuals was recorded. Fruit availability was classified as low, medium or high, as defined in Chapter 3. Time of day was grouped into morning (07:00-10:49), afternoon (11:00-14:49) and late afternoon/evening (15:00-19:00).

Party composition can be difficult to quantify because not all individuals may be visible in each scan period and determining association, particularly in less cohesive parties, is a judgement of the observer (Chapman et al. 1993). Chapman et al. (1995) used three methods to define a party: (i) all individuals visible during a scan; (ii) the party composition following a fission or fusion event; (iii) an “acoustic” party of all individuals within calling range, based on those recorded in the hour preceding and following an hourly scan. Some studies have defined a party within a set party spread, recording chimpanzees within a certain radius of the focal animal or within a set circumference (e.g. 30 m Hockings et al. 2012b; Newton-Fisher et al. 2000; 50 m: Carne et al. 2014).

Other studies have recorded party size and composition in a variety of ways: maximum party size per day (Hashimoto et al. 2003), the first scan at every fission or fusion event (Boesch 1996; Chapman et al. 1995) and party composition at first contact (Newton-Fisher et al. 2000). For this study, I defined a party as all independent individuals associating in the same area, as determined by their behaviour, and usually within a maximum diameter of 40 m since on a few occasions chimpanzees were clearly in an associated party but the distance between furthest individuals surpassed 30 m. I deemed it more important to record individuals present in an associated subgroup than to cut out individuals who were further than 30 m away. Considering the highly fluid nature of chimpanzee fission fusion dynamics (Ramos-Fernandez et al. 2018), if an individual was not visible for the following scan they were recorded as present but “unseen” for one consecutive scan unless they had been seen leaving the group.

6.2.2 Data analysis

Party size was summed for each scan by counting the number of individuals present. Habitat type categories were grouped into “forest”, including mixed forest, swamp forest, papyrus swamp, savannah-woodland, ecotone forest and “outside forest”, which included the gap (the main area chimpanzees spent time in, between the forest edge and the sugarcane; Plates 17-19 illustrate

this habitat), road, the sugarcane plantation (although most individuals were usually out of sight and party data incomplete and not used) and village-garden (used only infrequently when chimpanzees were opportunistically found in the village-garden matrix).

To assess the difference in the impact of leaving the forest on adult males and females, I created a value for the ratio of males in a party. I calculated the ratio of males in a party for every scan, with 0 denoting an all-female party, 1 denoting an all-male party and all values in between denoting a mixed party. The primary activity of the group was calculated as the activity engaged in by 50 percent or more of the party. Since the purpose of including party activity was to understand the impact of the overall activity of the party on grouping patterns, I did not include every behaviour, but defined party activity according to the potential impact it would have on party size, spread and composition. Party activities were defined as feeding, resting or travelling parties. Resting parties included individuals who were recorded as grooming or unseen in larger groups where other individuals were resting.

Party scans were recorded every 15 minutes; consequently, the data were heavily affected by pseudo-replication. For example, a party which was feeding would usually feed for longer than two consecutive scans. Similarly, a resting party could be resting for a considerable duration, particularly in the middle of the day. Travelling parties tended to travel for only one or two consecutive scans to reach a location, such as a feeding tree. Therefore, after a change of activity, the following data would be correlated to those data from the original scan until the activity changed again.

As a result of this autocorrelation, I grouped data according to party activity per day (i.e. the proportion of scans in each activity - feeding, resting and travelling - each day). Data were grouped according to party activity because fission and fusion would often precede and follow a change in activity. I created values for each day, averaging the dependent variables, party size, party spread and ratio of males for each party activity. For independent variables, I created a value for the proportion of time spent in the forest by dividing the number of data points per party activity per day by the corresponding number of data points chimpanzees spent in the forest. Similarly, the proportion of time per party activity per day where swollen females were present was calculated in this way. For several variables data were not normally distributed even after transformation. Therefore, I used non-parametric statistics throughout.

I performed a generalized linear mixed model (GLMM) to predict the effect of leaving the forest on party size, party spread and party composition (ratio of males in a party). Party size, spread and composition (male ratio) were the dependent variables, and independent variables included habitat (proportion of time outside the forest), party activity (feeding, resting, travelling), swollen females (proportion of time present in the party) and fruit availability (low, medium, high). I used a linear distribution because the target variables were continuous averages of grouping patterns. Since data were grouped by daily activity, the subject of the model was the day and party activity was entered as a repeated measure. I included the month as a random effect, since after plotting the data it appeared that grouping patterns differed between months. I checked the normality of the residuals and where they were not normally distributed I used the robust estimator. Pairwise comparisons for categorical variables were performed with a Bonferroni correction.

6.3 RESULTS

A total of 2046 records were used and after grouping the scan samples into daily party activities, 260 data points were included in the model, comprising feeding (30% of parties), resting (63% parties) and travelling parties (7% parties). Kasongoire chimpanzees spent 84% of observation time inside the forest compared to 16% outside the forest boundary. Table 6.2 presents a summary of the data. Party size, spread and composition varied according to the activity, habitat, presence of swollen females and availability of wild fruit. Full results from the GLMMs are presented in Table 6.3.

6.3.1 Party size

As predicted, when chimpanzees left the forest they formed significantly larger parties with a mean party size of $5.81 \pm SE 0.09$ inside the forest compared to $7.9 \pm SE 0.22$ outside the forest boundary ($p < 0.001$; Table 6.3, Figure 6.1a). The presence of maximally swollen females had a strong significant effect ($p < 0.001$; Figure 6.1b) as predicted, with party sizes increasing from a mean of $4.96 \pm SE 0.9$ with no maximally swollen females to $7.55 \pm SE 0.14$ when at least one maximally swollen female was present. Neither wild fruit availability nor the activity of the party had a significant influence in predicting party size (Figure 6.1c & d). Although not significant, party size was smaller when wild fruit availability was highest, against expectations.

Table 6.2: Mean party size, spread and proportion of males ($\pm$ SE) in chimpanzee parties in Kasongoire.

Factor	Condition	Party size	Party spread (m)	Proportion males (%)
Habitat	Forest	5.81 $\pm$ 0.09 (1-19)	15.68 $\pm$ 0.22	53.3 $\pm$ 0.86
	Outside forest	7.9 $\pm$ 0.22 (1-17)	17.10 $\pm$ 0.53	81.4 $\pm$ 1.21
Swollen females	Absent	4.96 $\pm$ 0.9 (1-14)	14.34 $\pm$ 0.27	65.7 $\pm$ 1.13
	Present	7.55 $\pm$ 0.14 (1-19)	17.78 $\pm$ 0.29	47.9 $\pm$ 0.97
Party activity	Feeding	6.42 $\pm$ 0.17 (1-19)	15.79 $\pm$ 0.38	55.5 $\pm$ 1.08
	Resting	5.99 $\pm$ 0.1 (1-19)	16.17 $\pm$ 0.25	61.3 $\pm$ 1.36
	Travelling	6.21 $\pm$ 0.29 (1-16)	13.91 $\pm$ 0.072	58.4 $\pm$ 1.99
Wild fruit availability	Low	6.09 $\pm$ 0.11 (1-17)	16.92 $\pm$ 0.26	54.6 $\pm$ 1.22
	Medium	6.67 $\pm$ 0.18 (1-19)	16.22 $\pm$ 0.4	56.6 $\pm$ 1.26
	High	5.43 $\pm$ 0.17 (1-15)	12.47 $\pm$ 0.43	66.4 $\pm$ 1.71
Time of day	07:00-10:49	6.42 $\pm$ 0.17 (1-19)	16.21 $\pm$ 0.31	58.9 $\pm$ 1.5
	11:00-14:49	5.99 $\pm$ 0.1 (1-19)	15.22 $\pm$ 0.32	56.8 $\pm$ 0.97
	15:00-19:00	6.21 $\pm$ 0.29 (1-16)	16.57 $\pm$ 0.46	60.6 $\pm$ 2.97

6.3.2 Party cohesion

Entering the risky habitat outside the forest did not impact party cohesion as predicted, and party spread increased from an average of 15.7 m in the forest to 17.1 m outside the forest, although this was not significant. The activity of the chimpanzees was the only factor that had a significant influence on party cohesion (fixed effect, $p=0.0041$; Figure 6.2d), with feeding and resting influencing party spread. Pairwise comparisons showed that travelling party spread (13.9 m) was significantly lower than that of feeding (15.8 m, $p=0.016$) and resting (16.2 m, $p=0.037$) parties.

6.3.3 Proportion of males

When chimpanzee parties left the forest, the ratio of males increased significantly ($p<0.001$; Table 6.3, Figure 6.3a), with males comprising 53.3% of party composition when inside the forest compared to 81.4% outside the forest.

Table 6.3: Results of the generalized linear mixed models showing factors influencing chimpanzee grouping patterns, including party size, party spread and the ratio of males in a party.

Factor	Condition	GLMM1: Party size				GLMM2: Party spread				GLMM3: Male ratio			
		Estimate	SE	t	P	Estimate	SE	t	P	Estimate	SE	t	P
	Intercept	6.311	0.915	6.900	<0.001	8.691	2.989	2.907	0.004	0.891	0.063	14.077	<0.001
	Month ¹	1.667	1.012	1.648*	0.099	20.432	12.056	1.695*	0.090	0.003	0.003	1.174*	0.241
Habitat	Forest ²	-2.784	0.502	-5.544	<0.001	-0.411	1.404	-0.293	0.770	-0.337	0.050	-6.744	<0.001
	-	-	-	-	-	-	-	-	-	-	-	-	-
Swollen females	Present ²	1.453	0.382	3.807	<0.001	1.736	1.078	1.610	0.109	-0.180	0.038	-4.752	<0.001
	-	-	-	-	-	-	-	-	-	-	-	-	-
Party activity	Feeding	0.326	0.393	0.831	0.407	2.638	1.087	2.427	0.016	0.003	0.039	0.068	0.946
	Resting	0.463	0.391	1.184	0.238	2.221	1.057	2.101	0.037	0.095	0.041	2.295	0.023
	Travelling	-	-	-	-	-	-	-	-	-	-	-	-
Wild fruit availability	Low	0.624	0.988	0.631	0.528	4.726	3.373	1.401	0.162	-0.041	0.055	-0.737	0.462
	Medium	0.681	1.130	0.603	0.547	4.279	3.867	1.107	0.207	0.024	0.062	0.380	0.704
	High	-	-	-	-	-	-	-	-	-	-	-	-

¹ Co-variance parameters of the random effect “month”, * denotes values that are Z scores.

² The factors ‘Habitat’ and ‘Swollen females’ were entered in the model as continuous variables.

P-values highlighted in bold are significant

N=260 in all cases

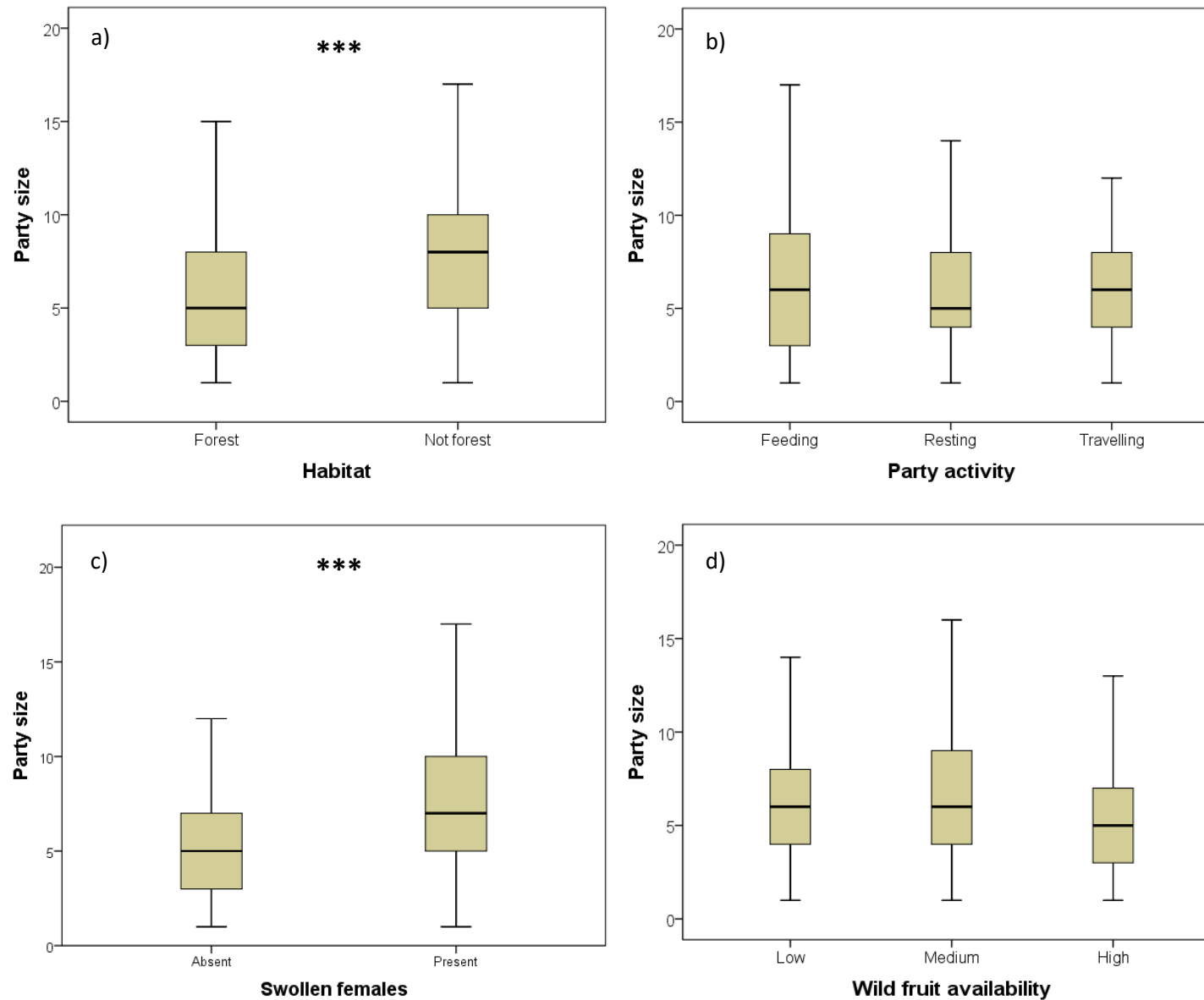


Figure 6.1: The influence of a) habitat, b) party activity, c) swollen females and d) wild fruit availability on chimpanzee party sizes at Kasongoire. Significant results are highlighted by asterisks: * $p < 0.05$; ** $p < 0.01$; * $p < 0.001$.**

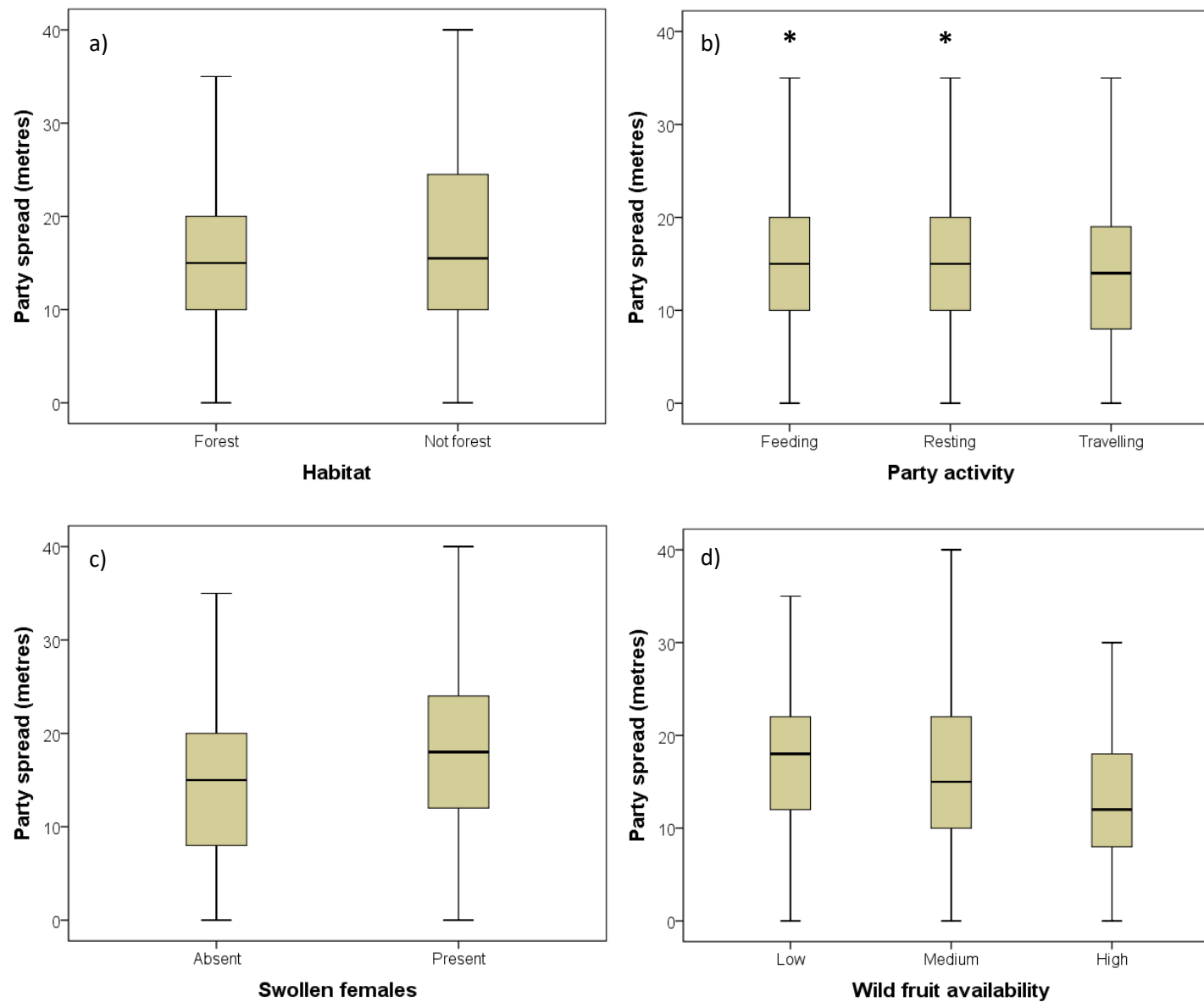


Figure 6.2: The influence of a) habitat, b) party activity, c) swollen females and d) wild fruit availability on chimpanzee party cohesion at Kasongoire. Significant results are highlighted by asterisks: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

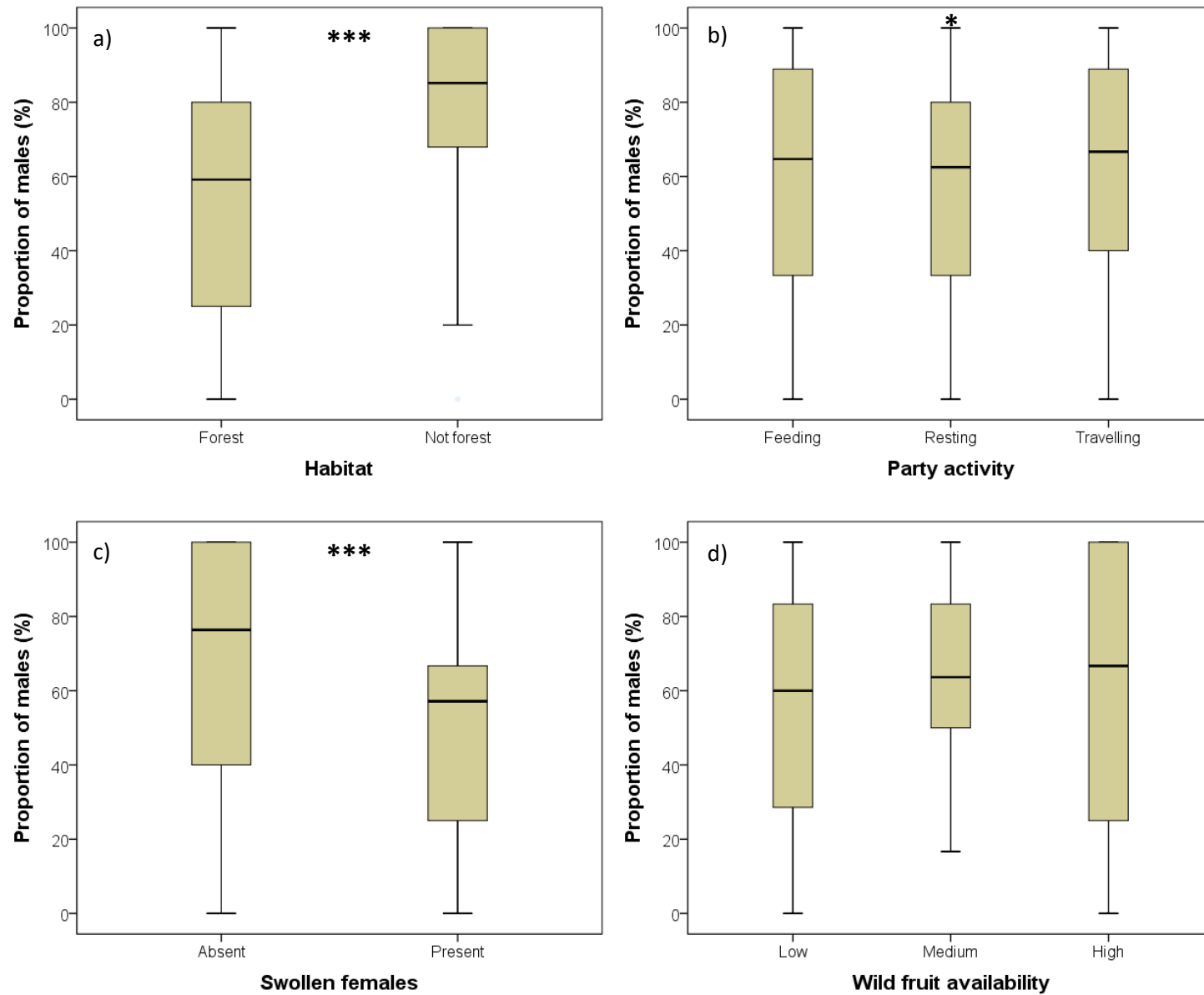


Figure 6.3: The influence of a) habitat, b) party activity, c) swollen females and d) wild fruit availability on the ratio of males in chimpanzee parties. Significant results are highlighted by asterisks: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

The number of maximally swollen females present also had a significant influence on the proportion of males ($p=0.001$, Figure 6.3c), but the opposite relationship was found than predicted: males accounted for 65.7% of parties with no swollen females, compared with 47.9% of parties when at least one maximally swollen female was present. Party activity also predicted the ratio of males to females in a party (fixed effect, $p=0.01$). Post-hoc tests revealed that the ratio of males was higher in resting parties as compared with both feeding ($p=0.005$) and travelling ($p=0.023$) parties. Against expectations, party cohesion was lowest during the period of high wild fruit availability (Figure 6.3d), although this was not significant.

6.4 DISCUSSION

6.4.1 Party responses to risk

The results of the models show that chimpanzees do respond flexibly to entering the risky anthropogenic habitat by adjusting their grouping patterns. As expected, leaving the forest led to larger party sizes with a higher proportion of males, as was the case at Bossou where chimpanzees leaving the forest to cross a road also formed significantly larger parties with a larger ratio of males than in the forest (Sakura 1994). Similarly, when foraging closer to anthropogenic landmarks, the number of chimpanzee males in a foraging party increased at Fongoli, Senegal, although they did not consume cultivated foods (Lindshield et al. 2017). In the same way, white-bellied spider monkeys (*Ateles belzebuth belzebuth*), which also have a fission-fusion social system, respond flexibly to predation risk by increasing group size (Link & Di Fiore 2013). In Link and Di Fiore's study (2013), they also found a higher rate of group fusion and fission before and after visiting a mineral clay lick where the risk of predation was high, demonstrating an anticipatory behavioural response to entering a risky area.

I predicted that party spread would be much lower in the habitat outside the forest, where there is the potential risk of a negative human encounter. Additionally, a large feeding group foraging on a limited resource would likely have to increase group spread (Chapman & Chapman 2000). Since forest resources are limited (in as much as they are exhaustible), and sugarcane is not, this would imply that chimpanzee party spread would be larger in the forest than outside. However, party cohesion did not appear to be affected by leaving the forest, and in fact party spread increased as a result of the larger party sizes outside the forest, although this was not significant. As predicted, feeding parties were more spread out than travelling parties as were resting parties, against predictions. No other factors significantly influenced party cohesion.

A likely reason explaining the looser party cohesion in the risky habitat outside the forest compared to inside the forest is that males and females exhibit different behavioural strategies to cope with the potential risks of sugarcane foraging. Male chimpanzees would often feed on sugarcane in different habitats, whereas females would often feed or rest in the ecotone forest, just within the protection of the forest boundary, rather than in the open gap between the forest and the sugarcane fields. When foraging on sugarcane, females usually crossed the open gap to the sugarcane field, picked as many stems of sugarcane as they could carry and speedily returned from the field to feed in the ecotone habitat. In contrast, male chimpanzees would usually feed in the gap between the forest boundary and the sugarcane. They also spent time resting and grooming in this open gap habitat. Therefore, in mixed-sex parties, there would be males feeding outside the forest and females just under the cover of the forest all in one party, resulting in a long distance between the two furthest individuals. In single-sex parties (male or female) or parties with a sex ratio score of close to 0 or 1, party spread was more cohesive, supporting this explanation. Accordingly, in larger mixed-sex chimpanzee parties at Kasongoire, males and females foraged on an abundant resource – sugarcane - in a widely spread party, forming units within a larger aggregation. Similar has been found in hamadryas baboons (*Papio hamadryas*) where during times of low feeding competition, baboons form smaller units within a large aggregation under high predation risk (Barton et al. 1996).

Travelling parties were not significantly larger than feeding or resting parties but were more cohesive and contained a lower proportion of males than resting parties. Smith et al. (2005) found that travelling parties of tamarins (*Saguinus fuscicollis* and *S. mystax*) showed lower group cohesion than parties engaged in other activities, although in a forest habitat. At Kasongoire, parties formed to travel in the edge habitat and chimpanzees would wait for their conspecifics before travelling out of the forest (pers. obs.). It was perhaps easier to traverse longer distances outside the forest on the grass in the open gap habitat rather than through the swamp, especially for females carrying infants. This shows some level of a behavioural response to potential risk, since when travelling outside the forest chimpanzees did so in a tight unit. When travelling in the forest, small parties or lone animals often maintain audio contact through pant hoots and travel hoos (Gruber & Zuberbühler 2013). It is possible that parties outside the forest are more cohesive since they maintain visual contact rather than audio contact: travel hoos were heard rarely outside the forest (pers. obs.).

Plumptre (2000) found that party spread changed in three monkey species in Budongo Forest according to the time of the day. He found a sharp increase in party size after the initial morning period of surveys (6am to 8am) and a decrease again for the last hour of the day. At Kasongoire, data collection usually started after chimpanzees had left their nesting group, meaning this effect, if present, would not skew the data.

6.4.2 Socio-ecological factors

The presence of cycling females was included as a variable to control for when looking at the effect of leaving the forest on grouping patterns and it was expected that parties with maximally swollen females would be larger. As predicted, the presence of maximally swollen females did lead to significantly larger parties, corroborating with the literature (Hockings et al. 2012b; Mitani et al. 2002; Sakura 1994). Interestingly, the proportion of males in the party was much lower in the presence of one or more swollen females, contrary to the findings of Sakura (1994). The data seem to show periods when multiple females were swollen at the same time, followed by periods when no females were swollen. I therefore interpret this result as a consequence of generally larger parties with multiple females who would not usually associate together joining the same party.

There are different implications for changes in the sex ratio for both males and females. The results of the model show that the ratio of males significantly decreases in the presence of swollen females, suggesting that there would be intense competition between males for mates when females were cycling. Observations in the field, though unsupported by systematic data, indicate that competition and aggression between males was lower at Kasongoire than at Waibira, with few instances of aggression observed when females were maximally swollen.

Wild fruit availability did not predict chimpanzee grouping patterns at Kasongoire. Although not significant, party spread was lower during the period of high wild fruit availability, as expected. However, this may reflect the lower party size during high fruit availability, which is contrary to predictions, since reduced feeding competition was expected to lead to larger parties. Similarly, a higher proportion of females in parties was expected when fruit was most abundant, and the opposite relationship was found in the data. It is possible that the expected effect of wild food availability on grouping patterns is not as strong an influence on grouping patterns at Kasongoire due to the continuous nearby presence of high quality abundant food (sugarcane).

6.4.3 Study limitations

The data will be generally biased towards larger party sizes, since smaller groups or lone individuals are less likely to be encountered since they are more elusive, as well as being more difficult to follow (van Schaik & van Noordwijk 1989). In addition to this, there is a bias towards male-dominated parties generally within the data: although there are more adult female individuals in the community than males, there were more males recorded in parties in almost all scenarios. While the system of rotating focal individuals for collecting behavioural data meant that all efforts were made to sample all individuals as evenly as possible, a slight skew remained. This is most likely explained by the lower habituation level of certain individuals, particularly peripheral females, meaning that small or lone female parties in particular are likely under-represented in the dataset. However, habituation levels of all individuals improved during the study. As a result of this, more data were collected in the latter half of the study period. This did not create a bias towards larger party sizes but did increase the data set towards the latter half of the study.

As mentioned in the previous chapter, dense vegetation would obscure visibility in certain habitats, particularly in ecotone forest and papyrus swamp, resulting in fewer data points in these habitats. When chimpanzees were outside the forest edge, data on grouping patterns was much more concise as there was no vegetation, apart from the times when chimpanzees entered the sugarcane fields. When they were in the field extracting sugarcane, data could still be collected as we could observe different individuals entering and coming out and could monitor their location through hearing the snapping of sugarcane.

Regarding the analysis for the party composition (the proportion of males), it may have also been informative to code the variable logistically (i.e. male, female and mixed parties). However, I created the score for proportion of males to make it a continuous variable since I wanted to ensure that the tests were consistent between the other dependent variables in the three models. Further analyses could potentially re-run the models using this system of coding to investigate the effects of risk and ecological variables on the party size and spread within each category of party composition type. However, if categorised into male, female and mixed parties, the data lose information about the ratio of males to females within mixed parties, showing the benefit of the higher degree of information provided by sorting the variable into a continuous proportion of males.

6.4.4 Further research

I would like to test specifically the impact that being outside the forest has on chimpanzee vigilance behaviour, particularly focusing on the difference between males and females and possibly including other age-classes. During this study female chimpanzees were notably more vigilant when exiting the forest and while at the edge than when in the forest (pers. obs.). Originally an analysis on vigilance behaviour was a goal of this study: I recorded chimpanzees during periods outside the forest with a handheld camera in order to analyse footage retrospectively with an ethogram focusing on vigilance behaviours, including monitoring, scanning and bipedalism as well as the amount of time spent outside the forest. However, the study of vigilance in wild animals is prone to many confounding factors, primarily due to potential threats from conspecifics. The most common method of investigating vigilance is by recording head turns (Treves 2000) but vigilance in chimpanzees has been found to be affected by various social factors, including proximity networks and, for females with infants, distance from infant (Kutsukake 2007). Therefore, vigilance studies require detailed information to control for these confounding factors and this was not possible with the video data I collected during this study.

Link and Di Fiore (2013) found that spider monkeys spent a long time scanning the environment before finally beginning to feed at a mineral lick. Similarly, Warren (2009) describes “elevated pre-vigilance” in olive baboons prior to entering fields in Gashaka. Understanding vigilance behaviours of Kasongoire chimpanzees in the period before, as well as during, leaving the forest could reveal whether chimpanzees show any anticipatory behavioural responses to risk. This could also potentially show the differences between foraging on sugarcane and leaving for the village gardens, where the chance of a human encounter is much higher.

As mentioned earlier, male chimpanzees at Kasongoire usually fed on sugarcane openly in the exposed gap habitat outside the forest, whereas females would usually harvest as many stems of sugarcane as they could carry and transport this back to the forest, feeding either on the ground (females with infants) or climbing a tree to feed (females without infants). Transporting crops from a risky habitat back to the safety of the forest has been reported in other species. Crop-foraging baboons (*Papio anubis*) in Nigeria stored food in their cheek pouches (Warren 2009), transporting crops to a safe refuge to feed. Bossou chimpanzees also regularly transport crops back to the forest to feed, with males carrying cultivated fruits and sharing with females (Hockings et al. 2007). When males did transport sugarcane back to the forest it was presumed that this was to shelter from the heat rather than from human risk (pers. obs.) although detailed information of

the whereabouts of guards are lacking. Further research recording chimpanzee scanning and monitoring when outside the forest, complemented by data on human presence and activity, will reveal further information about chimpanzees' perception of risk.

Van Schaik and Mitraseti (1990) found that long-tailed macaques (*Macaca fascicularis*) did not return to a site for several days after an encounter with a python and would alarm call near the site on subsequent days, showing a behavioural response not just to the actual risk but also in the period following a risky encounter. Kasongoire chimpanzees have demonstrated some level of response to risk by altering their grouping patterns, but it would be interesting to understand their response to, and after, an interaction with a human. Would chimpanzees avoid a 'hot spot' entirely after a negative encounter, or would their grouping patterns or behaviour change when returning to a location where they had previously experienced aggression from people? Some studies, such as that of van Schaik and Mitraseti (1990) have taken an experimental approach to investigating responses to predators (e.g. Karpanty & Wright 2007; Wich & Sterck 2003; Zuberbühler et al. 1999; Zuberbühler 2000), which would not be possible in the case of Kasongoire chimpanzees for obvious ethical reasons. Therefore, investigating animal responses to actual human encounters would have to take an opportunistic approach. It would also be necessary to ask local people to behave as they would normally and ignore the researchers in order to record chimpanzee responses. It would take a long time to acquire a large enough sample size since active interactions in the field (i.e. humans coming into close visual contact or responses by humans to the chimpanzees such as shouting or chasing) are rarely observed, but the results could be very interesting and deepen our understanding of chimpanzee responses to actual encounters with humans. Male chimpanzees may at times exhibit aggressive behaviour towards humans to intimidate them into leaving an area (McLennan & Hill 2010). Since fear from aggression by chimpanzees is a major factor affecting local people's support of chimpanzee conservation (Hockings & McLennan 2016), revealing chimpanzee behaviour during and after an encounter could provide vital information which may help mitigate future negative interactions.

6.4.5 Threat sensitive responses?

The size and cohesion of a social group are directly influenced by both feeding and anti-predation strategies (van Schaik & van Hooff 1983). Teasing out the influence of either factor independently is a tricky task. The lower party cohesion outside the forest may simply reflect a genuinely low level of risk. However, animals are known to respond to 'pulses' of risk (Boinski et al. 2000; Lima & Bednekoff 1999): responses to a low potential level of risk cannot be constantly high, since there

are costs of being vigilant as it is a time expense. Therefore, chimpanzees may respond to a general level of risk by increasing party size and the ratio of males, but increasing party cohesion may not be a necessary response in the absence of an imminent or actual danger.

Threat-sensitive responses to humans have been recorded in elephants: they are able to distinguish potential human threats from acoustic, visual and olfactory cues (Bates et al. 2007; McComb et al. 2014). African elephants (*Loxodonta africana*) showed a greater level of fear when detecting the scent and garments of Maasai men, who represent a high potential hunting threat, than those of Kamba men who represent a low threat (Bates et al. 2007). Similarly, elephants were significantly more likely to bunch together defensively, smell to investigate and retreat on hearing the voice of a Maasai man compared with a Kamba man, Maasai woman or Maasai boy (McComb et al. 2014). Asian elephants (*Elephas maximus*) have been shown to respond differently to vehicles of different sizes and towards different responses from motorists, becoming more agitated or aggressive towards motorists in large vehicles or who slowed or stopped or shouted at them (Vidya & Thuppil 2010).

With their advanced cognitive abilities, it is likely that chimpanzees can distinguish between humans who pose a threat and those who do not. This could even be down to the level of specific individuals which have behaved antagonistically towards them in the past, since chimpanzees are able to recognise human faces when exposed to them regularly (Martin-Malivel & Okada 2007). Even without individual recognition, chimpanzees can likely distinguish between different human roles which may pose different threats. Papworth et al. (2013) found that woolly monkeys (*Lagothrix poeppigii*) that were typically hunted behave more cryptically in the presence of hunters than humans gathering leaves or researchers. It is likely that chimpanzees also possess the ability to tell whether a human may pose an actual threat to them (e.g. a guard, or logger) or minimal/no threat (e.g. a villager traveling past, a researcher).

Just how risky Kasongore chimpanzees perceive the habitat outside the forest is not clear and I was not able to quantify this risk in this study, particularly the open gap between the sugarcane and the forest border (since they spend so much time in this habitat). Sugarcane foraging by chimpanzees is permitted by Kinyara Sugarworks Ltd., meaning that chimpanzees should be under no persecution from cane guards in theory. However, reports from cane guards suggest that they still chase chimpanzees away given the chance (C. Asiimwe, 2016, pers. comm.) and there is evidence that they collect stones and use dogs as methods of chasing crop-foraging primates

away generally (pers. obs.). One cane guard even used a mantrap (but did not set it) as a visual deterrent and used it to make a loud noise to scare off animals. Although Kasongoire chimpanzees were found in this study to adjust their grouping patterns in response to entering the risky habitat outside the forest, it is possible that the forest edge is genuinely perceived to be of low risk. Chacma baboons (*Papio ursinus*) chose to forage in a low-risk habitat but of low quality for feeding resources than the high-risk habitat, despite it being of better quality (Cowlshaw 1997). In a habitat with a high genuine risk of mortality from hunting it is likely that chimpanzee grouping responses would be more extreme, or that they may avoid an area entirely (as in Bili: Hicks et al. 2012, 2013).

CHAPTER SEVEN

PERCEPTIONS OF RISK AND MANGO FEEDING PREFERENCES OF
CHIMPANZEES IN A HUMAN-DOMINATED LANDSCAPE MOSAIC



Plate 20 (on previous page): View from a fallow field at sunset of the village-garden matrix. The tree furthest on the left is situated on the northern tip of the forest in the Kasongoire chimpanzee core home range: most of trees on the horizon are mango trees.

7.1 INTRODUCTION

Chimpanzees already face risks in the interior of their fragmented forest habitat, including snares and traps and interactions with humans harvesting timber and collecting firewood. In Kasongore, chimpanzees were found to adjust their grouping patterns when leaving the forest boundary (Chapter 6) showing that they exhibit some level of risk perception. However, those data were focused primarily on the open gap habitat between the forest edge and the sugarcane. Foraging on cultivated fruits in the village-garden matrix likely poses additional risks, namely hostile encounters with humans (McLennan 2008; McLennan & Hill 2012). This chapter investigates which aspects of risk might affect chimpanzee foraging choices in the village-garden matrix, focusing specifically on mango foraging. Studying chimpanzee responses to potentially dangerous situations in anthropogenic habitats allows us to better understand their behavioural flexibility and develop measures to improve future human-chimpanzee interactions (Hockings et al. 2015a).

7.1.1 Chimpanzees and risk in anthropogenic environments

As discussed in Chapter 6, many primate species are known to modify their behaviour according to anthropogenic risk (Hill 2017; McLennan et al. 2017; Nowak & Lee 2013; Nowak et al. 2014). From previous studies of chimpanzee responses to anthropogenic risks such as roads or crops, we know that they show behavioural flexibility and signs of heightened vigilance or stress in certain situations (Hockings et al. 2015a). For example, chimpanzees exhibited higher group cohesion and altered activity budgets during days when they foraged on crops as compared with days when no crops were consumed at Bossou, Guinea (Hockings et al. 2012b). When foraging on crops and in the presence of villagers, adult male chimpanzees at Bossou displayed much higher rates of rough self-scratching (RSS), a self-directed behaviour indicating anxiety (Hockings et al. 2007). In the Democratic Republic of Congo, chimpanzees in forests close to human settlements and roads produced fewer pant-hoot vocalisation and tree drums than those in more remote forest, showing responses to risk directly linked to the presence of humans (Hicks et al. 2013). At Bossou (Hockings et al. 2006; Sakura 1994) and Sebitoli (Cibot et al. 2015) chimpanzees modified their party structure or group positioning during road crossing, showing that while chimpanzees can and do modify their behaviour, they are often prepared or forced to enter into high-risk, potentially fatal situations (McLennan & Asiimwe 2016).

Some disturbance stimuli are analogous to predation risk (Frid & Dill 2002): as mentioned previously, humans have been known to injure or kill chimpanzees in agricultural habitats, both

directly (spear attack, Hyeroba et al. 2011; Reynolds 2005) and indirectly (setting mantraps, McLennan et al. 2012), within and outside the forest. Therefore, chimpanzee crop-feeding in villagers' crops gardens could potentially be an extremely risky activity.

7.1.2 Mangos: seasonal and nutritious fruits

Chimpanzees are known to consume mangos (*Mangifera indica*) predictably accross tropical Africa where they are grown (Hockings & McLennan 2012). For chimpanzees, which are ripe fruit specialists, mangos are a highly nutritious and attractive resource, although accessing mango fruits presents a risk for chimpanzees as they must travel beyond the forest edge into farmers' gardens. Since mangos are usually foraged on heavily by chimpanzees during the peak season(s) mango is known to be a "high-conflict" crop and was ranked by Hockings and McLennan (2012) in the top five (out of 30) "conflict" crops.

Mangos are a seasonal crop and in Uganda, there are two annual fruiting seasons: November-January and May-July (peak season). Because mangos are both highly seasonal and spatially abundant within the village-garden matrix, it can be expected that foraging on mangos would have the added benefit of increased foraging efficiency, making them an appealing food resource. While this fruiting event takes place in the risky landscape outside of the forest, chimpanzees appear willing to take the risks to obtain mango fruits. For example, in Bulindi mangos were the sixth most important food in the Bulindi chimpanzees' diet (McLennan 2013).

Mangos are high in simple sugars and easily digestible carbohydrates (Hockings et al. 2009; McLennan & Ganzhorn 2017) although the metabolisable energy of mangos as compared with an average for wild fruits is similar (McLennan & Ganzhorn 2017). The high sugar content of mangos will naturally make them an attractive and palatable resource to chimpanzees and humans alike. However, McLennan (2013) found that mango was not the most important food during the peak of mango fruiting for Bulindi chimpanzees (in terms of frequency in faecal samples) showing that, although mangos were consumed at high rates, wild fruits were still consumed (McLennan 2013).

During times of fruit scarcity, chimpanzees generally consume higher proportions of leaves, stems and terrestrial herbaceous vegetation as fallback foods (Harrison & Marshall 2011). However, if fruit is available, it would be expected for chimpanzees to consume the high sugar fruits preferentially even if the available fruits are cultivated and outside the forest (Hockings et al. 2009). Crops are sometimes considered fallback foods since chimpanzees often increase

consumption of cultivated foods when wild fruit availability is low (Naughton-Treves et al. 1998; Hockings et al. 2012b, McLennan 2013), although this is not always the case (Bessa et al. 2015; Tweheyo et al. 2005). This may depend on the attractiveness, availability and accessibility of specific crops (McLennan & Hockings 2014).

7.1.3 Mangos, conflict and conservation

Understanding chimpanzee mango-feeding behaviour is important for designing future strategies to mitigate negative human-chimpanzee interactions. At several field sites, particularly where forest edges have been encroached, chimpanzees are reported to feed on mangos, amongst other cultivated fruits (Mahale: Takasaki 1983; Gombe: Greengrass 2000; Budongo: Reynolds 2005). In the landscape bordering Budongo Forest Reserve, Uganda, it has been increasingly reported over the past decade that chimpanzees routinely exit the forest in May-July - the peak mango fruiting period - in search of mangos (Babweteera et al. 2012). Local people are generally afraid of chimpanzees (McLennan & Hill 2012) and when people see chimpanzees in the landscape it is likely that fear and hostility towards them will increase. Tensions may be particularly high considering the history of negative human-chimpanzee interactions in this area, and in Kasongire in particular, where chimpanzee attacks on local persons and retaliatory attacks on chimpanzees have been reported (McLennan 2008; Reynolds 2005). Therefore, mango season may be a critical time to understand chimpanzee crop foraging strategies and perception of risk for conservation and land management strategies.

The presence of a mango tree which is foraged on by chimpanzees may lead to damage of other crops, either by chimpanzees foraging on them or trampling over them. This in turn may lead the owner of the tree to cut the tree down, despite it being of value (either nutritionally or financially). There are several different varieties of mango tree, and local people stated that they preferred different varieties of mangos for certain qualities, such as sweetness or soft skin. However, nothing was known about whether chimpanzees exhibited any preference for specific varieties.

Most complaints from farmers about chimpanzee crop-foraging are in close proximity to the forest edge (pers. obs.; Hill 1997), although chimpanzees are also known to travel a long distance from the forest to exploit certain foods – mango being a particular favourite (pers. obs.; Greengrass 2000; Wallace & Hill 2012). Therefore, it is important to understand potential factors

relating to risk not only to help alleviate future negative interactions, supporting chimpanzee conservation.

Other forest fragments with resident chimpanzee communities within the landscape between Budongo and Bugoma forests (see McCarthy et al. 2015) are similar to Kasongire in habitat structure and high rates of deforestation (McLennan & Plumptre 2012). Chimpanzees are known to feed on mangos throughout this region (McLennan 2008). Therefore, understanding chimpanzee feeding behaviour during the peak time of the year when they leave the forest in search of cultivated food could provide valuable insights for other fragment communities.

7.1.4 Chimpanzee mango foraging strategies

Influence of wild fruit availability

Two alternating hypotheses could be made for whether chimpanzees would be more likely to take risks during periods of wild fruit scarcity or abundance. Gilby and Wrangham (2007) found that chimpanzees were more likely to engage in risky hunting practices when wild fruit was abundant rather than as a resort of necessity when fruit was scarce, supporting the “abundance/risk” argument (Gilby & Wrangham 2007). This would suggest that during periods of wild fruit abundance Kasongire chimpanzees would consume more mangos and would continue to consume wild fruits, as is the case in Bulindi (McLennan 2013). Chimpanzees can still find wild fruit if they fail in the risky activity of foraging on mangos. Alternatively, it may be expected that chimpanzees consume more mangos if wild fruits are scarce, following the “scarcity/risk” argument. This may be more likely since chimpanzees have been known to consume some cultivars as fallback foods during periods of wild fruit scarcity (Hockings et al. 2012b; McLennan 2013), and especially considering the nutritional attractiveness and high simple sugar content of mangos as a resource (McLennan & Ganzhorn 2017).

Influence of risk factors

Chimpanzees travel further from the forest to access palatable crops, including mangos, than do smaller bodied primates (Wallace & Hill 2012). However, because chimpanzees demonstrate some level of risk aversion during risky situations (Hockings et al. 2006, 2012b) it would be expected for a higher number of mangos to be consumed closer to the forest edge and in habitats which present fewer potential dangers.

Various chimpanzee communities have been shown to respond differently to humans in the landscape, potentially depending on their history with sharing the landscape with human neighbours. Chimpanzees may actively avoid or flee from an encounter with humans (Hicks et al. 2012, 2013; Tutin & Fernandez 1991) or simply ignore them (McLennan & Hill 2010). Therefore, human presence may have different effects on different chimpanzee communities, perhaps depending on whether humans are, and have historically been, tolerant of sharing the landscape with chimpanzees. It was expected that active guarding would deter chimpanzees from foraging on mangos since guarding is a common and often efficient method of protecting crops from animals foraging (Hill 1997; Hill & Wallace 2012; McGuiness & Taylor 2014; Priston et al. 2012; Warren 2009). Presence of a homestead nearby was also expected to deter chimpanzees from foraging on mango trees, since it was assumed there would be a higher level of human presence. However, the impact of this was expected to be lower than that of active guarding.

Other forms of crop protection include clearing ground vegetation in the vicinity around the crop (Hill 1997). A higher level of ground vegetation would likely provide more cover for chimpanzees allowing them to move stealthily in and out of the location of a tree, so it was expected for chimpanzees to forage more heavily on mango trees with a higher level of vegetation cover around the tree.

7.1.5 Study aims

In this chapter I investigate whether chimpanzees demonstrate a preference for certain mango trees and which factors influence their choice when selecting mango trees to forage from. I examine whether factors related to risk (including guarding presence and terrestrial vegetation cover) and characteristics of mango trees (mango variety, fruit availability) explain chimpanzee mango feeding tree choices and identify areas of potential high human-chimpanzee interaction levels. Specifically, I investigated the following questions:

- Do chimpanzees exhibit a level of risk perception when foraging on mangos in the village-garden matrix?
- Which risk factors are the most influential in selecting mango trees?

7.1.6 Hypotheses and predictions

Table 7.1 outlines the hypotheses and predictions tested in this chapter.

Table 7.1: Hypotheses and predictions relating to chimpanzee mango foraging preferences at Kasongoire, and the framework for testing them.

Hypothesis	Prediction	Analysis
Chimpanzees forage on crops when they are available.	1. Kasongoire chimpanzees will feed more on mangos when mango fruit availability is higher.	I use a generalised linear model to determine whether the number of mangos consumed (mango traces) and/or the number of days chimpanzees visited a tree is predicted by mango fruit availability (MFAI).
Chimpanzees in anthropogenic habitats respond flexibly to risk and will respond according to the level of risk of an encounter with humans.	2. Chimpanzees will consume more mangos and visit mango trees more regularly that: a. are closer to the forest edge; b. have a higher level of vegetation cover; c. are not within 30 m of a homestead; d. are not guarded.	I use a generalised linear model to determine whether the number of mangos consumed (mango traces) and/or the number of days chimpanzees visited a tree is predicted by a) distance of a mango tree from the forest edge; b) the percentage of vegetation cover around a mango tree within 30 m; c) the presence of a homestead within a 30 m radius of a mango tree and d) were not reported to have guarding presence within a 30 m radius of the mango tree.

7.2 METHODS

7.2.1 Study site

As described in Chapter 2, the landscape in Kasongoire is dominated by agriculture, from both small-scale farmers and a large-scale sugar plantation, which surrounds Kasongoire forest. Mango trees are located throughout the landscape outside the forest in the village-garden matrix, next to homesteads and in crop gardens (see Figure 7.1 for a schematic view of mango tree locations). A ‘garden’ in this study refers to a piece of land owned (usually customarily) by a local person which is used to grow subsistence crops.

7.2.2 Methodological considerations/development

Following chimpanzees into crop gardens to monitor foraging group size or behaviour during time spent in anthropogenic habitats is not desirable due to ethical considerations (Chapter 2). Therefore, I developed a method to examine chimpanzee risk perception and preferences using indirect observation. Primate crop-foraging has been previously studied through indirect or discreet observation using camera traps (Krief et al. 2014; Zak & Riley 2017), hides (Wallace & Hill

2012; Spagnoletti et al. 2017) or recording signs of crop damage (Naughton-Treves et al. 1998; Warren et al. 2007). Camera traps are useful to capture footage of events systematically without the presence of an observer, but they are costly, can be stolen (especially in a village-garden matrix), and only capture what falls directly in front of the frame. Additionally, camera traps can be ethically questionable as they can also capture people, potentially creating social fear and undermining conservation actions (Pebsworth & LaFleur 2014; Sandbrook et al. 2018). Their use may facilitate data collection on chimpanzee party size and composition outside the forest, but it would be difficult to collect quantitative data specifically on the consumption of one crop species.

Using hides can overcome this obstacle, allowing the observer to record data on consumption of specific crops, including harvest rate, party composition and also allowing direct behavioural observations (Priston et al. 2012; Wallace & Hill 2012). However, the observer would only be able to target a limited number of mango trees since it would be impractical to construct and maintain a high number of hides. An important additional consideration was that when simultaneously following chimpanzees for behavioural observations, the observer would still be “escorting” the study subjects from the forest to the garden area before becoming invisible in the hide. The problem then remains that the researcher would potentially be observing damage to local farmers’ food or livelihoods, which is the principal reason why following primates into crop gardens is inappropriate (Zak & Riley 2017).

Recording physical signs and traces is a common way to record information when direct observations are difficult or impossible. Sign surveys often aim to study elusive species population density and habitat use through recording signs such as faecal and feeding traces, tracks and scratch marks (Gompper et al. 2006; Fredriksson 2012; Karanth et al. 2011; Morgan et al. 2006; Tutin & Fernandez 1985), and if careful, can be used to deem detailed behavioural information (Pascual-Garrido 2018). The aim in this study is to investigate mango feeding from trees in a known area, so while the study species in this research was not necessarily elusive, we were able to go directly to specific trees and record traces after a feeding event. The additional benefit of using sign surveys is that monitoring trees which were not fed on provides valuable data on why a chimpanzee may *not* go to a tree, supplementing data on trees which are fed on. Recording crop feeding traces has been done previously to understand chimpanzee crop foraging behaviour (e.g. Bessa et al. 2015; McLennan 2013) but has not been used specifically to examine risk-taking behaviour.

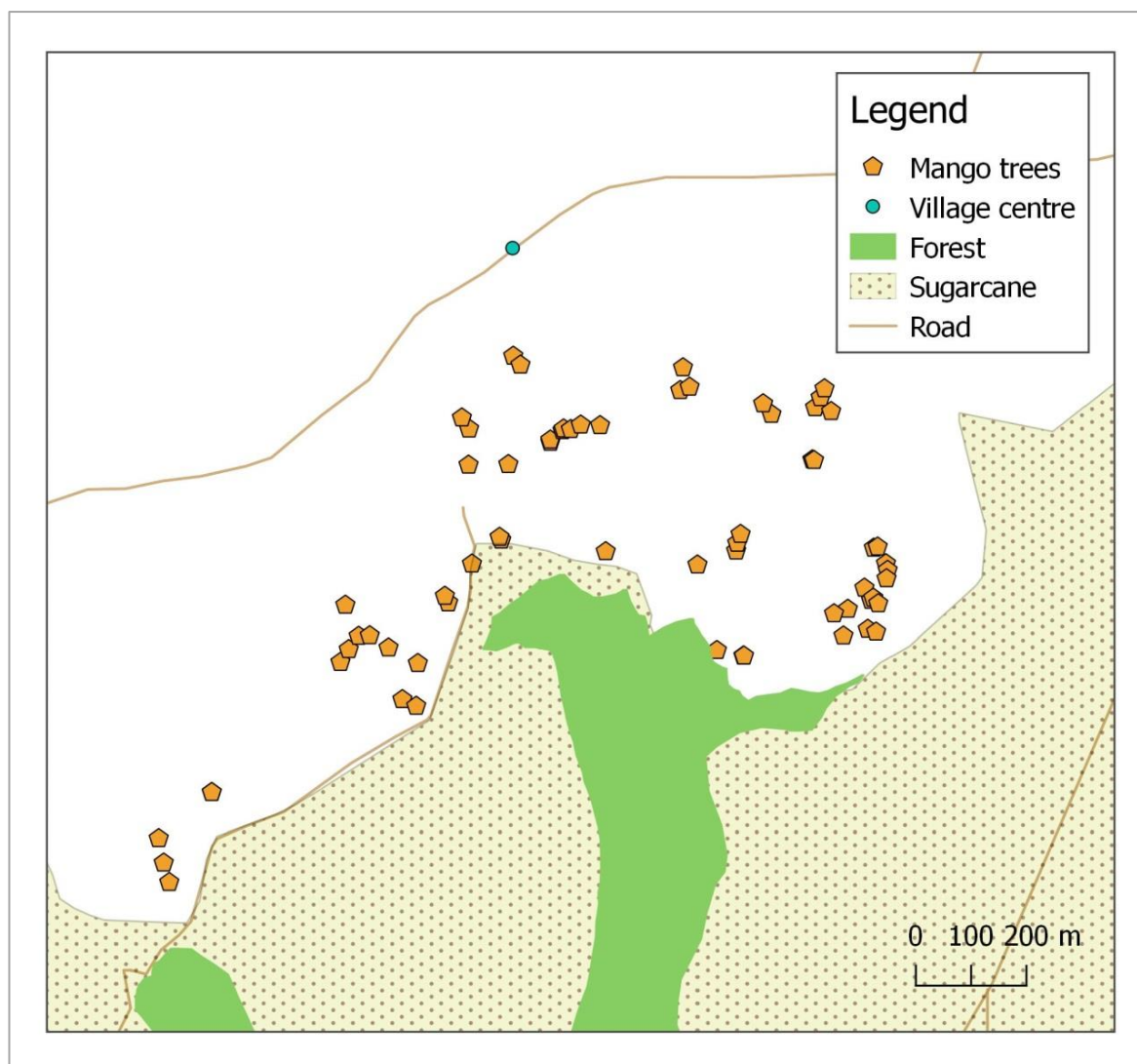


Figure 7.1: Map showing the distribution of monitored mango trees in Kasongoire.

7.2.3 Data collection

A total of 67 mango trees were selected between 40 and 410 metres away from the forest edge (Figure 7.1). I sought permission from the owners of each tree to monitor these trees during the mango season. One tree was cut down during the study and was not included in the analyses, leaving 66 trees. The number and location of trees chosen provided a sufficient sample size over a sizeable spread in distance but was also physically feasible to walk in a realistic time period. For each tree, diameter at breast height (DBH) taken at 1.3 m from the ground was recorded along with crown width and the variety of the mango tree. Information on the characteristics where the mango tree was located was also recorded, including the habitat type, presence of a homestead, terrestrial vegetation cover and guarding presence. The garden characteristics were recorded at the start of the study and at the mid-way point, since some variables changed over the duration of the mango season. For guarding presence, I asked the owner of the tree whether they guarded

the tree and/or the area of garden within 30 m of the tree. Table 7.2 presents a full description of tree and garden characteristics recorded.

Table 7.2: Mango tree and garden characteristic variables and definitions.

Variable	Description	Unit/category
DBH	Diameter at breast height	Cm
Crown	Crown width	Cm
Variety	Mango tree variety	Coded: 1-6 (with corresponding local name)
Distance from edge¹	Distance from the mango tree to the nearest forest point	m
Habitat	Primary habitat type	Coded: 1 = garden; 2 = homestead; 3 = tree cluster
Crop status	If garden habitat, whether crop present	Crop, fallow
Cover	Terrestrial vegetation over 1 m tall, within 30 m radius of tree	No cover, cover
Cover level¹	Proportion of tree covered, within 30 m	%
Homestead¹	Presence of a homestead, within 30 m	No homestead, homestead
Guard¹	Garden/area guarded, within 30 m, as reported by the owner. A guard might not necessarily be present at all times.	Unguarded, guarded

¹These factors were included as variables relating to risk in the analysis, see Section 7.2.4

Trees were monitored five days per week between 5 pm-7 pm over two months from mid-May to mid-July, the duration of the main mango fruiting season in the year (n=44 days). Mango stones (the leftover remains after being fed on) were collected from the ground underneath each tree and counted. Each stone was inspected to confirm it had been fed on by chimpanzees as they left distinctive teeth marks in the skin, remaining flesh and sometimes on the stone (see Plate 21). For each mango tree I calculated the total number of mango stones fed on by humans and chimpanzees as well as the number of times the tree was revisited on subsequent days. Total number of stones was assumed to represent the overall feeding investment in that tree by chimpanzees and number of visits represents the overall interest in the tree.

From behavioural observations, chimpanzees mainly entered the village-garden matrix in the mid-late afternoon, although they were occasionally seen feeding on mangos at other times. Therefore, trees were monitored in the evening so that we could record the mango traces for the whole day. Mango feeding traces that were over a day old were identifiable by the state of the remains: any flesh still on the stone would begin to decompose as seen by the colour and texture of the flesh and the skin would begin to shrivel. This meant that it was possible to identify the

traces fed on that day. To avoid potential error, mango stones that had been inspected and counted were disposed of in a pile away from the tree and covered with soil to enable us to distinguish new stones the following day.

As with other cultivated foods, it is possible that chimpanzees sometimes carried mangos back to the forest to eat (Hockings et al. 2007). However, from anecdotal and opportunistic observations, chimpanzees mostly consumed mangos on site – if some mangos were transported away from the feeding tree then the number was considered to be minimal. No mango traces were found in the forest while following chimpanzees.



Plate 21: Mango feeding trace from a chimpanzee. The trace is less than one day old, as seen by the bright flesh colour, and chimpanzee tooth marks can be seen on the stone.

Mango tree fruiting phenology was surveyed fortnightly over the study period (4 surveys in total) and each tree was scored for unripe and ripe fruit availability based on percent of canopy cover using the following scale, as per the methods used for wild fruit phenology (Chapter 3): 0: absent; 1: 1-25% cover; 2: 26-50% cover; 3: 51-75% cover; 4: 76-100% cover (Hockings et al. 2012b). Phenology surveys were also conducted within the forest recording wild fruit availability fortnightly during the mango study, concurrently with phenology surveys for mango trees, using the same 0-4 scale system recording percentage of fruit cover (see Chapter 3). Survey periods were broken down as follows: 1: mid-May - June; 2: early June - mid-June; 3: mid-June-July; 4: early July – mid-July.

7.2.4 Data analysis

For mango fruit availability, a fruit availability index (FAI) was created for each survey period ($n=4$) for each tree. This was calculated using a weighted scale to account for difference in tree size, and hence crop size, where the DBH was divided by the largest tree measurement and multiplied by the ripe fruit score. A Friedman test was used as a non-parametric repeated measures ANOVA to test whether the median fruiting scores of trees in each survey period were different.

Wild fruit availability sample size was too low to determine whether the period of mango availability coincided with a period of high or low wild fruit abundance, in relative terms. Therefore, statistical analyses to test whether wild fruit availability affected mango feeding were not conducted. However, it was useful to ascertain a general pattern of mango fruit productivity and consumption in comparison to wild fruit availability, so wild fruit availability values were plotted against mango fruit availability and consumption for an overall interpretation. For wild fruit availability, the proportional FAI values for each survey period during the mango study was used (Fawcett 2000; see Chapter 3).

I used a generalised linear model to examine which variables were most influential in chimpanzee mango tree selection. Because the dependent variables were counts ("mango stones", the number of traces per day; "tree visits", the number of days a tree was visited) the model was run with a Poisson and negative binomial loglink distribution and the model which fit best was selected, determined by the Akaike Information Criterion value, where the lowest value showed the better fit. When running the generalised liner model with the dependent variable "mango stones", the model fit with a negative binomial log distribution and when run with the dependent variable "tree visits" the model fit with a Poisson distribution. I used the robust estimator since the residuals were not normally distributed.

The number of mango stones showed the overall quantity of mangos consumed from each tree. Because chimpanzees were not followed to mango trees, it was not possible to say whether one chimpanzee or many had consumed the total number of mangos. I considered that the number of days chimpanzees visited a tree would show the potential risk in visiting a specific tree multiple times. Therefore, I performed the analysis using both the number of mango stones found under the tree and the number of days a tree was visited as dependent variables. Only days when traces were found were included. The models were run for the whole mango season to show overall influences on mango tree selection and again for the period of high and low mango fruit

availability, to investigate whether risk factors changed as fruit availability varied. I determined the high and low period by comparing the relative abundance of mango fruits: mango fruit availability was high during survey 1 and low during survey periods 2, 3 and 4 (see Figure 7.2).

Multi-collinearity of independent variables was tested using Spearman's correlation for continuous data and Chi square for nominal data and cases with a higher p value than 0.05 were excluded after adjusting with a Bonferroni correction. The variable "crown width" was excluded since it was highly correlated with mango fruit availability, as would be expected since a larger, more mature tree would likely produce more fruit. The variable "crop status" was also excluded as it was highly correlated with "guard" which would be expected since fallow fields would not be guarded. The variables "Cover" and "Cover level" were correlated. "Cover level" was used both because it gave a better fit in the model and provided more detailed information about the influence of terrestrial vegetation cover on tree selection rather than a binary presence/absence score. While the variable "habitat" was not significantly correlated with any other variable, it was deemed a redundant parameter, since whether the tree was in proximity to a crop or homestead was also recorded. Therefore, the following dependent variables were included in the model (Table 7.2): "Mango FAI" (Prediction 1), "Distance from edge" (Prediction 2a), "Cover level" (Prediction 2b), "Homestead" (Prediction 2c), and "Guard" (Prediction 2d). Trees which did not produce mango fruits during the study were excluded since a chimpanzee could not feed on a tree with no fruits. This left a total of 56 trees in the overall model, 41 trees in the high availability season and 44 in the low season.

7.3 RESULTS

I monitored 66 mango trees over 44 days, 75% of which were in a cropped area (n=51), 50% were guarded (n=33) and 50% had no vegetation cover (n=33), although a tree without cover was not necessarily guarded. Mango feeding traces from chimpanzees were found on 84% of survey days (n=36).

A total of 1633 mango stones were inspected, 1129 of which were from consumption by chimpanzees and 504 by humans. Chimpanzees were recorded feeding on 25 mango trees during the study period. Forty one percent of the mango trees monitored (n=27) were not recorded as fed on by chimpanzees or humans at all during the study. In 9 of 27 cases the trees did not produce ripe fruit during the study. A mean of 17 mango feeding traces were recovered from underneath each tree over the study period ($SD \pm 38.6$, range: 0-197, $N=1129$) and the highest

number of feeding traces recorded from a single tree in one day was 86. Each tree was visited by chimpanzees an average of once over the study period ($SD \pm 1.8$, range: 0-8; 1 day being the minimum period between surveys).

7.3.1 Mango fruit availability

A Friedman test showed that mango fruit availability varied significantly across survey periods ($\chi^2(3)=32.536$, $p<0.001$; Figure 7.2). There was a distinct spike in mango availability at the start of the season, and despite a large proportion of trees finishing fruiting in the last survey, overall mango fruit availability increased again towards the end of the season. Twenty-seven percent of the mango trees ($n=18$) had finished fruiting completely by the last phenology survey.

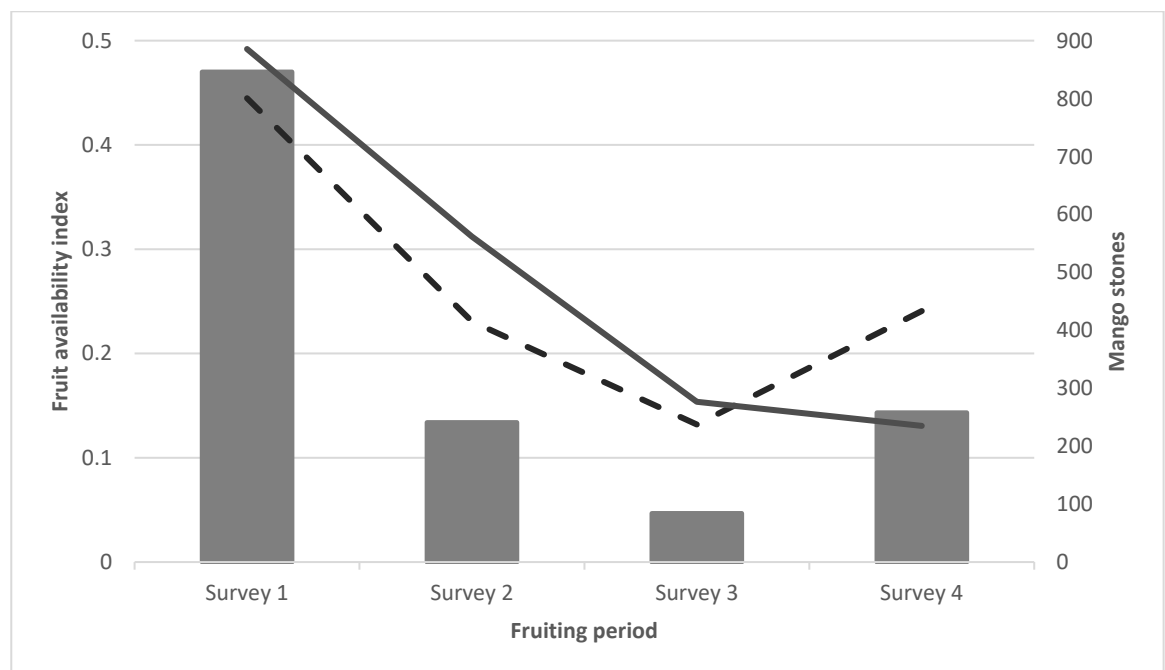


Figure 7.2: Mango (dotted line) and wild (solid line) fruit availability in each survey period against the number of mango stones fed on by chimpanzees (bars). Wild fruit availability is expressed as a proportional index to fit to scale but is not directly comparable to mango fruit availability.

7.3.2 Mango tree selection and risk perception

Overall, mango fruit availability was the strongest factor predicting both the number of mangos consumed by chimpanzees ($B=0.861$, Wald $\chi^2=9.559$, $p=0.002$, $n=56$) and the number of times a tree was revisited ($B=0.335$, Wald $\chi^2=4.272$, $p=0.39$, $n=56$). This strongly supports Prediction 1, and the hypothesis that chimpanzees will forage on crops when they are available. Regarding risk, chimpanzees consumed more mangos and revisited trees closer to the forest edge, supporting

Prediction 2a ($B=-0.005$, Wald $\chi^2=5.547$, $p=0.019$) and there was a trend showing chimpanzees consumed more mangos from trees which were reported to be unguarded, lending support for Prediction 2d ($B=1.199$, Wald $\chi^2=3.499$, $p=0.061$).

During the period of high mango fruit availability (Survey 1), the only variable predicting the amount of mangos fed on was the availability of fruit ($B=1.339$, Wald $\chi^2=6.620$, $p=0.01$, $n=41$) and there was a trend for chimpanzees to revisit trees with more fruit ($B=0.720$, Wald $\chi^2=3.656$, $p=0.056$). No risk factors predicted mango consumption in high season, but chimpanzees visited trees more often that were further from the forest ($B=0.004$, Wald $\chi^2=6.269$, $p=0.012$) - a result contrary to Prediction 2a and the results from the overall model - and which were not guarded ($B=1.285$, Wald $\chi^2=7.354$, $p=0.007$).

When mango fruits were relatively scarce (Surveys 2, 3 and 4), chimpanzees ate more mangos from trees that were not guarded ($B=4.318$, Wald $\chi^2=13.958$, $p<0.001$, $n=44$) and which had a higher level of terrestrial vegetation cover, in accordance with Prediction 2b ($B=0.037$, Wald $\chi^2=8.093$, $p=0.004$). There was a trend to consume more mangos from trees closer to the forest ($B=-0.008$, Wald $\chi^2=3.383$, $p=0.066$). The only factor predicting tree revisits in the low season (Surveys 2–4) was the amount of fruit, with chimpanzees revisiting trees with more fruit more often ($B=0.595$, Wald $\chi^2=4.862$, $p=0.027$), although there was a trend for chimpanzees to revisit trees that were guarded less often ($B=0.800$, Wald $\chi^2=3.063$, $p=0.08$).

7.3.3 Tree variety

There were 6 different varieties of mango tree, differentiated by their leaves and fruit, coded from 1 to 6. I was unable to identify two trees for their variety. Of the six varieties identified, three varieties were represented by only one fruiting tree and two varieties were not fed on by either humans or chimpanzees over the duration of the study (Table 7.3). Most trees monitored (64% of trees) were Variety 2 and chimpanzees consumed the majority of mangos from this variety. Humans also seemed to favour Variety 2. Chimpanzees ignored Variety 1 completely. With only four trees monitored, 8.8% of recorded mango stones recovered belonged to Variety 5.

Table 7.3: Summary of mango trees and mango stones per tree variety.

			Total number of stones	
Variety	n (trees)	n (trees with fruit)	Human	Chimpanzee
1	11	7	37	0
2	47	42	448	964
3	1	1	0	0
4	1	0	0	0
5	4	4	9	100
6	1	1	10	4
Unk	2	2	0	61

7.4 DISCUSSION

The aim of this study was to identify the key factors from all the tree and garden characteristics that may influence chimpanzee mango feeding behaviour, including chimpanzees' perception of risk in an anthropogenic environment. This is the first study to investigate in detail which specific aspects of the human-dominated matrix are considered in calculating feeding choices for chimpanzees by assessing each individual factor relating to risk within an anthropogenic habitat. Using sign survey techniques provided a systematic method to monitor feeding when direct observations were not possible, missing a minimal amount of information.

7.4.1 Fruit availability

In this study I found that chimpanzees consumed a substantial quantity of mangos during the peak season from the monitored trees, confirming the high level of mango foraging by chimpanzees at this time of year. Mangos are an integral part of the chimpanzees' diet at Kasongoire, as is also the case at similar highly human-disturbed sites like nearby Bulindi (McLennan 2013). These results corroborate other studies regarding the feeding of mangos in particular. Some crops have been described in previous studies as fallback foods (Naughton-Treves et al. 1998; Hockings et al. 2012b, McLennan 2013), but mango appears to be a preferential food item when it is available (Hockings et al. 2009; McLennan 2013). Kasongoire chimpanzees consumed significantly more mangos during the period of high wild fruit availability as compared with low, despite a relatively high level of wild food availability during the peak of the mango season, the opposite feeding behaviour seen in utilising fallback foods.

In Kasongoire, peak mango season coincided with a period of overall high wild fruit availability in relation to other months (see Figure 3.8, Chapter 3), yet chimpanzees still fed heavily on mangos suggesting that they were responding to the peak in availability of mangos irrespective of fruit in

the forest. The fact that mango foraging decreased over the season even though wild food availability was lower is perhaps a result of lower foraging efficiency explained by the lower availability of mango fruits. Conversely at Bossou, a period of low wild fruit availability coincided with the height of the mango season. While chimpanzees there foraged heavily on mangos when they were available, they constituted a much lower proportion of their diets when wild fruit availability was higher, despite high mango availability (Hockings et al. 2009). This suggests that chimpanzees at Bossou preferred to take the risk of accessing mangos when foraging efficiency was highest.

Overall, mango fruit availability in the high season at Kasongoire strongly influenced the quantity of mangos consumed by chimpanzees, and there was a trend for chimpanzees to revisit trees with more fruit. This may suggest that chimpanzees were exhausting the supply of mangos in each tree when they are most abundant, and then not revisiting the tree. No risk factors predicted how chimpanzees consumed mangos in the high season, although they were less likely to revisit guarded trees. This supports the idea that chimpanzees consume as many mangos as are available and when they revisit trees take guarding presence into account when selecting trees. It could be the case that as a result of lower foraging efficiency when mango availability was low, it was not worth risking entering the village-garden matrix to eat mangos, and when mango fruit availability increased towards the end this made the benefit sufficient to forage on mangos more heavily again.

Interestingly, chimpanzees revisited mango trees further from the forest during the first survey period when mango fruits were most abundant, although overall trees closer to the forest were more likely to be revisited and foraged on more heavily. There was no correlation found between mango fruit availability and distance from the forest edge in the high season, nor a correlation between guarding presence and distance from the forest. One possible explanation for this may be that chimpanzees simply prefer some of the trees further from the forest, and since this first survey period was also a period of high wild fruit availability, they were more prepared to make longer journeys into crop gardens. This lends support towards the “abundance/risk” hypothesis, where chimpanzees are more willing to take risks when there is an abundance of food to fall back on. As Gilby and Wrangham (2007) put it: “when diet quality is particularly high...they can simply recoup the costs of failure”.

Conversely, the “scarcity/risk” hypothesis was supported in the low season: mango fruit availability predicted mango tree revisits in the low season, but no variables relating to anthropogenic risks in the landscape. This shows that chimpanzees revisit trees with more fruit and are less concerned about risk, so increased foraging efficiency is the most important factor in tree selection. However, in the low season chimpanzees consumed more mangos from trees which were unguarded and had more terrestrial vegetation cover, perhaps because their lower perceived risk of being able to stay longer in these trees. The support of both the abundance- and scarcity-risk hypotheses suggests that rather than an either/or tactic, chimpanzees flexibly weigh up the risks with other factors including foraging efficiency and preference of trees when foraging on a highly preferred feeding species in the risky village-garden matrix.

7.4.2 Mango tree preferences and responses to risk

The distance a mango tree was from the forest edge was a significant factor predicting mango tree selection in the overall models, with chimpanzees generally choosing trees closer to the forest. Unsurprisingly, the distance from the forest edge has often been found a driving factor influencing the likelihood of primate crop-foraging, with crops grown close to the forest being favoured over those further away (Linkie et al. 2007; Naughton-Treves 1998; Nijman & Nekaris 2010; Wallace & Hill 2012). However, as Wallace and Hill (2012) point out, planting a crop further from the edge may not be an adequate deterrent for a large-bodied and highly mobile primate such as a baboon or chimpanzee.

When broken down by season, there was a trend for chimpanzees to consume more mangos from trees closer to the forest during low mango fruit availability, but, interestingly, the reverse was found for visiting trees during fruit abundance. This shows that the animals were still willing to travel long distances from the forest through a risky environment for a highly nutritious food. Kasongoire chimpanzees regularly travelled over 300 m from the forest to forage on mangos, as previously described by Greengrass (2000) for Gombe and Wallace and Hill (2012) for Budongo. On one occasion during this study (early May), a party of four chimpanzees was known to travel from the core range forest fragment across an extremely human-dominated and risky habitat where there is almost no remaining forest, including a busy road. Through reports from locals I traced this group (by finding their nests) as far as a cluster of mango trees 8 km away. Greengrass (2000) and McLennan (2010) both report chimpanzees travelling 3 km from the forest.

It is interesting to think about how chimpanzees are able to remember and locate trees far away from the forest, particularly since the analysis of tree visits in the high season found a negative relationship between distance from the forest edge and number of times a tree was visited. Mango trees are quite distinctive and can likely be seen from a long distance away. However, the landscape at Kasongoire is undulating, with the village and crop gardens on an uphill incline from the riverine forest: it is very likely that trees which are hundreds of metres away cannot be seen from the forest. In an anthropogenic landscape, chimpanzees are less able to move easily between trees to monitor their fruits. It is also less likely that chimpanzees would forage opportunistically: in a risky landscape, it may be more important to move directly to a specific food source. A study on the spatial memory of chimpanzees in locating fruiting trees in the Tai Forest in Cote d'Ivoire suggests that chimpanzees use their long-term memory to locate trees rather than visual cues (Janmaat et al. 2013). The authors suggest that chimpanzees remember specific trees which produce a high quantity of fruit across fruiting seasons, with a 'memory window' of up to three years. Since mango trees, among other cultivated foods, have been planted in areas that were once chimpanzee habitat, many of the trees monitored in this study would have been closer or adjacent to the forest at some point and after further land conversion are now farther away. Additionally, the landscape was likely much less intensively used by people a few decades ago. Therefore, it could be reasonable to assume that these trees were once known to chimpanzees when the forest was larger, and this could explain how chimpanzees travel so far from the forest to certain mango trees. Ban et al. (2014) found that chimpanzees were prepared to travel longer distances for trees that they had previously enjoyed, measured by a higher number of food pant grunt vocalisations and fewer rejected fruits. It is possible that certain trees, including trees which are further from the forest edge, are simply preferred, and that chimpanzees remember these locations and are willing to traverse the risky landscape for them. In another study, Janmaat et al. (2016) suggest that chimpanzees can plan times to return to specific trees using their spatio-temporal knowledge by monitoring the ripe fruit status of trees and using their memory of the expected quantity of fruit from specific trees. This then enables them to plan to travel to favoured trees efficiently, which may be how chimpanzees at Kasongoire plan their travel to further mangos trees in the village-garden matrix.

Guarding presence within the area of the tree seemed to deter chimpanzees from consuming as many mangos and revisiting the tree, particularly in the low season. Other studies have shown human guarding to be the most common, and sometimes the most effective, crop-feeding deterrent method (Hill 2000; Hsaio et al. 2013; McGuiness & Taylor 2014; Nijman & Nekaris 2010;

Wallace & Hill 2012; Webber 2006). This suggests that whilst chimpanzees in Kasongoire are generally accustomed to living in close proximity to humans, there is an impact of human presence on their perception of risk. However, trees with homesteads within 30 m were foraged on and revisited, and homestead as a risk factor was not significant in any model. A homestead would likely have some people around, although, unlike crop guarding, people would not necessarily be actively deterring chimpanzees from the area. From observation and reports during the study period, a tree near a homestead could be visited discreetly by a single chimpanzee, which may even be tolerated. Over the course of the study we received reports from local people that a female chimpanzee had been residing on the other side of the village over a period of a week or more and was being tolerated by the landowners. A larger party of chimpanzees might not be so discreet and would not usually be tolerated close to a homestead (pers. obs.).

McLennan and Hill (2012) report that farmers in nearby Bulindi were much more tolerant of chimpanzees foraging on domestic fruits compared to staple or cash crops. People eat and sell mangos, but they are neither a staple part of their diet nor are they a highly valuable crop. They are important however as a snack, particularly for children and older people who sell them to obtain small amounts of cash. In Kasongoire one person who reported that he guarded the crops in his garden was generally tolerant of chimpanzees, yet when we visited his garden we found a sizeable party foraging on mangos on his land. This also brings into question not only the reliability of a tree owner when reporting guarding, but also the method used when guarding. It could be the case that he was not actively guarding or was in another area of the garden at that time, or that he simply tolerates mango feeding. However, he was heard shouting at - but not chasing - chimpanzees foraging on jackfruit (*Artocarpus heterophyllus*) on other occasions. Guarding could be crop-specific: mangos are super-abundant at that time of year and not a staple crop, so it is possible that chimpanzee mango-foraging is not considered a big problem, whereas feeding on other crops is. For example, jackfruit is probably more economically viable and so chimpanzees may be more likely to be chased when foraging on them. Additionally, people do not tend to actively guard mango trees specifically, but the area around the tree where other crops are grown.

For higher foraging efficiency, if other cultivated foods were also available in the area as compared with a completely fallow field, chimpanzees may consider this tree more worth the risk. Alternatively, fallow fields would have few humans and a higher percentage of ground cover, making them attractive for crop-foraging forays. Whether the area around the tree was cropped

or left fallow could not be tested in the model due to multi-collinearity of the variable “crop status” with guarding presence. However, on the few occasions chimpanzees were observed leaving the forest to forage on mangos they were seen feeding on other cultivated foods on a couple of occasions and on fruit trees in particular: jackfruit and papaya (*Carica papaya*). No traces for other fruits were found under mango trees. Certainly chimpanzees knew of other fruit trees in the landscape, particularly of these two species, although in mango season chimpanzees would primarily feed on mangos since it is such a pronounced fruiting season.

7.4.3 Influence of mango tree variety

Chimpanzees showed a preference for Variety 2 (local name “Woosi”), consuming a total of 90% of mangos from this variety alone. Chimpanzees completely ignored mango trees which were Variety 1 (local name “Suna”), despite them comprising 17% of all trees monitored. This is explained in four out of eleven cases since the trees did not have ripe fruit. Further, the results of the model help explain why chimpanzees completely ignored this variety: of the seven trees which had fruit, five were reported to be in an area with a guard.

Both trees in Variety 5 which were foraged on were in an unguarded area, which could suggest that rather than showing a preference for this variety for taste or nutritional reasons, these individual trees were simply low risk. However, chimpanzees ignored a very large tree in this variety, which was unguarded, had a high level of ground cover and a large amount of fruit. This may illustrate that some trees are simply more known than others, and that there are additional factors involved when selecting trees to forage on than was recorded in this study. It may simply be that chimpanzees consumed the most number of fruits from the most common variety: this would not be surprising. A larger sample size for trees of all mango varieties, particularly Variety 5, would show whether chimpanzees did show particular preference for this variety or whether the high comparative level of feeding on this variety was genuinely due to factors related to risk.

7.4.4 Study limitations

One drawback in recording the total number of mango feeding traces is that it cannot be known whether one individual invested a long time foraging in a tree or many individuals consumed the same number of mangos. An association between crown size and the number of traces may have implied that a larger party of chimpanzees contributed to a higher number of mangos consumed, since a larger crown would presumably provide arboreal vegetation cover and visual protection.

This would be especially important for a larger party. In my analysis, crown size had to be omitted due to correlations with other factors, meaning that I was unable to investigate this further.

Since it was not feasible to monitor the trees for the duration of the day, it was not possible to assess whether there was any guarding presence during actual foraging events by chimpanzees. The question I posed to the owners of the trees about guarding the area was not specific to mangos, as I wanted to know whether there was a human guard in the area generally. Additionally, guards often sit in their huts during lunch time or the hottest part of the day, and also tend to other areas of the garden. Therefore, even though the owner may have reported that the area was guarded, the nature and intensity of this guarding is hard to specify. Despite not being able to record whether a human was actually there or not during the time when chimpanzees visited each tree, guarding was a significant predicting factor explaining mango tree selection. This may imply that chimpanzees remember which areas are generally guarded and avoid them.

It may be that chimpanzees forage from various trees for reasons other than those that were measured and/or controlled for in this study. Therefore, it could be worth performing the analysis again as a mixed model with the individual tree entered as a random effect. This could shed further light as to whether chimpanzees have 'preferred' trees and are selecting them based on their fruit availability and likelihood of a human encounter, or whether there is an additional unexplained variable worth considering.

7.4.5 Chimpanzee mango foraging party composition

Chimpanzees were present feeding in mango trees on 15 survey days during the study, so there was not sufficient data to analyse any patterns between the age/sex class of chimpanzees feeding on mangos and the factors of risk. However, on most occasions parties comprised only adult and subadult or juvenile males: on two occasions a female joined a party with other males. Chimpanzee risk perception would very likely be influenced by party size and composition, although in this study I was unable to record these data.

Adult females were observed feeding in a jackfruit tree less than 80 m from the forest edge on a couple of occasions prior to this study, but generally males were much more likely to enter the gardens. On the one occasion when a female foraged on mangos without adult males present, SYL, an adult female with an infant fed from a tree 100 m from the forest edge with her offspring

BLY, a juvenile male who usually travelled and foraged with the adult males. Females were not observed feeding on trees further than 175 m from the forest in this study, although from reports it was known that females did venture to further mangos discreetly on their own, and one female was in the party of four mentioned previously that foraged on mangos 8 km away from their core forest area.

It is already established that adult and subadult males are more likely to forage on crops (Hockings et al. 2007, 2012b; Wallace & Hill 2010) showing that they take more risks for high quality foods, although their behaviour in the village-garden matrix could not be recorded in this study. Krief et al. (2014) found that females were also crop-foraging after dark, meaning that potential interesting modifications of behaviour could be missed at Kasongoire. While ethically it is undesirable to follow chimpanzees in to crop gardens, and logistically it is difficult since chimpanzees move quickly and quietly in the anthropogenic matrix (pers. obs.), it would be useful to develop a method whereby the researcher could stay hidden and still be able to record chimpanzee behaviour. Although camera traps are a useful technology, if the subject species does not regularly revisit the exact same location, they cannot record this detailed information.

7.4.6 Conservation implications

Mangos are not a subsistence crop, yet the fact that chimpanzee mango-feeding was an almost daily occurrence shows the potential for hostility towards chimpanzees in the landscape. Several farmers at Kasongoire stated in informal discussions that they either had or were considering cutting down their mango trees because they attract chimpanzees, and they believed that removing them would lower the chance of chimpanzees coming out of the forest and damaging their crops (as is the case at nearby Bulindi, McLennan & Hill 2012). One tree which was monitored as part of the study was cut down by the owner's neighbour in revenge for bringing the chimpanzees close to his garden. At the same time, many community members, including the Kasongoire Chairman, were keen to plant more mango trees within or close to the forest to keep chimpanzees from entering the gardens.

I was unable to assess harvesting rates by humans for consumption at home or sale to market. However, Variety 2 was the most preferred mango variety for chimpanzees but was also found through feeding traces to be the most popular with humans too. Variety 5 was the second most preferred by chimpanzees, but feeding traces from humans were minimal. Future conservation strategies could consider planting this variety close to the forest to see whether its presence

deters chimpanzees from venturing further into the village-garden matrix. Similarly, Riley et al. (2013) suggest a buffer zone of cacao, an attractive crop for Tonkean macaques and high in metabolisable energy. This would be a long-term experimental strategy since mango trees take years to mature, but the situation is such in Kasongoire that drastic and creative measures may prove to be the best course of action to improve human-chimpanzee relations.

Considering the influence that guarding and vegetation cover had on reducing chimpanzee mango feeding, one obvious recommendation would be to increase guarding (Nijman & Nekaris 2010) and to keep the area around the tree free from ground vegetation. However, although chimpanzees showed a preference for trees with ground vegetation cover during the low mango fruiting season, trees which were completely exposed were still foraged on: it is not possible to prevent chimpanzees from leaving the forest. Humans are more likely to feel threatened by adult and subadult chimpanzee males than females since they are larger in body mass and have the propensity to display more agonistic behaviours (McLennan & Hill 2010). Given crop-foraging parties are mainly comprised of males, reducing cover around the tree may only increase the visibility of chimpanzees to humans and increase fear and hostility.

Hill and Wallace (2012) found active guarding (regularly patrolling the perimeter of the farm) to be an effective crop-foraging deterrent for a variety of species, although part-time guarding was not always effective in deterring baboons. However, these results are not corroborated everywhere where guarding is not performed so actively. For example, in Gashaka Gumti National Park in Nigeria, Warren (2009) found that guards only actively reacted to crop-foraging by baboons around 50% of the time, taking over 20 minutes on average to respond, resulting in their guarding efforts being generally ineffective. However, guarding is still recommended as the most effective way to protect from crop losses (Hill & Wallace 2012; Nijman & Nekaris 2010; Warren et al. 2007). If increased guarding was advised in Kasongoire then it would be important that farmers do not leave small children alone in the garden: not only does this take children away from school (Linkie et al. 2007; Mackenzie et al. 2015) but the target of attacks on local persons by chimpanzees is ordinarily children, which can potentially be fatal (Hockings & McLennan 2016; McLennan 2008; Reynolds et al. 2003; Wrangham 2000). In nearby villages, as well as at other sites, up to two thirds of crop guarding is reportedly performed by women and children (Hill 2000; Linkie et al. 2007; McGuinness & Taylor 2014; Ogra 2008), although crop-foraging animals are more likely to be deterred by adult men (Osborn & Hill 2005).

Even when guards are present, they may be ineffective: in a study in villages around Budongo Forest, Wallace and Hill (2012) found that guards were equally as likely to actively respond to primates foraging on their crops as to ignore the primates, which meant that farmers' guarding response did not actually influence the duration of the foraging event. Additionally, guarding is the largest cost for farmers in economic and opportunity costs (Howard 1995, cited in Hill 2000; Linkie et al. 2007; Webber 2006). Developing strategies for alleviating the impact of chimpanzee crop-foraging and the potential for human-interactions is complicated: the situation is complex, and unique to each chimpanzee community and the surrounding village environment. However, the first step is further understanding foraging behaviour and highlighting factors that determine preferences.

Mangos are not a staple crop, although chimpanzees, among other primate species, are known to forage on non-fruit crops which are important to the livelihoods of local people (Hill 2017). Crop losses of non-fruit crops such as maize and cassava and fruits such as bananas, which are locally important staple crops, can result in tension and negative interactions between humans and wildlife. For crops which are less seasonally available and more intensely guarded as result of being more important to peoples' livelihoods, risk factors may likely play a more important role in foraging decisions. Further research, potentially involving hides or camera traps, should investigate the factors involved in primate risk perception when foraging on these crops. It would also be interesting to know how much mango season impacts perceptions towards chimpanzees and to see whether this changes over the duration of the season, reflecting crop loss, for example using a Likert scale-type questionnaire to households on a bi-monthly basis.

Understanding the complex dynamics of crop-foraging behaviour and chimpanzee perceptions of risk is vitally important for conservation planning. Chimpanzee foraging on crops, and mangos and sugarcane in particular, has been increasingly documented around Budongo Forest where anthropogenic influences and deforestation is increasing (Babweteera et al. 2012; Reynolds 2005). Even though mangos are not a subsistence crop, crop losses - whether substantial or not - hamper conservation efforts. This study has shown that chimpanzees feed heavily on mangos when they are available and are therefore more likely to be encountered in the village during this period, which could lead to an increase in negative interactions or perceptions.

CHAPTER EIGHT

CONCLUSION: IMPLICATIONS FOR ANIMALS IN HUMAN-MODIFIED LANDSCAPES



Plate 22 (on previous page): A lone male resting in the open gap outside the forest. Kasongoire hill can be seen in the background.

8.1 Summary and analysis of results

This study sought to gain a better understanding of how chimpanzees respond to living in a human-modified landscape at a new study site in the Albertine Rift. As was the case in Bulindi, the neighbouring site (McLennan & Plumptre 2012), despite being heavily impacted by human activities the forest at Kasongoire maintains a high diversity of tree species and does not currently experience a shortage of wild fruit. Chimpanzees at neither Kasongoire nor Waibira appeared to increase their dietary diversity when wild fruits were less abundant: at Kasongoire this is likely explained by the fact that chimpanzees met their metabolic needs through the exceptionally high integration of sugarcane into their diet, with males spending more time foraging on sugarcane than wild fruits. This is the first study to report the effects of a monoculture crop on chimpanzees' diet and activity patterns. Kasongoire chimpanzees spent a significantly higher proportion of their activity budgets resting and less time feeding than did chimpanzees at Waibira, likely as a result of the high contribution of sugarcane (among other crops) in their diet, corroborating with results where other primates incorporate human foods in their diet (Altmann & Muruthi 1988; Saj et al. 1999; Strum 2010). Although I was unable to follow chimpanzees into crop gardens it is evident that the anthropogenic matrix provides additional resources for chimpanzees at Kasongoire: in addition to sugarcane chimpanzees foraged heavily on cultivated fruit trees, namely mangos, and traces of jackfruit were encountered often. Since chimpanzees are able to supplement their diet on wild foods with cultivated foods, this suggests that they are able to find sufficient resources to survive, for the time being at least. This study provides further evidence showing that in cases of severe forest loss, primates can respond flexibly by using the agricultural matrix in order to survive.

Kasongoire chimpanzees modify their grouping patterns when leaving the forest by increasing the size of parties and the ratio of males, as was predicted in response to higher risk. When foraging on mangos in the village-garden matrix, chimpanzees consumed mangos when they were available despite high wild fruit availability, showing that chimpanzees are prepared to enter a risky habitat for certain cultivated foods. Chimpanzees at Kasongoire showed an overall preference for mango trees which were closer to the forest and which were not guarded, suggesting that the potential risk of encountering humans is something that they consider when foraging within the village-garden matrix. However, where predictions were not supported, caution must be taken when making generalisations about Kasongoire chimpanzees' perception of risk: it could be that the landscape outside of the forest is not perceived as that risky by the

chimpanzees. For example, Kasongoire chimpanzee party cohesion was not tighter when leaving the forest, and chimpanzees did not avoid mango trees close to homesteads. This could be explained by the fact that animals may react to specific risks as they arise through threat-sensitive responses (Helfman 1989), whereby animals change their behaviour according to the degree of perceived actual danger from the predator (in this case humans).

If animals are flexible they can utilise areas outside of the forest boundary to their advantage: for Kasongoire chimpanzees, their use of the agricultural matrix is integral to their daily survival, as is the case for primates in other human-modified habitats. Chimpanzees in nearby forest fragments within the Budongo-Bugoma forest corridor have responded flexibly to forest loss by nesting in plantation forests (McCarthy et al. 2017). In southern Kenya, colobus monkeys (*Colobus angolensis palliatus*) in extremely small forest fragments have been reported to use the agricultural matrix for dispersal (Anderson et al. 2007). Elsewhere, primates have been found to develop sympatric relationships with humans and their cultivated foods, creating a level of benefit from their behaviour and reducing the costs for local people of living close to animals foraging on crops. For example, red colobus monkeys in Zanzibar 'prune' harvested coconut trees, although many local people perceive them to damage rather than aid the crop (Siex & Struhsaker 1999). In Cantanhez National Park in Guinea-Bissau chimpanzees consume the pseudofruit of cashew, making it easier for humans to harvest the edible nuts (Hockings & Sousa 2012). Primates have also been reported to act as seed dispersers for cultivated plants (e.g. cacao: Estrada et al. 2012; Hockings et al. 2017).

Through investigating animals' use of these habitats and understanding their responses to different anthropogenic factors, future conservation and conflict mitigation strategies can be tailored to specific situations according to the responses and limits of flexibility of the species. The growing literature on primates' use of resources outside the forest boundary highlights the importance of the agricultural matrix. In addition to conserving and restoring wild habitats, there may also be conservation value in the anthropogenic habitats, including specific cultivated species (Chaves & Bicca-Marques 2017; Estrada et al. 2012).

8.2 Aggressive apes: an obstacle to co-existence

In Kasongoire, no symbiotic interactions were discovered between chimpanzees and humans whereby chimpanzee responses created a benefit. In contrast, human-chimpanzee co-existence is threatened by two-way negative interactions including directed aggression by both chimpanzees

and humans towards each other. Apart from damage and loss to crops, the biggest obstacle in the way of peaceful human-chimpanzee co-existence in Kasongoire is people's fear of attack. This is often the case where chimpanzees and humans share landscapes (Hill & Webber 2010; Hockings & Humle 2009; Hockings & McLennan 2016; McLennan & Hill 2012; McLennan & Hockings 2016). Understanding perceptions and responses to entering the risky anthropogenic matrix, including encounters with humans, from the point of view of the species is therefore a crucial step towards unravelling, predicting and possibly preventing future negative interactions.

Why chimpanzees might show different responses on different occasions is something worth analysing in further detail. Kavaliers & Choleris (2001) point out that an individual's previous experience, in addition to their innate response, will shape their response to a threat. In the case of Bulindi chimpanzees, encountering researchers inside the forest fragment and in recently cleared patches (as opposed to other habitats outside of the forest) dramatically increased the likelihood of a threatening response (McLennan & Hill 2010). Chimpanzees in Bulindi showed different behavioural responses to researchers during the initial stages of McLennan's study there (McLennan & Hill 2010), from ignoring researchers to aggressively mobbing them and even pursuing them to the point until they left the forest (as also happened during this study in Kasongoire). As the study period continued, chimpanzees' rate of intimidating behaviour decreased likely because they learnt that the researchers were not a threat to them.

Occurrences of predation by chimpanzees on human children have been documented (Wrangham 2001), although such cases are extremely rare. For chimpanzees, most physical attacks on humans have not been witnessed by researchers, but it has been reported that serious aggression is often in response to intimidation by humans, such as shouting or throwing stones (Hockings & McLennan 2016; McLennan & Hockings 2016). Like chimpanzees, elephants are known to have caused human fatalities (Dunham et al. 2010; Thekaekara & Thornton 2016; Thouless 1994) and to a much higher degree than chimpanzees. Elephants have shown threat-sensitive responses to humans that are known to persecute them over non-threatening humans (Bates et al. 2007; McComb et al. 2014). Such studies show that flexible species with high cognitive capabilities can exhibit extremely high awareness of threats and either protectively modify their behaviour accordingly or show signs of fear. The problem remains, however: even if species' responses are understood, how can aggressive behaviour be reduced and eliminated? In order to improve human-wildlife co-existence it will be imperative to reduce the rate and severity of negative interactions.

McLennan and Hockings (2016) discuss the precarious nature and complexity of potential strategies for mitigating human-ape 'conflicts'. These include: culling 'problem' individuals, which is inappropriate for endangered species; translocating animals, which is wrought with difficulties since translocations may not be successful in addition to finding suitable locations in the face of diminishing habitats; and financial compensation for loss or injury, which can lead to local people feeling that researchers or conservation organisations 'own' the animals. Researching species' responses therefore provides essential information for developing educational strategies for local people regarding how to behave when encountering potentially dangerous species based on data of species' responses to human interaction. However, whilst understanding the behavioural responses of chimpanzees can help to inform conservation mitigation strategies, ultimately their survival relies on tolerance from the local human population: where animals are not tolerated by humans, behavioural flexibility may not be enough to survive in the long-term.

8.3 Implications for chimpanzee survival in Kasongoire

The loss of resources within remnant forests in anthropogenic habitats will undoubtedly have an impact on primate survival in the long-term. At Kasongoire, wild fruit availability seems to be stable for the time being. However, the loss of large tree stems and the current state of timber extraction and forest clearance is indicative of further decline in species richness and diversity (Lindborg & Eriksson 2004). If the future of important trees can be secured and Kasongoire chimpanzees continue to have access to energy- and nutrient-rich foods, then the habitat may be of adequate quality to sustain the chimpanzees there. But how much habitat loss is too much? In neighbouring Bulindi, chimpanzees have recently lost forest at an alarming rate: in addition to a high level of initial forest loss and fragmentation (McLennan 2008), around 80% of the remaining forest was cleared between 2006 and 2014 (McLennan & Ganzhorn 2017). In the face of this monumental habitat loss, Bulindi chimpanzees are still persisting in extraordinarily little habitat (McLennan 2013; McLennan & Plumptre 2012), although recent and ongoing forest loss means that their wild food supply is seriously reduced, and chimpanzees now forage even more extensively on cultivated fruit trees than previously reported (M. McLennan, 2018, pers. comm.).

Extensive foraging on high-sugar cultivated foods must also have implications for chimpanzee health. Although Kasongoire chimpanzees have access to a highly abundant, low-risk cultivated food, this will likely come at a health cost: excessive intake of sugar in humans (Karam et al. 1963; Lustig 2016) and captive chimpanzees (Harwood et al. 2012; Rosenblum et al. 1981) is a known cause of Type 2 diabetes. Future studies will investigate whether diabetes can be confirmed in

Kasongoire chimpanzees and explore the long-term health implications of consuming large quantities of sugarcane over a long time period for chimpanzee health. For example, dental cavities may be a serious consequence of a diet comprising so much sugarcane: tooth decay could reduce feeding capacity, potentially very significantly. During this study, an older male (GRZ) was noticed to have lost most, if not all, of his teeth. Additionally, obesity has been recorded in human-commensal Barbary macaques (Maibèche et al. 2015): while I did not observe any clearly over-weight chimpanzees at Kasongoire, visiting observers from BCFS commented on the large body size of the fragment chimpanzees in comparison to those in Budongo Forest. Collecting data on some physiological markers through non-invasive sample collection methods (Behringer & Deschner 2017) will shed a lot of light on the true state of the health of the Kasongoire chimpanzees.

Recording indicators of anxiety, both behavioural and hormonal via faecal gluco-corticoid measurements, could also give an indication of to what degree living in a human-influenced landscape impacts stress levels, and therefore health, in different individuals. Chimpanzees at Bossou were found to exhibit higher levels of rough self-scratching, an anxiety-related behaviour, both when foraging on crops in the presence of local people (Hockings et al. 2007) and when crossing roads (Hockings 2007), showing that chimpanzees may show behavioural stress-related responses to being in risky situations.

Gill et al. (2001) highlight potential errors when interpreting results from behavioural responses to human disturbances regarding whether or not animals avoid human disturbances. They state that animals that do not avoid human disturbances do not necessarily do so because they choose not to: species and groups of animals which avoid humans and anthropogenic disturbances may do so simply because they have the available habitat. They suggest that in fact populations which appear to be coping with anthropogenic disturbances best in terms of appearing flexible and strong in the face of human activities may in fact be the very ones which need the most protection. Species may even show responses that are ultimately maladaptive to anthropogenic disturbance which can reduce individual fitness and decrease population viability in the long term (Tuomainen & Candolin 2011). For example, consuming crops increases body mass in elephants, a signal of fitness for females, meaning that male elephants that forage on crops may be sexually selected for (Chiyo et al. 2011a). Therefore, more reproductively successful individuals (crop-foraging individuals) are putting themselves in high risk situations, a trait that may be maladaptive over time if human tolerance for crop-foraging animals declines. Even where chimpanzees are not

hunted, farmers angry about crop losses can kill animals to take revenge (e.g. Hyeroba et al. 2011; McLennan 2008; McLennan et al. 2012; Reynolds 2005), showing that there can be an impact on longevity for individuals that take risks to forage on crops.

How and whether chimpanzees in diminishing forest fragments will ultimately be able to survive in the future remains a critical question. As habitat cover further declines and the extent and nature of human landscape modifications continue, chimpanzees may face novel threats which may be fatal, such as the introduction of a tarmac road in Bulindi (McLennan & Asiimwe 2016), in addition to the ongoing risk of hostile encounters with humans (McLennan & Hill 2012). Food scarcity can also potentially affect primate fecundity, reducing birth and growth rates and ultimately having an impact on survival (Hemingway & Bynum 2005). However, McCarthy et al. (2015, 2018) found that the chimpanzee population in the corridor forest fragments between Budongo and Bugoma Forest Reserves (including Kasongore) was much higher than some previous estimates and genetic analyses show that animals are still dispersing in this risky landscape. In Kasongore, preliminary observations of adult females with two offspring of ages where they are still carried suggest that the inter-birth interval may be lower in Kasongore than in a more in-tact forest setting. Strum (2010) also reported lower inter-birth intervals in human commensal baboons. While no long-term data exists for fragment chimpanzees, lower inter-birth intervals may well be prevalent among communities with access to crops (T. Humle, 2018, pers. comm.; M. McLennan, 2016, pers. comm.). Although female chimpanzees in Kasongore consume fewer crops than males, the presence of crops nevertheless contributes to their diets with sugarcane available year-round. Emery Thompson and Wrangham (2008) found that female chimpanzees that constantly maintained a high energy balance both cycled and conceived more often. Long-term studies will be able to address how the anthropogenic matrix impacts individual chimpanzee fecundity and dispersal which will help predict whether, if protected from direct persecution from humans, chimpanzees might survive in the long term.

8.4 Future directions and considerations for studies in human-modified habitats

Dickman (2012) highlights six main drivers of conflict between humans and primates: the economic costs of damage (principally to crops), the visibility of the species, wealth/power, cultural norms, social tensions, and fear or lack of knowledge. In Kasongore, damage to crops and fear of attack are obviously detrimental to human-chimpanzee co-existence, but the contribution

of the other factors is unknown. Ethnoprimateology is a growing field based on the idea that humans and nonhuman primates share social and ecological spaces, and recognises that social and political influences impact nonhuman primates as co-inhabitants of an area (Fuentes 2012; Lee 2010; Parathian et al. 2018; Setchell et al. 2017). As humans and nonhuman primates increasingly share space as a result of forest loss and fragmentation, it has never been more important to give equal consideration to understanding human-primate interactions from this angle.

Future work at Kasongoire will take an ethnoprimateological approach to develop a thorough understanding of human perceptions of the forest and chimpanzees from a cultural, historical and socio-economic perspective. This, combined with the results of this study, in addition to further research on chimpanzee behaviours and perceptions of risk, will provide a rounded framework to develop a strategy for co-existence that works for both humans and wildlife.

Caro (1999) points out that studying the behavioural ecology of species should also be complemented by other studies, highlighting the need for cross-disciplinary studies. Any solution to conservation conflicts must take into account the views and socio-economic situations of the local people (Priston et al. 2012). There are, however, a number of difficulties in collecting cross-disciplinary data which are important to recognize. Within a set time-frame, researchers cannot always collect a wide array of data sets encompassing species behaviour, habitat ecology and socio-economic and/or ethological studies of the local human population. Of course in principle a holistic array of these three areas would create the ideal complementary study for human-wildlife co-existence, but logistically fitting three studies into one may not be feasible.

Measuring anthropogenic factors in itself presents a challenge. Other studies have attempted to categorise and score sites based on their position along the anthropogenic disturbance continuum (e.g. Hockings et al. 2015a; McKinney 2015), although the resulting scores provide either too broad or too complicated a description and comparisons across sites remains difficult. In this study I had intended to use all-occurrence sampling of anthropogenic factors, but the reality of working in a highly human-modified landscape was that even all-occurrence sampling proved unfeasible since no one spot was free from some sort of human trace. However, in order to make broader comparisons across sites and species, some kind of standard method would be useful.

The benefit of devising a standardised method of habitat disturbance factors and species responses would be for comparing disturbance factors between sites to provide more efficient ways to make overall guidelines about potential behavioural responses, such as the IUCN Guidelines on Human-Great Ape Conflict (Hockings & Humle 2009). Targeted species- and even site-specific strategies are optimal, but conducting in-depth research on every population or group of primates (among other orders and taxa) is unrealistic. With a little bit of information (rather than a long-term study), certain elements of a situation can be matched with what is already known about animals facing similar threats elsewhere to create a fast response based on what is already known (e.g. animals are not directly persecuted, animals are known to forage on crop a, b and c but not x, y and z, responses to specific deterrents have been quantified elsewhere). Previous research has used scale rankings (e.g. Hockings et al. 2015a; Table 5.3), categorised systems (McKinney 2015) or Principal Components Analysis (Bersacola et al. 2018) to tease out the different factors and their relative influence in human-modified habitats. In this study I used variables such as distance from forest edge and guarding status of crop gardens around mango trees (Chapter 7), which can be useful for drawing comparisons with other studies when another researcher has used the same variables. However, in order to make more general comparisons of the responses of animals between different sites, quantifying and characterising human disturbances and their impact on species' socio-ecology remains a problem.

Lastly, it is important to consider that even with an effective set of methods to collect and analyse data on species' responses and/or human attitudes and behaviours, there remains a gap between academic studies and conservation practise (Arlettaz et al. 2010; Knight et al. 2008; Toomey et al. 2017). It is surely imperative for the translation of data to effective strategies that communication between the two arenas is improved, in both directions. This should ensure that studies conducted by academic researchers have a function, addressing important gaps in information needed for local management strategies (Braunish et al. 2012; Knight et al. 2008). Similarly, data must be made available to those responsible for designing and implementing conservation policies in a format that it useful and accessible (Gossa et al. 2014). Although this does not guarantee the success of conservation strategies, bridging the research-implementation gap is a crucial step which will ensure that conservation strategies have foundations based on evidence, enabling more effective and flexible policies that can adapt over time.

8.5 Final remarks

Kasongoire chimpanzees may be flexible enough to adapt their foraging strategy to a high energy diet, but unless they can continue to exploit human-influenced resources which benefit them, behavioural flexibility alone may not be enough to ensure long-term survival (McLennan et al. 2017). Whichever strategy an animal may be able to take to adapt to human influences, as Schwitzer et al. (2011) point out, the ultimate survival of populations, whether in an urban, rural or agricultural setting, will depend on the tolerance of humans.

These results provide new information about chimpanzee behavioural flexibility in a human-impacted environment. However, it is not possible to extend these findings and apply the results of this study to make general statements about chimpanzee strategies wherever they are found in anthropogenic environments since the response of one community may not reflect that of the whole species (Tablado & Jenni 2017). The specific circumstances, including which crops are available and consumed, the history of interactions with humans and the level of tolerance given to crop-foraging animals, will directly influence the behavioural and dietary strategies of animals inhabiting human-modified landscapes. While chimpanzees have been shown to display a high level of flexibility in their behaviour, diets and grouping patterns, if they are fearful of entering the agricultural matrix outside the forest (for example, due to high hunting pressure), their strategies for survival will likely be very different from that reported in this study.

Studies in the area around Budongo Forest Reserve have found that farmers were historically tolerant of chimpanzees, although this appears to be changing with ongoing forest conversion into agriculture and settlements (Babweteera et al. 2012; Hill & Webber 2010; McLennan & Hill 2012; Reynolds 2005). These studies highlight that tensions, particularly around crop losses - whether measured or perceived - have exacerbated conflicts about chimpanzees. Since the completion of data collection for this study, the BCFS veterinary intervention team has been called to Kasongoire four times to attend to chimpanzees injured in mantraps and snares. On the two occasions where chimpanzees were injured in matraps, the animals lost their limb. Hopefully, in the future there will be a continued research presence in Kasongoire that will reduce the number of these interventions, given that researcher presence has sometimes been shown to have a positive effect on rates of forest exploitation by local people (Campera et al. 2017; Laurance 2013). Ultimately, chimpanzees may be able to respond flexibly to risk to a certain degree by entering risky areas in larger parties and with more males, but if negative human-

wildlife interactions increase in severity as a result of deteriorating perceptions from locals, then Kasongoire chimpanzees may be in perilous danger.

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Appendices

Appendix 1: Chimpanzee study sites in the Albertine Rift and across Africa, with anthropogenic disturbance ratings and information.

Site, Country	Key ¹	Habitat	Human activities ²	Disturbance rating ³	References
<i>This study</i>					
Waibira (Budongo), Uganda	1	Semi-moist continuous forest	S: Protected (Forest Reserve) L: Occasional illegal pit-sawing. H: Snare traps (19% of chimps with snare injuries); chimpanzees not directly targeted for hunting. A: No agriculture; chimpanzee home range does not share a boundary with the forest edge. O: An unused road runs through the chimpanzees' home range.	8	Pers. obs.
Kasongore, Uganda	2	Riverine corridor forest fragment	S: Unprotected. Logging: timber extraction (poles, pit-sawing), fuel wood. H: Crop guarding, traps laid: mantraps, snare traps, "triangle" traps. Chimpanzees not hunted for meat. A: Subsistence farming, commercial sugarcane, timber plantations; cattle herding on forest edge (occasionally inside the forest). O: Roads cutting through forest, settlements within 100m of forest.	13	Pers. obs.
<i>Albertine Rift</i>					
Sonso (Budongo), Uganda	3	Semi-moist deciduous continuous forest	S: Protected (continuous forest block managed by governmental agency). L: Selective logging over 80+ years, stopped in 1997. H: Chimpanzees not actively hunted for meat but sometimes in retaliation for crop-foraging. Snare traps common. A: Subsistence agriculture outside the forest boundary,	11	Plumptre 1996; Plumptre et al. 2007; Reynolds 2005.

			including sugarcane; pine plantations on forest border. O: Largest forest block in Uganda. Some forest compartments where resource use by local people is allowed. Settlements and roads close to forest border.		
Bulindi, Uganda	4	Riverine corridor forest fragments	S: Unprotected (privately owned forest fragments). L: Intensive forest clearance: 80% forest loss in period 2006-2014. H: Chimpanzees not actively hunted for meat but sometimes in retaliation for crop-foraging. Snares and man traps. A: Subsistence agriculture, cash crops: namely tobacco, rice and, recently, sugarcane. O: Road cuts through home range.	14 ³	McLennan & Asimwe 2016; McLennan pers. comm.; McLennan & Hill 2015; McLennan & Plumptre 2012.
Kasokwa, Uganda	5	Riverine corridor forest fragments	S: Both protected (Kasokwa Central Forest Reserve) and unprotected (remainder of forest fragments). L: Kasokwa CFR is more intact than unprotected private forests which have been extensively logged over the past decades to present. H: Chimpanzees not actively hunted for meat but sometimes in retaliation for crop-foraging. Snare traps are used as well as mantraps occasionally. A: Subsistence agriculture. The forest is situated in the heart of the sugarcane plantation, with the KSWL factory only 1 km away. O: The main forest fragment sites adjacent to the main road from Masindi (made of maram clay). A large village	13 ⁴	Reynolds et al. 2003; Reynolds 2005; Zommers 2013.
Semiliki, Uganda	6	Savannah with riverine gallery forest	S: Protected: gazetted as a game reserve in 1932.. L: nd H: Some snares but no snare injuries on chimpanzees. Extensive history of poaching. Low current levels of poaching; whether chimpanzees are actively hunted is unknown. A: Tea plantations and subsistence farming outside	nd	Hunt 2000; Hunt & McGrew 2002; Patrick et al. 2012.

			reserve boundary. O: Oil drilling exploration in Lake Albert at north of reserve.		
Sebitoli (Kibale), Uganda	7	Medium altitude tropical moist forest-farm mosaic	S: Protected: Kibale National Park L: 4 of 11 forest compartments used for commercial timber extraction. H: Chimpanzees not actively hunted for meat. A: Subsistence crops grown around forest edge. O: Most of chimpanzee home range bordering forest edge. A tarmac road runs through home range.	12 ⁵	Bortolamiol et al. 2014; Cibot et al. 2015.
Ngogo (Kibale), Uganda	8	Medium altitude tropical moist forest	S: Protected: Kibale National Park L: No logging, but old human settlement, now grassland. H: Chimpanzees not actively hunted for meat. A: None O: Chimpanzee home range shares no borders with the forest edge.	8 ⁴	Bortolamiol et al. 2014.
Kanyawara (Kibale), Uganda	9	Medium altitude tropical moist forest	S: Protected: Kibale National Park L: Areas with history of no, medium and high logging intensity. Currently some pitsawing. H: Chimpanzees not actively hunted for meat. Many individuals with snares and chimpanzees have been caught in mantraps when entering crop fields. Additionally, there is a report of a chimpanzee being speared after entering crop gardens. A: Pine plantation. O: Chimpanzee home range shares western border with forest edge.	11 ⁵	Hyeroba et al. 2011; Sekercioglu 2002; Wilson et al. 2007.
Kalinzu, Uganda	10	Medium altitude tropical moist forest	S: Protected: Forest Reserve. L: A sawmill was located in one section of the forest, although extraction was limited to stems of one species (<i>Parinari excelsa</i>). Commercial selective logging continues. Pit-sawing and harvesting of stems for construction and firewood occurs.	8	Kagoro-Bugunda & Hashimoto 2015; Hashimoto 1999

			H: Chimpanzees not actively hunted, but snares are common, leading to a high proportion of chimpanzees with limb losses and injuries. A: Forest surrounded by agriculture. O: Around 100 people live in the site of the sawmill. Villages in landscape outside the forest.		
Gishwati, Rwanda	11	Moist afro-montane forest fragment	S: Gazetted status as Gishwati-Mukura National Park as of 2015. L: Loss of 80% forest cover within century down to 9km²; forest cover is now expanding; local people have restricted access for forest resources. H: nd A: Smallholder subsistence farming: crops grown up to forest boundary; livestock grazing. O: nd	13 ⁴	Chancellor et al. 2012; McGuinness & Taylor 2014.
Gombe, Tanzania	12	Medium altitude forest-woodland mosaic	S: Protected: National Park. L: Logging within the park is minimal, but outside the border in unprotected forest, forest cover has declined dramatically. H: Chimpanzees traditionally not hunted, but several individuals have been confirmed killed by poachers since late 1990s. Snares and men with hunting dogs, spears and guns present. A: Expanding subsistence agriculture outside of the park boundary. O: Chimpanzees impacted fatally by diseases transmitted by humans and domestic animals. Bordered by Lake Tanganyika on western edge. Large fishing villages on northern and southern borders.	8	Pusey et al. 2007.
Mahale, Tanzania	13	Medium altitude forest-woodland	S: Protected: National Park. L: Logging outside forest park boundary. H: Chimpanzees not hunted for meat, poaching levels low.	5	Bakusa & McManus 2005; Kaur et al. 2008.

		mosaic	A: Outside the park. O: Tourists have been known to come as close as 1-2 m to chimpanzees. Fatal respiratory disease outbreaks have badly affected the chimpanzee population, possibly of human origin.		
Ugalla, Tanzania	14	Savannah-woodland mosaic	S: Not protected L: nd H: Chimpanzees not directly targeted; hunters from villages using snares. A: Some tobacco crops, other data lacking. O: Main road through western Tanzania (although narrow and unpaved).	nd	Moore & Vigilant 2014; Piel et al. 2017.
Other sites					
Fongoli, Senegal	15	Savannah-woodland mosaic	S: Not protected, but only 4-5% of chimpanzee home range encroached by human activities. L: Timber extraction; wood for fuel. H: Shouting/throwing rocks when foraging on wild tamarind trees within or near crops. A: Crops; free-range cattle, herded sheep. Humans also harvest and consume wild species which are consumed by chimpanzees, including use as cash crops (e.g. <i>Saba senegalensis</i>), O: Human settlements (permanent and seasonal); roads; bush fires; artisanal gold mining; recent large-scale human immigration.	12	Lindshield et al. 2017; Pruetz 2002, 2006.
Cantanhez, Guinea-Bissau	16	Subhumid forest-mangrove-agriculture landscape mosaic	S: Protected: Cantanhez National Park. Category V Protected area, allowing for humans to live in the park and use resources. L: Extraction and use of trees for construction (including the protected species <i>Borassus Aethiopum</i>). H: Chimpanzees not directly hunted (local Nalu people hold beliefs about primates), although there is evidence of hunting chimpanzees for medicine. Within Guinea-	13 ⁴	Bersacola et al. 2018; Bessa et al. 2015; Hockings & Sousa 2013; Sa 2012.

			Bissau chimpanzees are trafficked as pets. A: Subsistence agriculture inside the park (crops including rice, cassava, beans and fruit trees), cultivation of cashews (cash crop) widespread. Slash and burn agriculture. O: There are over 100 villages within the park.		
Bossou, Guinea	17	Tropical forest-farm mosaic	S: Informally declared as a reserve. L: Forest clearance for expanding agriculture. H: Chimpanzees not hunted due to totemic beliefs. A: Cultivated, mainly subsistence crops, including fruit trees, cassava, oil palm (native but also cultivated by people). Abandoned crop gardens in home range. History of slash and burn agriculture. O: Two roads run through home range (one wider used by trucks and cars), neither is paved.	13	Hockings et al. 2006; Hockings et al. 2009; Hockings & McLennan 2012.
Tai, Ivory Coast	18	Evergreen lowland rainforest	S: Protected: National Park - the largest protected forest in West Africa. L: Forest clearance on forest boundary. H: Low levels of poaching, although hunting chimpanzees for consumption and illegal trafficking has been common in Ivory Coast. A: Subsistence and slash and burn agriculture on forest boundary. Cocoa grown as a cash crop. O: na	6	De Rouw 1993; Herbinger et al. 2011; Marchesi et al. 1995.
Gashaka-Gumti National Park, Nigeria	19	Savannah /riverine forest mosaic	S: Protected; national park gazetted in 1991, although some areas inhabited by humans illegally within the park. L: No large scale timber extraction. H: Illegal poaching of pigs and ungulates; chimpanzees are not targeted due to religious taboos, although poaching of primates may occur near to the Cameroonian border. A: Maize the most important subsistence crop, grown by	nd	Sommer et al. 2004; Warren et al. 2007; Warren 2008.

			majority of households. Rice, cocoa, yam, papaya, cassava and sweet potato are also grown. Crop-foraging reported in nearby village, but mainly for baboons. O: Cattle grazed occasionally. Non-timber forest products collected from the forest.		
Lopé, Gabon	20	Tropical rainforest/savannah-riverine forest fragment mosaic	S: Protected: national park since 2002 and UNESCO World Heritage site since 2007. An "Area of Traditional Use" (ATU) exists in the north eastern part of the park where local people are allowed to hunt, grow crops and raise cattle. L: Some selective logging, leading to local extinction of certain tree species over 30 years ago. Some trees (<i>Ceiba</i> sp.) have been locally protected due to totemic beliefs. H: Hunting allowed in ATU with traditional methods (no guns or wire snares allowed). Illegal hunting also reported. A: Crops grown in ATU including cassava. Further details of which crops and whether chimpanzee forage on them is available. O: No human settlements in the protected area, but bordered by a railway and major road and villages to the north and east of the park boundary. Park managers use controlled fires. Primate tourism operates in one of the field stations. Some cattle grazing.	nd	Tutin 1999, Ukizintambara et al. 2007, Wheeler 2010.
Goualougo, Republic of Congo	21	Equatorial lowland forest	S: Mix: Chimpanzees inhabit the protected Nouabalé-Ndoki National Park and areas outside the park planned to be a logging concession. L: None, but a third of the home range due to become a logging concession. H: None. A: None. O: Two rivers have formed an effective barrier to human encroachment, leaving the site the least disturbed	4	Morgan & Sanz 2003; Morgan et al. 2006.

			chimpanzee study site to date: no humans or human signs encountered.		
Bili, DRC	22	Tropical moist forest mosaic	S: Unprotected forest fragments and blocks across the Bili-Uele landscape. L: Land clearance for agriculture, harvesting stems for construction of huts. H: Chimpanzees are actively hunted. Guns used. Snares set. A: Subsistence farming. O: Some gold mining, fishing and bird hunting in area. Several villages. It is worth noting that these studies refer to the whole landscape, in which there is a large amount of variation of level of anthropogenic disturbance factors between forested areas.	nd	Hicks et al. 2012, 2013.

¹ Key number refers to Figure 1.1, Chapter 1, showing location of study sites.

² Disturbance rankings as according to Hockings et al. 2015. Where sites were not included in the rankings and I had enough data available I created a score.

³ S=Status (protected, unprotected); L=Logging history; H=Hunting pressure; A=Agricultural practises; O=Other information relating to human activities in and/or around the site.

⁴ Site where ranking data were not available in Hockings et al. 2015.

⁵ Kibale was ranked in Hockings et al. 2015 as one site, but three chimpanzee studies exist there, where chimpanzees are exposed to varying levels and types of anthropogenic disturbances. I have re-ranked these sites individually based on data available.

nd= no data available

Appendix 2: Waibira chimpanzee list. Asterisks denote dependent offspring, which were not recorded in scan samples.

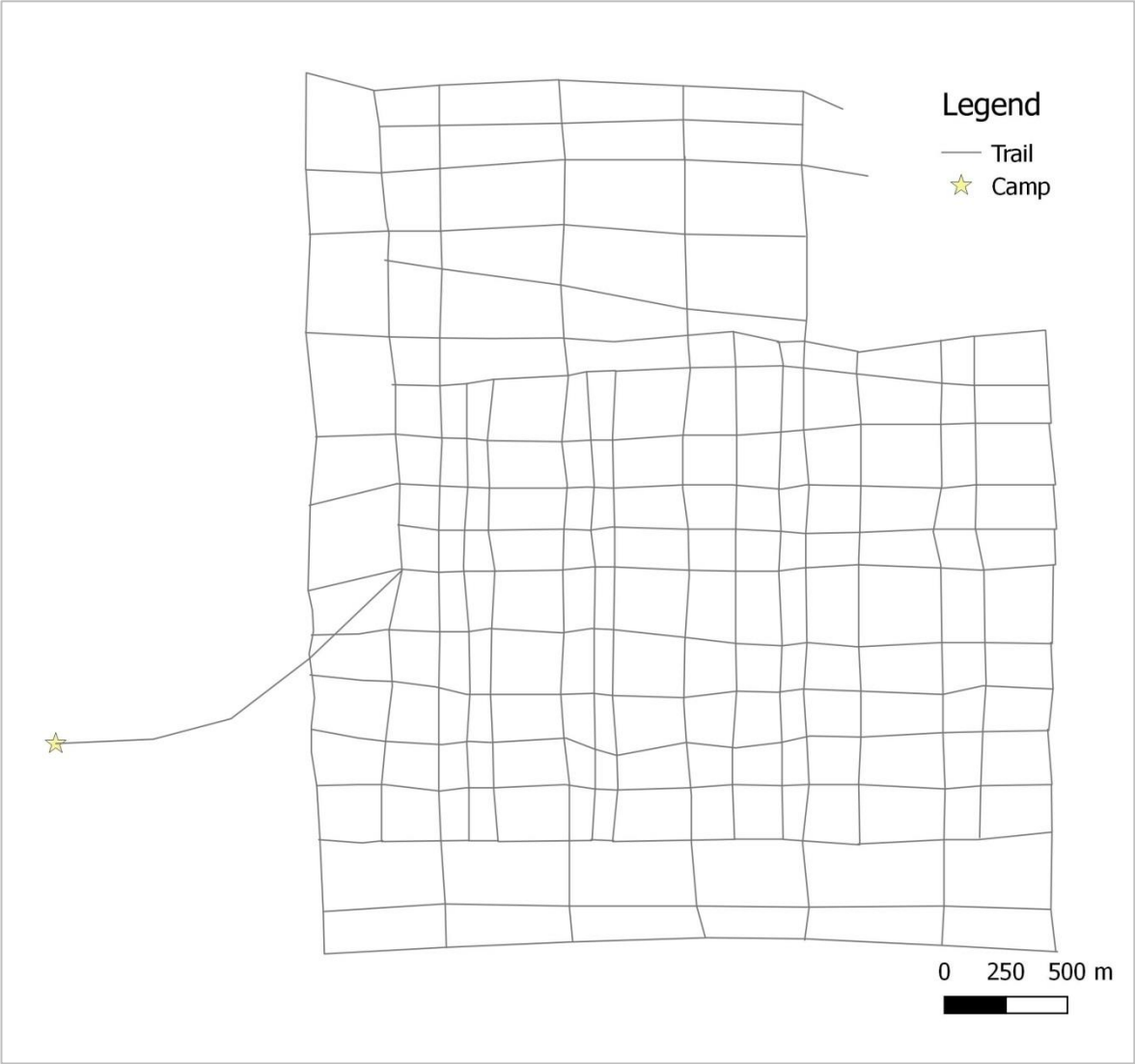
Code	Name	Sex	Age class	Year of birth	Notes
Males					
ABO	Abooki	M	Adult	1997 ± 2 yrs	
AKL	Akilli	M	Adult	1986 ± 3 yrs	
ALF	Alf	M	Subadult	1998 ± 1 yr	
ATA	Atayo	M	Adult	1996 ± 1 yr	Snare injury, R hand
BEN	Ben	M	Adult	1993 ± 2 yrs	Snare injury? L index finger
CHN	Chandia	M	Adult	1991 ± 3 yrs	Snare injury, L foot 3 toes
DOU	Douglas	M	Adult	1976 ± 5 yrs	Snare injury? L toes deformed
FID	Fiddich	M	Juvenile	2003 ± 1 yr	Travels independently.
GER	Gerald	M	Adult	1993 ± 2 yrs	Snare injury, L foot toes missing
ILA	Ila	M	Subadult	1999 ± 1 yr	
KAS	Kasongoire	M	Adult	1995 ± 2 yrs	
KEV	Kevilee	M	Adult	1981 ± 3 yrs	
LAF	Lafoig	M	Subadult	2003 ± 1 yr	Snare injury, R hand
MAC	Macallan	M	Subadult	1998 ± 1 yr	Snare injury, L hand
MAP	Mapasa	M	Adult	1983 ± 4 yrs	Snare injury, R hand
MAS	Masariki	M	Juvenile	2002 ± 1 yr	
MOR	Morangie	M	Adult	1984 ± 3 yrs	
MUG	Mugisha	M	Subadult	2003 ± 1 yr	
SAM	Sam	M	Adult	1999 ± 1 yr	
TAL	Talisker	M	Adult	1981 ± 5 yrs	
TRS	Tristan	M	Adult	1986 ± 5 yrs	Snare injury? L hand
URS	Ursus	M	Adult	1987 ± 5 yrs	
Females					
AKK	Akiki	F	Adult	1988 ± 3 yrs	
ARD	Ardbeg	M	Subadult	2006 ± 1 yr	Began collecting data Feb 2016
AIM	Aimee	F	Infant*	2015	
ARU	Arua	F	Adult	1981 ± 5 yrs	
AND	Andrua	M	Juvenile*	2008 ± 1 yr	Snare injury, missing L hand
ASM	Asiimwe	F	Infant*	2013	
BAH	Bahati	F	Adult	1994	Known from Sonso
BAL	Balvenie	M	Infant*	2012	Died October 2014
BYZ	Byazi	F	Adult	1987 ± 3 yrs	
BAR	Baraka	M	Infant*	2012	
CHP	Chapati	F	Adult	1990 ± 5 yrs	Snare injury, R hand maimed
CAE	Caelidh	F	Juvenile*	2008 ± 1 yr	
CIS	Ciska	F	Infant*	2012	
DAD	Dada	F	Adult	1987 ± 5 yrs	
DUN	Dun-Edin	M	Juvenile*	2005 ± 1 yr	
D	Unnamed	U	Unknown*	2013	
DAI	Daima	F	Adult	1987 ± 5 yrs	
DAU	Daudi	M	Subadult	2004 ± 1 yr	Snare injury, L hand
DAR	Darwin	M	Juvenile*	2010 ± 1 yr	
GAY	Gaya	F	Adult	1988 ± 5 yrs	
GPH	Gophin	M	Juvenile*	2008 ± 1 yr	

HOB	Hobaiter	F	Adult	1980 ± 5 yrs	
HAR	Harris	M	Juvenile*	2009 ± 1 yr	
IMP	Impia	F	Juvenile*	2006 ± 1 yr	
JIN	Jinja	F	Adult	1988 ± 3 yrs	Snare injury, missing R hand
KET	Ketie	F	Adult	1998	Known from Sonso
KID	Kidepo	F	Adult	1978 ± 5 yrs	
KAR	Karamoja	F	Juvenile*	2008 ± 1 yr	
KIP	Kipepeo	F	Adult	1997 ± 1 yr	
KIL	Kilimanjaro	M	Infant*	2014	
LIR	Liran	F	Adult	1981 ± 5 yrs	
LAN	Lahni	M	Subadult	2002 ± 1 yr	Snare injury, L hand, 4 fingers
LKU	Lokuyu	M	Juvenile*	2010	
LOT	Lotty	F	Adult	1984 ± 5 yrs	
LIZ	Liz	F	Infant*	2012	
MSD	Masindi	F	Adult	1985 ± 3 yrs	Snare injury, R hand & L foot
MER	Merkley	M	Juvenile*	2008 ± 1 yr	
MIK	Micky	M	Infant*	2014	
MAT	Mathaai	F	Adult	1990 ± 2 yrs	Snare injury, R & L hands
M	Unnamed	U	Infant*	2012	
MON	Monika	F	Adult	2003	Known from Sonso
NEV	Ndito-Eve	F	Adult	1984 ± 3 yrs	
NAT	Natan	M	Juvenile*	2006 ± 1 yr	
NOA	Noah	M	Infant*	2010	
NOR	Nora	F	Adult	1996	Known from Sonso; snare injury R hand
NAL	Nalala	M	Infant*	2013	
ONY	Onyofi	F	Adult	1998 ± 2 yrs	Snare injury, R hand
PEN	Penelope	F	Adult	1987 ± 3 yrs	
PHI	Philipo	M	Juvenile*	2008 ± 1 yr	Snare injury, missing L foot
PAV	Pavela	F	Infant*	2013	
RAC	Rachna	F	Adult	2000 ± 2 yrs	
SAN	Santa	F	Adult	2000 ± 1 yr	Snare injury, R leg
S	Unnamed	U	Infant*	2015	
SHY	Shay	F	Adult	1993 ± 3 yrs	Possible snare injury, L hand
SUL	Sula	F	Juvenile*	2010	
TAT	Tatu	F	Adult	2000 ± 1 yr	Snare injury, L leg missing
TIB	Tibu	F	Adult	2000 ± 1 yr	
VIR	Virunga	F	Adult	1984 ± 3 yrs	Snare injury, R hand

Appendix 3: Kasongoire chimpanzee list. Asterisks denote dependent offspring.

Code	Name	Sex	Age class	Year of birth	Notes
Males					
BES	Besige	M	Adult	1982 ± 5 yrs	
EDD	Eddie	M	Adult	1994 ± 3 yrs	Missing since Oct 2015
GAR	Garibaldi	M	Adult	1988 ± 3 yrs	
GRZ	Graziano	M	Adult	1980 ± 5 yrs	Missing most teeth
JOV	Jovan	M	Subadult	2001 ± 2 yrs	
LBE	Clooney	M	Adult	1987 ± 4 yrs	
OPE	Openmouth	M	Adult	1986 ± 5 yrs	
PAU	Paul	M	Adult	1992 ± 3 yrs	Probable alpha. Snare injury, L hand
THO	Thor	M	Adult	1987 ± 5 yrs	Snare injury, L hand
SCA	Scar	M	Adult	1985 ± 4 yrs	
SPO	Spotty	M	Adult	1984 ± 4 yrs	
UM1	Unnamed	M	Adult	2000 ± 2 yrs	Seen Aug 2015 only. Snare injury, L hand
Females					
AID	Aida	F	Adult	1984 ± 5 yrs	
BLY	Blyth	M	Subadult	2007 ± 2 yrs	Snare injury, R hand
AND	Andromeda	F	Juvenile*	2010 ± 1 yr	
APH	Aphrodyte	F	Infant*	2015	
BRL	Beryl	F	Adult	1995 ± 3 yrs	
BUB	Bubbles	F	Infant*	2014/5	
COC	Coco	F	Adult	1988 ± 4 yrs	
CHA	Chalou	F	Juvenile*	2011 ± 1 yr	
CIS	Ciska	F	Infant*	2015/6	
GRE	Gremlin	F	Adult	1988 ± 5 yrs	Snare injury, R hand [Mantrap Aug 2016, lost L foot]
G	Unnamed	U	Infant*	2015	Died June 2016
HEL	Hellen	F	Adult	1988 ± 8 yrs	
H	Unnamed	U	Infant*	2015	
MAR	Margaret	F	Adult	1993 ± 5 yrs	
M	Unnamed	U	Infant*	2016	
MEL	Melan	F	Adult	1999 ± 2 yrs	
NRE	Noreen	F	Adult	2000 ± 2 yrs	
SAR	Sarah	F	Adult	2000 ± 1 yr	
SYL	Sylvia	F	Adult	1987 ± 5 yrs	
KGE	Gerald	M	Subadult	2005 ± 2 yrs	[Mantrap Dec 2016, lost L hand]
STO	Stoney	F	Juvenile*	2009 ± 2 yrs	
SAB	Saba Saba	F	Infant*	2013 ± 0.5 yrs	
THU	Thursa	F	Adult	1996 ± 3 yrs	
TYR	Tyrrion	M	Infant*	2013/4	Died Dec 2014-Jun 2015
VER	Verity	F	Adult	1990 ± 5 yrs	
VTK	Voytek	M	Juvenile	2009 ± 2 yrs	Began collecting data Feb 2016
V	Unnamed	U	Infant*	2016	
WEY	White-eye	F	Adult	1986 ± 5 yrs	
UF1	Unnamed	F	Subadult	2002 ± 1 yr	Missing since 2015, dispersed? Snare injury, R hand
UF2	Unnamed	F	Subadult	2002 ± 1 yr	Missing since 2015, dispersed? Snare injury, L hand

Appendix 4: Map of BCFS’ trail system in the Waibira chimpanzee home range



Appendix 5: Complete species list found in plots at Waibira, showing for each species the frequency (the percentage of plots in which a species was recorded), density (trees per hectare), average basal area (BA) and species importance values (SIV).

Species	Family	Frequency (% of plots)	Density (trees/ ha ⁻¹)	BA (m ² ha ⁻¹)	SIV
<i>Alangium chinense</i>	Alangianceae	3.85	0.96	0.08	0.85
	Leguminosae -	8.97	2.24	0.49	2.83
<i>Albizia glaberrima</i>	Mimosoideae				
<i>Albizia zygia</i>	L. - Mimosoideae	5.13	1.28	0.31	1.71
<i>Alchornea laxiflora</i>	Euphorbiaceae	41.03	20.19	0.30	9.55
<i>Alstonia boonei</i>	Apocynaceae	8.97	2.56	1.47	5.67
<i>Aningeria altissima</i>	Sapotaceae	7.69	2.88	0.05	1.60
<i>Antiaris toxicaria</i>	Moraceae	12.82	3.85	0.15	2.63
<i>Antidesma membranaceum</i>	Euphorbiaceae	3.85	0.96	0.05	0.76
<i>Argomuellera macrophylla</i>	Euphorbiaceae	1.28	0.32	0.00	0.21
<i>Balsamocitrus dawei</i>	Rutaceae	1.28	0.32	0.03	0.30
<i>Baphia wollastonii</i>	L. - Papilionoideae	1.28	0.32	0.00	0.22
<i>Belonophora glomerata</i>	Rubiaceae	3.85	0.96	0.02	0.67
<i>Bequaertiodendron ob lanceolatum</i>	Sapotaceae	2.56	1.28	0.05	0.69
<i>Blighia unijugata</i>	Sapindaceae	2.56	0.64	0.02	0.46
<i>Bosqueia phoberos</i>	Moraceae	6.41	1.60	0.08	1.27
<i>Bridelia brideliifolia</i>	Euphorbiaceae	1.28	0.64	0.11	0.59
<i>Caloncoba schweinfurthii</i>	Flacourtaceae	11.54	3.53	0.14	2.39
<i>Canarium schweinfurthii</i>	Burseraceae	1.28	0.32	0.01	0.22
<i>Celtis durandii</i>	Ulmaceae	38.46	15.38	2.33	13.98
<i>Celtis mildbraedii</i>	Ulmaceae	82.05	62.50	3.90	33.06
<i>Celtis wightii</i>	Ulmaceae	12.82	4.17	0.07	2.46
<i>Celtis zenkeri</i>	Ulmaceae	39.74	19.23	0.89	10.86
<i>Chrysophyllum albidum</i>	Sapotaceae	20.51	6.73	0.66	5.51
<i>Chrysophyllum muerense</i>	Sapotaceae	5.13	1.28	0.13	1.20
<i>Chrysophyllum perpulchrum</i>	Sapotaceae	5.13	1.28	0.02	0.89
<i>Cordia millenii</i>	Boraginaceae	5.13	1.60	0.55	2.45
<i>Croton sylvaticus</i>	Euphorbiaceae	19.23	8.01	0.55	5.33
	L. -	61.54	30.45	9.63	40.27
<i>Cynometra alexandri</i>	Caesalpinioideae				
<i>Desplatsia dewevrei</i>	Tiliaceae	6.41	1.92	0.08	1.32
<i>Diospyros abyssinica</i>	Ebenaceae	1.28	0.32	0.02	0.27
<i>Dombeya mukole</i>	Sterculiaceae	1.28	0.64	0.11	0.58
<i>Drypetes ugandensis</i>	Euphorbiaceae	5.13	2.56	0.03	1.18
<i>Ehretia cymosa</i>	Boraginaceae	6.41	1.60	0.07	1.24
<i>Entandrophragama angolense</i>	Meliaceae	1.28	0.32	0.01	0.22
<i>Entandrophragama cylindricum</i>	Meliaceae	1.28	0.32	0.13	0.58
<i>Entandrophragama utile</i>	Meliaceae	2.56	0.64	0.02	0.46
	L. -	3.85	0.96	0.34	1.58
<i>Erythrophleum suaveolens</i>	Caesalpinioideae				
<i>Fagaropsis angolensis</i>	Rutaceae	7.69	1.92	0.20	1.80
<i>Ficus exasperata</i>	Moraceae	1.28	0.32	0.01	0.23
<i>Ficus mucoso</i>	Moraceae	6.41	1.60	0.60	2.73
<i>Ficus sur</i>	Moraceae	16.67	6.41	0.89	5.68
<i>Ficus variifolia</i>	Moraceae	5.13	1.28	0.72	2.86
<i>Funtumia elastica</i>	Apocynaceae	67.95	48.40	1.54	21.89

<i>Glyphaea brevis</i>	Tiliaceae	3.85	1.92	0.03	0.89
<i>Greenwayodendron suaveolens</i>	Annonaceae	7.69	1.92	0.03	1.34
<i>Guarea cedrata</i>	Meliaceae	3.85	0.96	0.07	0.81
<i>Holoptelea grandis</i>	Ulmaceae	3.85	0.96	0.14	1.03
<i>Khaya anthotheca</i>	Meliaceae	17.95	5.13	1.37	6.90
<i>Kigelia africana</i>	Bignoniaceae	1.28	0.32	0.01	0.22
<i>Lannea welwitschii</i>	Anacardiaceae	1.28	0.32	0.01	0.25
<i>Lasiodiscus mildbraedii</i>	Rhamnaceae	76.92	92.63	1.55	32.21
<i>Leptaulus daphnoides</i>	Icacinaceae	1.28	0.32	0.01	0.24
<i>Leptonychia mildbraedii</i>	Sterculiaceae	1.28	0.32	0.01	0.23
<i>Lychnodiscus cerospermus</i>	Sapindaceae	6.41	1.60	0.04	1.14
<i>Maerua duchesnei</i>	Capparaceae	10.26	3.21	0.04	1.90
<i>Maesopsis eminii</i>	Rhamnaceae	6.41	2.24	0.58	2.81
<i>Majidea fosteri</i>	Sapindaceae	1.28	0.32	0.00	0.21
<i>Mammea africana</i>	Guttiferae	2.56	0.64	0.01	0.45
<i>Manilkara obovata</i>	Sapotaceae	3.85	1.28	0.02	0.73
<i>Margaritaria discoidea</i>	Euphorbiaceae	20.51	7.37	0.90	6.33
<i>Markhamia platycalyx</i>	Bignoniaceae	2.56	0.64	0.04	0.51
<i>Mildbraediodendron excelsum</i>	L. - Caesalpinoideae	2.56	0.96	0.13	0.84
<i>Milicia excelsa</i>	Moraceae	1.28	0.32	0.04	0.32
<i>Mitragyna stipulosa</i>	Rubiaceae	1.28	0.32	0.02	0.25
<i>Monodora angolensis</i>	Annonaceae	2.56	0.64	0.01	0.43
<i>Monodora myristica</i>	Annonaceae	3.85	1.60	0.10	1.03
<i>Morus mesozygia</i>	Moraceae	3.85	0.96	0.03	0.69
<i>Myrianthus holstii</i>	Moraceae	11.54	5.13	0.17	2.80
<i>Newtonia buchananii</i>	L. - Mimosoideae	1.28	0.32	0.00	0.22
<i>Pseudospondias microcarpa</i>	Anacardiaceae	1.28	0.32	0.37	1.25
<i>Psidium guajava</i>	Myrtaceae	2.56	0.96	0.03	0.58
<i>Pycnanthus angolensis</i>	Myristicaceae	1.28	0.32	0.01	0.23
<i>Ricinodendron heudelotii</i>	Euphorbiaceae	6.41	1.92	0.83	3.44
<i>Rinorea ardisiaeflora</i>	Violaceae	43.59	38.78	0.52	14.35
<i>Ritchiea albersii</i>	Capparaceae	1.28	0.32	0.04	0.33
<i>Rothmania urcelliformis</i>	Rubiaceae	2.56	0.64	0.01	0.43
<i>Sapium ellipticum</i>	Euphorbiaceae	1.28	0.32	0.01	0.24
<i>Sterculia dawei</i>	Sterculiaceae	1.28	0.32	0.03	0.29
<i>Strombosia scheffleri</i>	Olacaceae	2.56	1.28	0.15	0.97
<i>Strychnos mitis</i>	Loganiaceae	2.56	0.96	0.33	1.40
<i>Tabernaemontana holstii</i>	Apocynaceae	10.26	2.56	0.04	1.75
<i>Tapura fischeri</i>	Dichapetalaceae	24.36	7.05	0.16	4.58
<i>Teclea nobilis</i>	Rutaceae	14.10	3.85	0.08	2.55
<i>Tetrorchidium didymostemon</i>	Euphorbiaceae	2.56	1.60	0.10	0.90
<i>Trema orientalis</i>	Ulmaceae	3.85	1.28	0.06	0.84
<i>Trichilia dregeana</i>	Meliaceae	1.28	0.32	0.00	0.21
<i>Trichilia prieuriana</i>	Meliaceae	20.51	5.77	0.14	3.83
<i>Trichilia rubescens</i>	Meliaceae	14.10	6.09	0.14	3.20
Unknown sp. 1	Unknown	1.28	0.32	0.07	0.40
Unknown sp. 2	Unknown	2.56	0.64	0.04	0.53
<i>Uvariopsis congensis</i>	Annonaceae	6.41	2.56	0.06	1.40
<i>Zanthoxylum leprieurii</i>	Rutaceae	1.28	0.32	0.01	0.24

Appendix 6: Complete species list found in plots at Kasongoire, showing for each species the frequency (the percentage of plots in which a species was recorded), density (trees per hectare), average basal area (BA) and species importance values (SIV).

Species	Family	Frequency (% of plots)	Density (trees/ ha ⁻¹)	BA (m ² ha ⁻¹)	SIV
<i>Acacia</i> spp.	L. - Mimosoideae	1.10	0.55	0.02	0.52
<i>Albizia grandiflora</i>	L. - Mimosoideae	1.10	0.27	0.02	0.42
<i>Albizia coriaria</i>	L. - Mimosoideae	2.20	0.55	0.05	0.95
<i>Albizia glaberrima</i>	L. - Mimosoideae	1.10	0.27	0.11	0.97
<i>Albizia grandibracteata</i>	L. - Mimosoideae	3.30	0.82	0.09	1.52
<i>Albizia zygia</i>	L. - Mimosoideae	2.20	0.55	0.07	1.09
<i>Alchornea cordifolia</i>	Euphorbiaceae	1.10	0.27	0.01	0.36
<i>Alstonia boonei</i>	Apocynaceae	1.10	0.27	0.02	0.43
<i>Aningeria altissima</i>	Sapotaceae	4.40	1.37	0.09	1.92
<i>Anonna senegalensis</i>	Annonaceae	1.10	0.27	0.00	0.35
<i>Antiaris toxicaria</i>	Moraceae	3.30	1.37	0.95	6.97
<i>Antidesma laciniatum</i>	Euphorbiaceae	3.30	1.10	0.03	1.19
<i>Antidesma membranaceum</i>	Euphorbiaceae	5.49	1.92	0.06	2.15
<i>Bersama abyssinica</i>	Melanthaceae	1.10	0.55	0.01	0.48
<i>Blighia unijugata</i>	Sapindaceae	14.29	5.49	0.32	6.67
<i>Bosqueia phoberos</i>	Moraceae	15.38	6.04	0.14	5.98
<i>Bridelia micrantha</i>	Phyllanthaceae	16.48	9.07	0.30	8.17
<i>Broussonetia papyrifera</i>	Moraceae	1.10	0.27	0.00	0.33
<i>Caloncoba schweinfurthii</i>	Flacourtaceae	3.30	0.82	0.03	1.16
<i>Canarium schweinfurthii</i>	Burseraceae	1.10	0.27	0.02	0.44
<i>Cassia spectabilis</i>	L. - Caesalpinioideae	1.10	0.27	0.00	0.34
<i>Chaetechme aristata</i>	Ulmaceae	1.10	1.10	0.03	0.74
<i>Coffea canephora</i>	Rubiaceae	1.10	0.27	0.01	0.36
<i>Cola gigantea</i>	Malvaceae	6.59	1.65	0.12	2.63
<i>Combretum molle</i>	Combretaceae	1.10	0.27	0.00	0.33
<i>Cordia africana</i>	Boraginaceae	1.10	0.27	0.00	0.33
<i>Croton macrostachyus</i>	Euphorbiaceae	1.10	0.27	0.10	0.94
<i>Croton megalocarpus</i>	Euphorbiaceae	1.10	0.27	0.04	0.58
<i>Croton sylvaticus</i>	Euphorbiaceae	14.29	3.85	0.21	5.49
<i>Dictyandra arborescens</i>	Rubiaceae	1.10	0.27	0.00	0.33
<i>Dombeya mukole</i>	Sterculiaceae	2.20	1.10	0.02	0.91
<i>Dovyalis macrocalyx</i>	Flacourtaceae	1.10	0.27	0.00	0.33
<i>Entandrophragma cylindricum</i>	Meliaceae	1.10	0.27	0.01	0.36
<i>Erythrina excelsa</i>	Fabaceae	3.30	0.82	0.01	1.02
<i>Ficus bubu</i>	Moraceae	4.40	1.10	0.13	2.06
<i>Ficus exasperata</i>	Moraceae	1.10	0.27	0.04	0.54
<i>Ficus natalensis</i>	Moraceae	2.20	0.82	0.06	1.11
<i>Ficus ovata</i>	Moraceae	1.10	0.27	0.06	0.69
<i>Ficus polita</i>	Moraceae	1.10	0.27	0.12	1.03
<i>Ficus saussureana</i>	Moraceae	1.10	0.27	0.04	0.55
<i>Ficus stipulosa</i>	Moraceae	1.10	0.55	0.01	0.44
<i>Ficus sur</i>	Moraceae	10.99	2.75	0.06	3.56

<i>Ficus vallis-choudae</i>	Moraceae	9.89	5.77	0.60	7.61
<i>Funtumia africana</i>	Apocynaceae	23.08	9.62	0.36	10.06
<i>Funtumia elastica</i>	Apocynaceae	1.10	0.27	0.02	0.44
<i>Harungana madagascariensis</i>	Guttiferae	2.20	1.92	0.06	1.46
<i>Khaya anthotheca</i>	Meliaceae	1.10	0.55	0.02	0.56
<i>Khaya grandifoliola</i>	Meliaceae	1.10	0.27	0.01	0.35
<i>Leptaulus daphnoides</i>	Icacinaceae	3.30	0.82	0.01	1.01
<i>Lovoa swynnertonii</i>	Meliaceae	2.20	0.55	0.03	0.82
<i>Lovoa trichilioides</i>	Meliaceae	1.10	0.27	0.03	0.51
<i>Macaranga monandra</i>	Annonaceae	1.10	0.27	0.00	0.33
<i>Macaranga schweinfurthii</i>	Euphorbiaceae	31.87	32.69	1.28	24.92
<i>Maesopsis eminii</i>	Moraceae	2.20	0.55	0.02	0.75
<i>Manilkara butugi</i>	Sapotaceae	1.10	0.27	0.10	0.91
<i>Margaritaria discoidea</i>	Euphorbiaceae	2.20	0.82	0.07	1.12
<i>Mildbraediodendron excelsum</i>	L. - Caesalpinioideae	1.10	0.27	0.09	0.88
<i>Mitragyna stipulosa</i>	Moraceae	2.20	1.37	0.04	1.15
<i>Monodora angolensis</i>	Annonaceae	2.20	0.55	0.02	0.76
<i>Morus mesozygia</i>	Moraceae	6.59	2.75	0.39	4.62
<i>Myrianthus holstii</i>	Cecropiaceae	5.49	6.04	0.12	3.83
<i>Neoboutonia macrocalyx</i>	Euphorbiaceae	16.48	19.78	0.43	12.40
<i>Olea welwitschii</i>	Oleaceae	4.40	1.10	0.03	1.47
<i>Oncoba spinosa</i>	Flacourtaceae	4.40	1.37	0.02	1.45
<i>Oxyanthus speciosus</i>	Rubiaceae	3.30	1.92	0.03	1.46
<i>Pachystela brevipes</i>	Sapotaceae	1.10	0.27	0.02	0.43
<i>Parkia follicoides</i>	Fabaceae	5.49	1.65	0.32	3.64
<i>Phoenix reclinata</i>	Arecaceae	53.85	107.42	3.12	64.70
<i>Phyllanthus discoilis</i>	Euphorbiaceae	3.30	0.82	0.08	1.45
<i>Piptadeniastrum africanum</i>	L. - Mimosoideae	3.30	1.10	0.12	1.80
<i>Pseudospondias microcarpa</i>	Anacardiaceae	50.55	26.92	2.63	35.28
<i>Pycnanthus angolensis</i>	Myristicaceae	14.29	3.85	0.32	6.16
<i>Rothmania urcelliformis</i>	Rubiaceae	2.20	0.55	0.00	0.66
<i>Sapium ellipticum</i>	Euphorbiaceae	17.58	7.42	0.97	11.99
<i>Spathodea campanulata</i>	Bignoniaceae	3.30	0.82	0.02	1.05
<i>Sterculia dawei</i>	Sterculiaceae	1.10	0.27	0.03	0.50
<i>Strombosia scheffleri</i>	Olacaceae	1.10	0.55	0.10	1.04
<i>Syzygium guineense</i>	Myrtaceae	17.58	9.07	0.88	11.98
<i>Tabernaemontana holstii</i>	Apocynaceae	9.89	4.67	0.07	4.01
<i>Teclea nobilis</i>	Rutaceae	3.30	1.37	0.07	1.54
<i>Terminalia glauscens</i>	Combretaceae	1.10	0.27	0.01	0.36
<i>Trema orientalis</i>	Ulmaceae	5.49	1.37	0.03	1.77
<i>Trichilia dregeana</i>	Meliaceae	3.30	1.10	0.11	1.72
Unknown sp. 2	Unknown	1.10	0.27	0.00	0.33
Unknown sp. 3	Unknown	1.10	0.27	0.01	0.40
<i>Vernonia amangdelena</i>	Asteraceae	1.10	0.27	0.00	0.34
<i>Vitex doniana</i>	Lamiaceae	1.10	0.27	0.01	0.38
<i>Voacanga thouarsii</i>	Apocynaceae	5.49	3.02	0.12	2.86
<i>Zanha golungensis</i>	Sapindaceae	1.10	0.27	0.02	0.45

Appendix 7: Shared species and densities at each site.

Species	Waibira	Kasongoire
<i>Albizia glaberrima</i>	2.24	0.27
<i>Albizia zygia</i>	1.28	0.55
<i>Alstonia boonei</i>	2.56	0.27
<i>Aningeria altissima</i>	2.88	1.37
<i>Antiaris toxicaria</i>	3.85	1.37
<i>Antidesma membranaceum</i>	1.92	0.96
<i>Blighia unijugata</i>	0.64	5.49
<i>Trilepisium madagascariensis</i>	1.60	6.04
<i>Caloncoba schweinfurthii</i>	3.53	0.82
<i>Canarium schweinfurthii</i>	0.32	0.27
<i>Croton sylvaticus</i>	8.01	3.85
<i>Dombeya mukole</i>	0.64	1.10
<i>Entandrophragma cylindricum</i>	0.32	0.27
<i>Ficus exasperata</i>	0.32	0.27
<i>Ficus sur</i>	6.41	2.75
<i>Funtumia elastica</i>	48.40	0.27
<i>Khaya anthotheca</i>	5.13	0.55
<i>Leptaulus daphnoides</i>	0.32	0.82
<i>Maesopsis eminii</i>	2.24	0.55
<i>Margaritaria discoidea</i>	7.37	0.82
<i>Mildbraediodendron excelsum</i>	0.96	0.27
<i>Mitragyna stipulosa</i>	0.32	1.37
<i>Monodora angolensis</i>	0.64	0.55
<i>Morus mesozygia</i>	0.96	2.75
<i>Myrianthus holstii</i>	5.13	6.04
<i>Pycnanthus angolensis</i>	0.32	3.85
<i>Rothmania urcelliformis</i>	0.64	0.55
<i>Sapium ellipticum</i>	0.32	7.42
<i>Sterculia dawei</i>	0.32	0.27
<i>Strombosia scheffleri</i>	1.28	0.55
<i>Tabernaemontana holstii</i>	2.56	4.67
<i>Teclea nobilis</i>	3.85	1.37
<i>Trema orientalis</i>	1.28	1.37
<i>Trichilia dregeana</i>	0.32	1.10

Appendix 8: Contributions to chimpanzee diets at Waibira and Kasongoire per species consumed, shown by proportion of feeding observations per month. “x” denotes no data for proportional contribution to diet as records were made through indirect observations.

Species	Jul15	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul16	Months fed on
Waibira														
<i>Antiaris toxicaria</i>	-	-	-	-	-	-	/	7.59	17.86	-	-	/	/	2
<i>Balsamocitrus dawei</i>	-	-	4.30	-	6.45	-	/	-	-	-	-	/	/	2
<i>Celtis mildbraedii</i>	-	-	15.05	12.20	6.45	66.15	/	-	-	-	73.44	/	/	5
<i>Celtis wightii</i>	-	17.39	-	-	-	-	/	-	-	-	-	/	/	1
<i>Celtis zenkeri</i>	-	-	-	-	-	-	/	-	-	2.90	-	/	/	1
<i>Cordia millenii</i>	75.00	-	-	-	-	-	/	-	-	-	-	/	/	1
<i>Cynometra alexandri</i>	-	-	-	-	18.43	33.85	/	28.97	2.38	-	-	/	/	4
<i>Desplatsia dewevrei</i>	-	-	10.75	-	-	-	/	-	-	-	-	/	/	1
<i>Dialium excelsium</i>	-	-	-	-	-	-	/	-	33.33	19.71	-	/	/	2
<i>Erythrophleum suaveolens</i>	-	-	-	2.44	-	-	/	-	-	-	-	/	/	1
<i>Ficus exasperata</i>	-	-	-	7.32	-	-	/	4.83	20.24	20.87	-	/	/	4
<i>Ficus mucoso</i>	-	-	-	-	64.06	-	/	-	-	34.78	-	/	/	2
<i>Ficus nantalensis</i>	-	-	-	-	-	-	/	-	-	9.57	-	/	/	1
<i>Ficus saussureana</i>	-	-	-	-	-	-	/	6.21	1.79	-	-	/	/	2
<i>Ficus sur</i>	-	-	-	-	-	-	/	24.14	13.69	0.87	-	/	/	3
<i>Ficus variifolia</i>	-	-	-	-	-	-	/	9.66	3.57	1.74	-	/	/	3
<i>Honey</i>	-	-	-	13.41	-	-	/	-	-	-	-	/	/	1
<i>Mammea africana (traces)</i>	-	-	-	-	-	-	/	x	-	-	-	/	/	1
<i>Mildbraediodendron excelsum</i>	-	-	-	-	-	-	/	-	-	3.19	20.31	/	/	2
<i>Morus mesozygia</i>	-	-	-	-	-	-	/	-	4.76	-	-	/	/	1
<i>Myrianthus holstii</i>	-	-	-	-	-	-	/	-	-	1.74	-	/	/	1
<i>Pseudospondias microcarpa</i>	-	-	-	-	-	-	/	-	-	x	-	/	/	1
<i>Sterculia dawei</i>	16.67	-	-	-	-	-	/	-	-	-	-	/	/	1

<i>Strychnos mitis</i>	-	-	-	-	-	-	/	17.24	-	-	-	/	/	1
<i>Terrestrial piths</i>	-	-	2.15	-	-	-	/	-	-	-	-	/	/	1
<i>Tree cabbage</i>	-	-	-	-	-	-	/	-	-	3.19	-	/	/	1
<i>Unknown sp.1</i>	-	-	-	15.85	-	-	/	-	-	-	-	/	/	1
<i>Unknown tree spp.</i>	4.17	-	-	-	-	-	/	-	-	-	3.13	/	/	2
<i>Unseen climber sp.1</i>	-	56.52	56.99	-	-	-	/	-	-	-	-	/	/	2
<i>Unknown climber spp.</i>	4.17	26.09	10.75	48.78	4.61	-	/	1.38	2.38	1.45	-	/	/	8
<i>Unseen</i>	-	-	-	-	-	-	/	-	-	-	3.13	/	/	1
Kasongoire														
<i>Acacia spp.</i>	-	-	-	-	-	22.86	-	0.60	-	-	-	-	-	2
<i>Acanthas pubescens</i>	-	-	-	-	-	-	-	0.60	-	-	2.88	-	1.35	3
<i>Alaphia lowdoides</i>	45.83	-	-	-	-	-	-	-	0.52	-	-	-	4.05	3
<i>Albizia sp.</i>	-	-	-	-	-	-	-	0.60	-	-	-	-	-	1
<i>Aningeria altissima</i>	-	-	-	-	-	-	-	-	-	7.22	52.88	1.91	-	3
<i>Ants</i>	-	-	-	-	-	-	-	-	-	-	-	-	2.70	1
<i>Antiaris toxicaria</i>	-	-	-	-	-	5.71	33.33	21.08	3.65	-	-	1.27	1.35	6
<i>Blighia unijugata</i>	-	-	-	-	-	-	-	-	2.08	-	-	-	-	1
<i>C. g. occidentalis</i>	-	-	-	-	-	-	-	-	-	-	-	10.19	1.35	2
<i>Cola gigantea</i>	-	-	-	-	-	-	-	-	-	-	x	-	-	1
<i>Cyperus papyrus</i>	-	-	-	-	-	-	-	-	-	-	3.85	1.27	1.35	3
<i>Ficus bubu</i>	-	-	-	-	-	-	-	-	1.04	1.03	0.96	-	-	3
<i>Ficus exasperata</i>	-	-	-	-	-	-	6.31	2.41	-	-	-	-	-	2
<i>Ficus nantalensis</i>	-	-	-	-	-	-	2.70	-	7.81	-	-	-	-	2
<i>Ficus ovata</i>	-	-	-	-	-	-	-	-	0.52	-	-	2.55	-	2
<i>Ficus sansibarica</i>	-	-	-	-	-	-	-	-	-	-	-	4.46	-	1
<i>Ficus saussureana</i>	-	-	-	-	-	-	-	3.01	12.50	-	-	1.91	-	3
<i>Ficus sur</i>	-	-	-	-	-	8.57	1.80	1.20	1.56	2.06	0.96	3.18	-	7

<i>Ficus vallis-choudae</i>	16.67	3.45	50.00	18.75	14.29	2.86	7.21	10.84	1.04	5.15	-	1.91	20.27	12
<i>Honey</i>	-	-	-	-	-	-	-	0.60	-	-	-	0.64	-	2
<i>Lantana camara</i>	-	-	-	-	-	-	-	-	-	1.03	-	-	-	1
<i>Macaranga schweinfurthii</i>	-	10.34	-	-	-	-	-	-	-	-	-	-	-	1
<i>Maesopsis eminii</i>	-	-	-	-	-	-	-	-	-	x	-	-	-	1
<i>Morus mesozygia</i>	-	-	-	-	-	-	-	12.65	38.02	-	-	-	-	2
<i>Myrianthus holstii</i>	-	-	-	-	-	-	-	-	-	-	1.92	-	1.35	2
<i>Parkia filicoidea</i>	-	-	-	-	-	-	-	-	0.52	23.71	-	-	-	2
<i>Pennisetum purpureum</i>	-	-	-	-	-	-	-	x	-	-	-	x	-	2
<i>Phoenix reclinata</i>	-	-	15.00	62.50	71.43	5.71	3.60	0.60	-	-	-	3.82	2.70	8
<i>Pseudospondias microcarpa</i>	-	-	-	-	-	17.14	13.51	9.04	1.04	29.90	9.62	11.46	-	7
<i>Pycnanthus angolensis</i>	-	-	-	-	-	8.57	-	-	-	-	-	-	-	1
<i>Saccarum officinarum</i>	37.50	75.86	15.00	18.75	14.29	22.86	24.32	30.12	22.92	24.74	14.42	49.04	40.54	13
<i>Sterculia dawei</i>	-	-	-	-	-	-	-	-	0.52	-	-	-	-	1
<i>Syzygium guineense</i>	-	-	-	-	-	-	-	-	-	4.12	9.62	1.27	-	3
<i>Terrestrial piths</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0
<i>Unknown sp.2</i>	-	-	-	-	-	-	-	-	2.60	-	-	-	-	1
<i>Unknown sp.3</i>	-	-	-	-	-	-	-	0.60	-	-	-	-	4.05	2
<i>Unknown sp.4</i>	-	-	-	-	-	-	-	-	1.56	-	-	-	-	1
<i>Unknown sp.6</i>	-	-	-	-	-	-	-	-	0.52	-	-	-	-	1
<i>Unknown tree spp.</i>	-	-	-	-	-	-	5.41	5.42	-	1.03	-	-	-	3
<i>Unknown climber spp.</i>	-	-	-	-	-	-	0.90	-	1.04	-	2.88	5.10	18.92	5
<i>Unseen</i>	-	10.34	20.00	-	-	5.71	0.90	0.60	-	-	-	-	-	5
<i>Vernonia amangdelena</i>	-	-	-	-	x	x	-	-	-	x	-	-	-	3
<i>Zanha golungensis</i>	-	-	-	-	-	-	-	-	0.52	-	-	-	-	1