MAKERERE  UNIVERSITY

NUTRITIONAL ECOLOGY OF MANGABEYS (*Lophocebus ugandae*, GROVES) IN MABIRA AND LWAMUNDA FOREST RESERVES, UGANDA

Margaret Masette

B.Sc (Hons-Dar es- Salaam); MSc (Lincoln University - UK)

2003/HD13/2444U

A THESIS SUBMITTED TO THE DIRECTORATE OF RESEARCH AND GRADUATE TRAINING FOR THE AWARD OF THE DEGREE OF DOCTOR OF PHILOSOPHY OF MAKERERE UNIVERSITY

October 2016

DECLARATION

I, Masette Margaret, declare that this study is original and it has not been published or submitted for any other degree award to any other university.

Signed.....

Date.....10th October 2016

Masette Margaret

B.Sc (Hons - Dar es Salaam); MSc (Lincoln University - UK)

This thesis has been submitted for examination with our approval as the University appointed supervisors.

Signed.....

Date.....11 October 2016

Assoc. Prof. G. Isabirye-Basuta

Signed .....

Date.....11 October 2016

Prof. D. Baranga

Signed .....

Date.....

Prof. C. A. Chapman

DEDICATION

To all folks who have devoted their time and resources to study nutritional ecology of non-human primates

ACKNOWLEDGEMENTS

This thesis has evolved over several years and it would not have been possible without the help and moral support from some people. Prof Baranga proposed my candidature to NUFU that funded this work. Permission to conduct research in Mabira and Lwamunda forest reserves was granted by the National Council for Science and Technology. National Agricultural Research Organization (NARO) and particularly the late Dr Aluma, Director of Research (1998-2005), granted partial study leave for me to undertake prolonged periods of time in the forests. The proposal was vetted by a 12-man panel from the then Faculty of Science who made useful suggestions. Mrs Ruth Mubiru was indispensable in the Animal Nutrition Laboratory. My field assistant, Wilber - whose knowledge of Lwamunda forest reserve and keen interest in mangabeys was commendable. Godfrey Kubiriza, Moses Chemurot and Edgar Tinyiro were at hand with statistical packages and graphic options. I am highly indebted to my principal supervisor Assoc. Prof Gilbert Isabirye-Basuta for the initiation into primatology and particularly foraging behaviour. During the writing of this thesis, he invested a lot of his time reviewing manuscripts. Prof Colin Chapman and Dr. Jessica Rothman offered invaluable advice that contributed to the transformation of this work into publishable papers. Without the encouragement and moral support from Dr E. Sande and Dr J. Kwetegyeka and my nucleus family, this work would still be pending.

To all these people and organizations, I am very grateful for all your support. Thank you again for being there for me. Finally to God be the Glory for thus far has He enabled me.

ABSTRACT

The nutritional ecology of Grey-cheeked Mangabey (*Lophocebus ugandae* Groves) inhabiting Mabira and Lwamunda, two of Lake Victoria Basin (LVB) forest reserves is not well understood. Yet this knowledge would provide relevant information for formulation of an effective management strategy that would guarantee the health of the forests and synchronously conserve their forest fauna. The principal objective of this study therefore was to investigate the nutritional ecology of mangabeys inhabiting three contrasting habitats; fairly undisturbed Mabira (M1), regenerating Mabira (M2) and severely degraded Lwamunda (LD) with different management histories within the LVB. To achieve this objective, a three year study was undertaken to generate information on the diet, fruiting phenology and quality of fruits from ten priority trees species commonly utilized as food by 3 groups of habituated mangabeys. In each of the three habitats, phenological data was collected to provide information on fruit availability, quality and timelines for their consumption.

The phenology of 10 individual trees of 10 priority fruit trees species utilized by mangabeys in each study area was documented on a monthly basis to establish fruit abundance and availability. A systematic 5 minute-scan sampling was supplemented with ad libitum observations to collect feeding data for 5 consecutive days at the end of the month for a study period of 24 months. On each day, mangabeys were trailed from 7am to 3pm. Fruit remains under trees where mangabeys were feeding and throwing on the forest floor were carefully examined and the exact parts that were being fed on by mangabeys were identified. Mechanisms of fruit processing prior to consumption were also recorded. In order to get an insight of the macronutrients contained in the most utilized fruits, samples for nutritional analyses of different fruit parts and stages of development were collected on a monthly basis and analyzed using standard laboratory methods. One km^2 area was randomly selected in each study habitat to collect a single data set on the number and size of forest gaps for assessment of deforestation and its effect on food availability.

Results showed that there were several inter-related factors that influenced dietary composition and foraging behaviour of mangabeys in Mabira and Lwamunda forests. The principal factors included fruit availability and quality. Fruit availability varied seasonally and according to type of habitat while quality varied with fruit type/part, stage of fruit development and level of secondary compounds. It was observed that as food availability declined, fruit processing by mangabeys increased in Lwamunda and M2 but it was non-existent in M1 of Mabira forest. Of the ten priority fruits commonly consumed by mangabeys in Lwamunda, M2 and M1, about 60%, 20% and <1% respectively were processed to access endosperm or pulp. The stage of fruit development dictated the specific part(s) of fruit consumed and the mode of ingestion. The skin of ripe fruits was peeled off and discarded while the pulp gnawed off in the mouth and ingested. The intermediate ripening stages of most fruits were avoided except for a few genera. Level of fruit ripeness also determined pattern of fruit processing. *Ficus* species (*sur* and *exasperata*) were consumed whole while unripe fruits of *Canarium indicum, Maesopsis eminii, Pseudospondias microcapa* were processed. Large-sized fruits were consumed in piece-meal portions; medium-sized fruits were gnawed at to access the desired part(s) and small-sized ones were invariably ingested whole. Immature fruits belonging to *C. indicum, P. microcapa* and *M. eminii* and *Myrianthus arboreus* were processed to access endosperm; while pulp of most fruits was consumed when fruits were ripe. Abundance of fruits commonly eaten by mangabeys did not translate into availability. The number of fruiting trees was significantly higher in M2 than M1 and LD. However, edible fruits in M1 were significantly higher than in LD ($P<0.001$ using one-way ANOVA).

Availability and nutrient content of priority fruits in LVB also influenced Mangabey nutritional ecology. Fall-back fruits (FBFs) that were available for most of the time contributed to Mangabey diet during periods of low food availability. Nutritionally, seasonal fruits had twice as much protein, fat and sugars as FBFs. Protein seemed to be an important nutrient component in Mangabey diet as exemplified by the consumption of seeds and endosperms. It was closely followed by fat as indicated by preference for *B.unijugata* (Baker) aril and *Celtis* spp seeds with $\geq$ 10% fat levels. However, the phenological data indicated that the number of fruiting FBF trees appeared insufficient to sustain Mangabey populations in M2 and LD. It was therefore concluded that the actual

FBFs in the two habitats were probably the raided crops and domestic fruits growing in the wild respectively since they sustained mangabeys during fruit scarcity. In a health ecosystem (forest), the proportion of FBFs in comparison with preferred fruits should be small but it was observed that in Lwamunda and M2, the ratio of FBFs to preferred fruits was 2:1 and 1:1 respectively. This implied that Lwamunda was ecologically unhealthier than M2 in terms of Mangabey diet.

The level of secondary compounds, particularly tannins, which are known to have anti-digestive properties among primates also seemed to have influenced Mangabey diet. During periods of food scarcity, mangabeys selectively consumed parts of unripe fruit (endosperms of *P. microcapa*, *M. aboreus*, *C. indicum* and *M. eminii*) that were known to contain relatively low levels of condensed tannins below a threshold of 2.6g/100g catechin equivalent. Fruit parts with tannins levels above the threshold were avoided and rarely consumed by mangabeys unless they contained relatively high protein content and low fibre. This type of trade-off was exemplified by consumption of *Celtis* seeds with relatively high levels of protein (≈10%) and tannins (3.08g/100g). Fruit processing behaviour to select specific fruit parts for consumption seems to be related to the level of tannins and an adaptation to cope with food scarcity.

In a forest environment, gap size seemed to have influenced food availability. The mean gap size varied from 50.12±24.8 m^2 in fairly undisturbed Mabira (M1) to 96.42±24.9 m^2 in regenerating Mabira (M2) and 644.58±53.98 m^2 in severely degraded Lwamunda (LD) forest reserves. Generally, fruits utilized by mangabeys as food declined as the number and sizes of gaps increased. The level of decline was significant (one way ANOVA $p < 0.05$). During periods of fruit scarcity, mangabeys devised different patterns of fruit processing as a coping strategy.

However, it was noted that interpreting interrelated factors influencing Mangabey diet and foraging behaviour was complex. To unravel some of these complexities, the consumption or rejection of specific fruit parts of *B. unijugata* at different developmental stages was investigated. The nutritional criteria used depended on level of fat and condensed tannins. When seeds or arils had low tannins, mangabeys ate them but rejected them when tannin levels increased beyond 2.6g/100g catechin equivalent. While fat

content in seeds and aril increased with increasing maturity, it only influenced aril consumption but not seed consumption because of its high tannin level.

In conclusion, nutritional content of food items appeared to be pivotal to understanding primate foraging decisions including trade-offs between consumption of critical macro-nutrients and secondary metabolites. Generally, mangabeys in the three forests selected fruit parts that were low in fibre and tannins, but rich in protein, high in sugars and fats. These included ripe fruit pulp of *Rheedia edulis*, aril of *B. unijugata* and seeds of *Celtis* species. The quality and quantity of fruits appear to be the main factors that influenced mangabey nutrition. Several recommendations were drawn from the study; for instance, development of credible strategies and policies for conservation of forest reserves to sustain Mangabey population in LVB, repetition of the study with increased study sites, mangabey groups, sample size of monitored tree species and inclusion of other secondary metabolites like terpenoids and alkaloids.

Key words: Fruit availability, quality, tannins, adaptation mechanisms and Mangabeys

LIST OF PAPERS AND MANUSCRIPTS

The results are presented in form of five publishable papers and manuscripts:-

1. Masette M, Isabirye-Basuta G, Baranga D and Chapman C. A.. Patterns of fruit processing by Grey-cheeked mangabeys (*Lophocebus ugandae* Groves) in Mabira and Lwamunda forest reserves, Uganda
2. Masette M, Isabirye-Basuta G, Baranga D, Chapman C. A, & Rothman J. M. (2015). The challenge of interpreting primate diets: mangabey foraging on *Blighia unijugata* fruit in relation to changing nutrient content. *African Journal of Ecology*. Vol. 53 (3) 259-267. doi: 10.1111/aje.12174. Received in August 2014 and published Sept 2015
3. Masette M, Isabirye-Basuta G, Baranga D and Chapman C. A. The importance fall-back fruits on the nutritional ecology of Grey-cheeked mangabeys *(Lophocebus ugandae*, Groves*)* in Mabira and Lwamunda forest reserves, Uganda
4. Masette M., Isabirye-Basuta G., Baranga D., & Chemurot M. (2015). Levels of tannins in fruit diet of grey-cheeked mangabeys (*Lophocebus ugandae*, Groves) in Mabira and Lwamunda forest reserves. *Journal of Ecology and the Natural Environment* Vol. 7(5), pp. 146-157, May 2015, DOI: 10.5897/JENE2015.0499, Article Number: F60599752732,
5. Masette M, Isabirye-Basuta G, Baranga D and Chapman C. A. Effect of gaps on fruit availability for mangabeys in Mabira and Lwamunda forest reserves, Uganda.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF ACRONYMS AND ABBREVIATIONS

CBO	Community Based Organization
CITES	Convention on International Trade in Endangered Species
CFR	Central Forest Reserve
COFSDA	Future Sustainable Development Association
GoU	Government of Uganda
FAO	Food and Agricultural Organization of United Nations
IUCN	International Union for the Conservation of Nature
LD	Lwamunda forest reserve
LVB	Lake Victoria Basin
M1	Mabira study site described as fairly undisturbed forest reserve
M2	Mabira study site described as regenerating forest reserve
MWLE	Ministry of Water, Lands and Environment
NACOBA	Nagojje Conservation Biodiversity Association
NaFORRI	National Forest Resources Research Institute
NARO	National Agricultural Research Organization
NEAP	Uganda National Environmental Action Plan
NEMA	National Environmental Management Authority
NFA	National Forest Authority
NUFU	Norwegian Programme for Development, Research and Education
PRPs	Proline-rich proteins
PSM	Plant secondary metabolites
UBOS	Uganda Bureau of Statistics
UMD	Uganda Metrological Department
UNEP	United Nations Environment Programme
UNESCO	United Nations, Educational Scientific and Cultural Organization
UNPF	United Nations Population Fund
UWA	Uganda Wildlife Authority
VAS	Visual Abundance Score
WCMC	World Conservation Monitoring Centre

CHAPTER ONE

1 GENERAL INTRODUCTION

1.1 Background

Primate nutritional ecology may be defined as the interactions between the environment and the primate in terms of nutrient intake and its resultant physiological state (Felton *et al.*, 2009). One of the overarching goals of nutritional ecology among primates is to establish what they consume and understand what governs their dietary food selection. The mangabeys (*Lophocebus ugandae* Groves, 2007) commonly known as Grey-cheeked mangabeys were targeted among the sympatric primate species within the Mabira and Lwamunda (ML) for several reasons. First, nutrient compositional information on the dietary items of this frugivorous primate is scanty being a recent discovery with restricted range in Uganda (Groves, 2007). Secondly, several studies (Onderdonk and Chapman, 2000, Howard, 1991) recommended generation of authentic data that focus on forest fauna susceptible to extinction or potential forest habitats capable of supporting species like mangabeys. Thirdly, although mangabeys are not currently threatened with extinction, their population might drastically decline due to habitat loss or unregulated bush-meat trade (De Merode and Cowlishaw, 2006; Davis, 2002; Bowen-Jones and Pendry, 1999). Finally, the sensitivity of primates to environmental degradation provides a useful tool for assessment of forest health status and its structure. As such, mangabeys are regarded as flagship species for wildlife conservation and they were identified as potential good primate species as indicators of forest health (Onderdonk and Chapman, 2000).

The feeding behaviour of primates is best understood by detailed analysis of nutritional ecology (Houle *et al.*, 2007; Conklin-Brittain *et al.*, 1998). According to Rothman *et al.* (2012) understanding nutritional needs of primates is crucial to understanding their other ecological variables. Furthermore, understanding of Mangabey habitat requirements, limitations and flexibilities in both primary and degraded forests is paramount for their

conservation (Worman and Chapman, 2006). Besides, knowledge of the causative factors that influence primate populations and abundance, is paramount for the formulation of conservation and management plans of their forest habitat (Hanya and Chapman, 2013; Isabirye-Basuta and Lwanga, 2008; Harris and Chapman 2007; Rodes *et al.*, 2006; Wasserman and Chapman, 2003). Relevant information is however scarce because of the considerable challenges involved when collecting and interpreting such data (Felton *et al.*, 2009). This is in spite of the alarming rate of habitat alteration, degradation and the urgency required to conserve the forest fauna and particularly the primates inhabiting M&L forests. The nutritional ecology of mangabeys is essentially unknown in these forest reserves. Consequently, strategies to effectively manage their habitat have not been adequately formulated for lack of relevant information which this study has endeavoured to generate.

Previous studies (Baranga, 1983; have generated scanty information on nutritional ecology of other primates but none has been conducted on mangabeys inhabiting M&L. Baranga (1983) studied white colobus (*Colobus guereza occidentalis*) at Kanyawara, Kibale Forest, Uganda and determined seasonal variations in the chemical composition of parts consumed by these animals. Rode *et al.* (2003) also studied mineral resources available and consumed by individuals of the same species and in the same Kibale forest. Chapman *et al.*, (2003) evaluated variations in protein, fiber, digestibility, alkaloids, saponins, cyanogenic glycocides, and minerals of leaf material from species eaten by Red Colobus (*Piliocolobus tephrosceles*) and black-and-white colobus (*Colobus guereza*) of Kibale National Park, Uganda. Generally, food choices among primates are governed by the nutritional and toxic contents of the fruit/fruit part consumed and their spatiotemporal availability (Milton,1984). However, Janson and Chapman (1999) observed that most primates preferred a diet that is rich in protein and carbohydrates but low in fibre. In the absence of preferred food items during periods of general scarcity, primates usually shift to low quality foods or fall-back items (Chapman *et al.*, 2012; Marshall *et al.*, 2009; Marshall and Wrangham, 2007; Lambert *et al.*, 2004). With the current incessant degradation of Mangabey habitat in M&L forest reserves, their diet may have changed significantly in the recent past. Over a decade and a half ago, a study conducted in Kibale

national park (Olupot, 1999) asserted that habitat degradation impacted directly on the nutritional ecology of mangabeys. Furthermore Chapman (1988) specifically noted that habitat degradation reduced potential food resources and its availability. As a result, group size, composition and diversity among primates reduced considerably compared to social groups studied earlier by Freeland (1979).

The declining biodiversity appears to be intrinsically linked to increasing scarcity of natural resources that may be brought about by anthropogenic induced activities (Stickler, 2004). Food scarcity ultimately compromises the nutritional ecology of forest fauna including mangabeys. There are several human-induced activities which compromise food availability for mangabeys. These include high water pollution levels, alarming deforestation rates (Becker and Ostrom, 1995), thinning ozone layer and global warming which is exacerbated by increasing carbon dioxide release in the atmosphere (Fearnside, 2005) and increasing human populations especially in developing economies like Uganda (Livi-Bacci, 2012). In addition, most valuable resources like forests are accessed liberally by communities (da Fonseca, 2007; Fisher, 2004; Banana and Gombya-Ssembajjwe, 2000; Bromley, 1992). This liberal access to forest resources has inadvertently led to conflicts between humans and non-human primates, over exploitation of natural resources and decline in biodiversity (Glew and Hudson, 2007; Okello and Kiringe, 2004; McNeely, 2003). In the process, habitat for forest fauna has declined drastically. Besides, access to high quality fruit has become a critical challenge for forest frugivores including mangabeys.

Loss of habitat for forest fauna has been exacerbated by man's insatiable demand for forest products. About three decades ago, Hamilton (1984) predicted that demage would lead to accelerated decline in forest cover all over the African continent. Barnes (1990) also warned of dramatic forest loss across the African continent by 2040 with the exception of only Gabon and Congo which will lose small proportion of their forests (Bush, 2009). According to Burgess *et al.* (2007) the Eastern Arc Mountains supporting around 3300 km^2 of sub-montane, montane and upper montane forest have declined to less than 30% of the estimated original forested area in the last century. These mountains

are renown in Africa for high concentrations of endemic species of animals and plants including the Sanje Mangabey. It has been estimated that tropical countries harbouring large populations of primates were losing approximately 12.5 million hectares of forest annually (Chapman *et al.*, 2006). The subtle consequence of habitat loss through forest degradation worldwide appears to be the sole major causal factor for the declining biodiversity and abnormally high extinction rates among primates (Becker and Ostrom, 1995). The declining biodiversity was exemplified in the heterogeneous Rungwe–Livingstone forests, of southwest Tanzania where the critically endangered Kipunji *Rungwecebus kipunji* inhabits (Bracebridge *et al.*, 2012). Chapman *et al.* (2006) asserted that the available empirical evidence suggests that the increasing threat to primate populations is principally due to these anthropogenic actions.

In small economies like Uganda, impacts of deforestation (Obua *et al.*, 2010; NEMA, 2010) has not only contributed to habitat loss for mangabeys but it has also undermined the sustainable economic, societal and environmental development of the people living in close proximity to forests (NEMA, 2010; NFA, 2008; Baranga, 2004; Kayanja and Byarugaba 2001). Owing to their close proximity to major urban centres, Mabira and Lwamunda forest reserves have been prime targets for degradation. Essentially, deforestation threatens the very existence of forest fauna including mangabeys by denying them the basic necessities of life like suitable habitats, protection and food. Undeniably, food quantity and quality for mangabeys inhabiting M&L forests has become uncertain due to severe fragmentation, degradation and clearing as a result of increased anthropogenic pressure (Obua and Agea, 2010; NEMA, 2010; NEMA, 2006).

The choice of M&L forest reserves for the present study is based on their geographical location and their different management histories. The latter factor has led to the culmination of contrasting levels of degradation and presumably the current exhibition of different nutritional ecologies for mangabeys. For example, the 1993, UNESCO management strategy that was implemented in most of the Lake Victoria Basin (LVB) forest reserves prohibited human encroachment (Alpert, 1996). In Mabira where supervision was strict after expiry of the intervention, the forest recovered to a certain

extent which resulted into mangabeys extending their home range. On the contrary, in Lwamunda where the supervision was relaxed, the encroachers returned and mangabeys were hounded (Basuta, *unpublished data*). As a response to this strategy, the quality of Mangabey food in Mabira may have presumably improved but there is lack of information, the assumption has not been verified. On the other hand, the food quantity and quality in Lwamunda may have been harshly compromised and Mangabey populations may be on the decline and under threat due to habitat loss. In both cases however, the stated assumptions remain speculations. This comparative study investigated the hypothesis that degradation influences the dietary ecology of mangabeys because it affected food availability. Although M&L forest reserves are not rain forests per se, the rate of fragmentation and degradation due to anthropogenic pressure re-enforced the urgent need for formulation of conservation strategies. In addition, the dietary composition and balanced food intake may have been altered owing to the reduction in the availability of potential food resources. The change in diet is usually a reflection of the environmental alteration within a home range (Olupot *et al.*, 1994; Hamilton, 1984; Waser, 1977). In spite of these glaring pointers to reduction of Mangabey quantity and quality of food, none of these presumptions have been investigated. Habitat degradation changes forest structure and composition which inadvertently affect food availability and ultimately the nutritional status of the primate as conjectured in conceptual framework (Fig. 1.1).

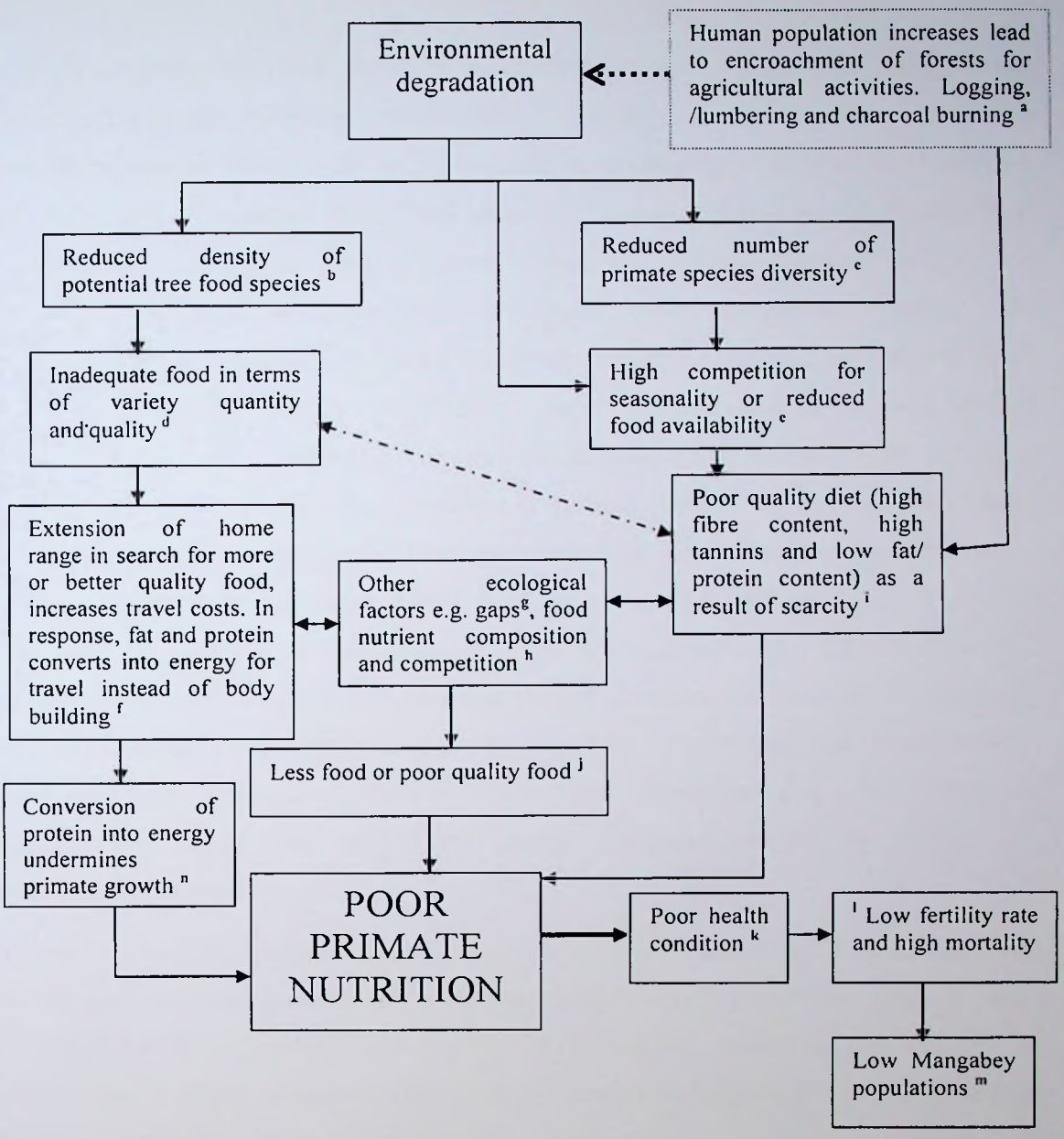


Figure 1.1 Schematic sequence of events likely to compromise the nutritional ecology of primates following habitat loss due to degradation

Superscripts refers: [a]NEMA (2008); Chapman *et al.* (2006) [b]Olupot (2000; 1999) [c](Kayanja and Byarugaba (2001), [d]Chapman and Onderdonk (1998), [e]Baranga (2004), Poulsen *et al.* (2001), [f]Milton (1998), [g]Isabirye-Basuta and Lwanga (2008), [h]Butynski and de Jong (2007), Struhsaker (1997), [i]Wrangham *et al.* (1993), [j]Worman (2004), [k]McCabe *et al.* (2013) Rode *et al.* (2006), [l]Arlet *et al.* (2014) [m]Olupot (1999) and [n]MAFF (

Although mangabeys may be classified as omnivorous, they are primarily frugivorous. Janson and Chapman (1999) categorized their wide range of food choice into three major components namely insect, fruit and leaves. However, during periods of food scarcity, mangabeys tend to consume other food items for example, young leaves, flower buds (Olupot *et al.,* 1997; Waser, 1975) and other animals (Janson and Chapman, 1999). Food scarcity may be due to habitat degradation (Olupot, 1999), seasonality (Poulsen *et al.*, 2001; Kaplin *et al.*, 1998), competition (Struhsaker, 1997; Conklin and Wrangham, 1994) and presence of high level of secondary compounds like tannins in seed or leaf (Wrangham *et al*, 1993) which may require detoxification (Nabihamba, 1996), a process that may not be cost-effective. Insufficient protein intake as a result of habitat degradation compels mangabeys to supplement their diet through consumption of unpalatable plant parts (Chalmers, 1968). Scarcity of minerals in fruit and seed compels mangabeys to consume leaves and clay like-soils (Janson and Chapman, 1999). Frugivores are known to respond to variation in fruit abundance and nutritional quality by changing metabolism and energy balance (Knott, 1998), ranging behaviour (Remis, 1997; Olupot *et al.*, 1997), and food selection (Peres, 1994; Wrangham *et al.*, 1998). None of these responses have been established among mangabeys inhabiting Mabira and Lwamunda forest reserves.

It is probable that all these factors may be at play in both Mabira and Lwamunda forest reserves and yet their interactions with regard to Mangabey nutrition had not been established. Habitat degradation being pivotal to Mangabey nutritional ecology and the consequences of forest degradation has been elaborated to demonstrate the dire need for information generation in the present study.

1.2 Problem Statement

The feeding ecology of mangabeys has been affected by severe degradation of their habitats within Mabira and Lwamunda forest reserves. The pressure on their habitat exacerbated by high human populations (UBOS, 2014), has been so enormous (NEMA 2006) that availability of sufficient balanced food for the mangabeys and other forest fauna on a long time basis may be doubtful. Degradation results in loss of suitable natural habitat and scarcity of food resources which has direct impact on food choice and

ultimately population size as well as health of primates. Knowledge of priority food choice, its chemical composition and abundance in M&L forest reserves would give an indication of the forest health as Mangabey' dietary adaptations are a reflection of environmental changes (Olupot *et al.*, 1994). It appears conservation of the forest reserves would guarantee a balanced diet of high quality food resources for mangabeys and their conservation. However, the forest policy (MWLE, 2002) is less emphatic on the conservation strategies of forest fauna despite the severe threat posed to their habitat. This lack of conservation strategy was vividly demonstrated in 2006 when a proposal was made to apportion part of Mabira forest reserve to entrepreneurs for sugarcane production.

Whereas management strategies of 1993 in Mabira forest reserve (Alpert, 1996) stemmed degradation, it continued unabated in Lwamunda with potential disastrous consequences for mangabey food quality and availability. A comparative study to generate information on the nutritional ecology of mangabeys would be a basis for formulation of an effective management system for Lwamunda. Implementation of such a management system guarantees the sustainability of the forest whilst meeting the nutritional requirements of forest fauna including mangabeys. The recent identification of *Lophocebus ugandae* in Uganda as a "new" species and it is likely to be endangered owing to increased loss of its habitat (Groves, 2007). There is therefore need for its conservation which requires generation of sufficient baseline information on its nutritional ecology. Its conservation would enhance the biodiversity of these highly fragmented, deforested and degraded Mabira and Lwamunda forest reserves.

There are several factors influencing nutrition among primates. They include geographical variation of habitat, activity budgets and travel patterns (Kaplin *et al.*, 1998; Poulsen *et al.*, 2001) seasonality (Baranga, 1983), competition and food availability, chemical constituents of ingested food (Chapman, 1988), fruit/seed/leaf maturity and location in the tree canopy (Danish *et al.*, 2006; Rode *et al.*, 2006; Worman and Chapman, 2005). The relationship between these factors and food selection among mangabeys in Mabira and Lwamunda has not been established. There is limited

information on the impact of anthropogenic activities on Mangabey food availability, fruit abundance and nutrition. Deforestation creates gaps in tree canopy which forces arboreal primates to change their movement and ranging patterns (Olupot *et al.*, 1997, Ganzhorn, 1986). This change entails high energy budgets and change in dietary composition, which has a bearing on primate nutrition (Olupot, 1999). However, this dietary shift has not been established in either Mabira or Lwamunda mangabeys. This study was therefore aimed at investigating Mangabey nutritional ecology in relation to food availability and quality.

1.3 Overall Objective

The principal objective of this study was to investigate the nutritional ecology of Grey-cheeked mangabeys inhabiting three contrasting habitats within the Mabira and Lwamunda (M&L) forest reserves.

1.3.1 Specific objectives

The specific objectives of the study were to

i. Assess influences of fruit macro-nutrient content on Mangabey feeding behaviour when utilizing different fruit parts at different stages of development
ii. Investigate dietary adaptations of mangabeys to declining fruit availability and quality quality in Mabira and Lwamunda forest reserves
iii. Assess influence of tannins levels (secondary metabolites) on Mangabey fruit dietary selection
iv. Investigate the importance of fall-back fruits in Mangabey diet
v. assess the effect of gap size on availability and quality of fruit for mangabeys in study sites subjected to different management regimes.

1.4 Scope of the study

This study was part of a bigger project on ecology and sustainable natural resource management for development in Uganda. It was funded by Norwegian Programme for Development, Research and Education Project abbreviated in Norwegian as NUFU that was implemented by Makerere University from 2000-2003. The present study was a

much smaller component and it was limited to nutritional ecology of mangabeys inhabiting the three different habitats within Mabira and Lwamunda forest reserves. The study sites or habitats for mangabeys consisted of two portions of Mabira forest reserve; one fairly undisturbed and the other regenerating after two decades of encroachment for agricultural purposes. The third habitat was Lwamunda forest reserve located about 71Km away from Mabira and severely degraded. These three habitats have been subjected to varying environmental pressures and disturbances. Because of the different management histories, the three habitats formed a basis for comparative studies. In essence, the study focussed on four major areas that influence Mangabey dietary requirements consisting of fruit and seed: -

- fruit abundance/availability that may induce fruit processing and use of fallback fruits as coping strategies during periods of fruit scarcity;
- fruit chemical nutrient composition as a major influence on choice and food source diversity as a function of fruit quality.
- the effect of plant secondary compounds like tannins on fruit/fruit part selection
- gap numbers and sizes as indices of forest degradation.

The nutritional and ecological studies revolved around the ten priority fruit trees commonly utilized as food by mangabeys in both forest reserves. These studies included monthly collection of fruit abundance and ripeness or availability of 10 individual trees of the 10 priority fruit trees. Field observations of what part of fruit mangabeys consumed and coping mechanisms employed to access the desired part during periods of food scarcity. Samples in form of whole or parts of fruits were collected from these same trees for macro-nutrient analyses and secondary compounds (tannins). The study uses the generated data to identify inter-related factors that influence Mangabey diet in three contrasting habitats. For purposes of this study, only fruits and seeds have been considered since they constitute over 50% of the Mangabey diet.

However, there were several viable research activities that were outside the scope of the present study. They included energetics (i.e. travel costs, feeding bouts, energy content per fruit and development stage), actual food components assimilated by different

mangabey age groups and sexes, other secondary compounds like terpenoids, alkaloids and most components of phenolics like lignins, flavonoids and saponins. In-depth studies involving habitat degradation vis-a-vis Mangabey population declines and their dynamics including causative intrinsic factors are also conspicuously absent from the present study.

1.5 References

Alpert, P. (1996). Integrated conservation and developmental projects. Examples from Africa. *BioScience*, **46** (11), 845-855.

Arlet, M.E., Isbell, L.A., Molleman, F., Kaasik, A., Chancellor, R.L., Chapman, C.A. &Carey, J.R. (2014). Maternal investment and infant survival in gray-cheeked mangabeys (*Lophocebus albigena*). *International Journal of Primatology* **35**(2), 476-490.

Banana, A.Y. & Gombya-Ssembajjwe, W. (2000). Successful Forest Management: The importance of security of tenure and rule enforcement in Ugandan forests. In Gibson, C.C., McKean, M.A., Ostrom, E. (Eds), *People and Forests: Communities, Institutions, and Governance*, 1 Review (pp 87-97). MIT Press, Science.

Baranga, D. (2004). Forest fragmentation and primate survival status in non-reserved forests of the Kampala area, Uganda. *African Journal of Ecology* **42** (1), 70-77.

Baranga, D. (1983). Changes in chemical composition of food parts in the diet of colobus monkeys. *Ecology*, **64**(4), 668-673.

Barnes, R.F.W. (1990). Deforestation trends in tropical Africa. *African Journal of Ecology*, **28**(3), 161–173.

Becker, C.D. & Ostrom, E. (1995). Human ecology and resources sustainability: The importance of institutional diversity. *Annual Review of Ecology and Systematics* **26**(1995): 113-133.

Bowen-Jones, E. & Pendry, S. (1999). The threat to primates and other mammals from the bushmeat trade in Africa, and how this threat could be diminished. *Oryx*, **33**(3), 233–246.

Bracebridge, C.E., Davenport, T.R. & Marsden, S.J. (2012). The Impact of Forest Disturbance on the Seasonal Foraging Ecology of a Critically Endangered African Primate. *Biotropica*, **44**(4), 560–568.

Bromley, D.W. (1992). The commons, common property and environmental policy. *Environmental and Resource Economics* **2**(1), 1-17.

Burgess, N.D., Butynski, T.M., Cordeiro, N.J., Doggart, N.H., Fjeldså, J., Howell, K.M., Kilahama, F.B., Loader, S.P., Lovett, J.C., Mbilinyi, B., Menegonm, M., Moyern, D.C., Nashandaj, E., Perking, A., Roverom, F., Stanley, W.T. & Stuart, S.N. (2007). The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation* **134**(2), 209–231.

Bush, G.K. (2009). *The economic value of Albertine Rift Forests; applications in policy and programming.* Economics eThesis Published by University of Stirling. STORRE: Stirling Online Research Repository

Butynski, T.M. & de Jong, Y.A. (2007). Distribution of the potto Perodicticus potto (Primates: Lorisidae) in eastern Africa, with a description of a new subspecies from Mount Kenya. *Journal of East African Natural History* **96**(2), 113-147.

Chalmers, N.R. (1968). The visual and vocal communication of free inhabiting Mangabeys in Uganda. *Folia Primatologica,* **9**(3-4), 258-280.

Chapman, C. A., Rothman, J. M. & Lambert, J. E. (2012) Food selection in primates. In: *The Evolution of Primate Societies* (Eds. J. Mitani, J. Call, P. Kappeler, R. Palombit & J. Silk). Chicago University Press, Chicago.

Chapman C.A., Lawes, M.J. & Eeley, H.A.C. (2006). What hope for African primate diversity? *African Journal of Ecology* **44**(2), 116-133.

Chapman, C. A., Chapman, L. J., Rode, K. D., Hauck, E. M., & McDowell, L. R. (2003). Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal of Primatology* **24**(2), 317-333.

Chapman, C.A. & Onderdonk, D.A. (1998). Forests without primates: primate/plant co-dependency. *American Journal of Primatology* **45**(1), 127-141.

Chapman, C.A. (1988). Patterns of foraging and range use by three species of Neotropical primates. *Primates*, **29**(3), 177-194.

Conklin, N.L. & Wrangham, R.W. (1994). The Value of Figs to a Hind-gut Fermenting Frugivore: a Nutritional analysis. *Biochemical Systematic and Ecology* **22**(2), 137-151.

Conklin-Brittain, N.L., Wrangham, R.W. & Hunt, K.D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *International Journal of Primatology* **19**(6), 971-998.

Da Fonseca, G.A.B., Rodriguez, C.M., Midgley, G., Busch, J., Hannah, L. & Mittermeier, R.A. (2007). No Forest Left Behind. *PLoS Biol,* **5**(8): e216.

Danish, L., Chapman, C.A., Hall, M.B., Rode, K.D. & Worman, C.O. (2006). The role of sugar in diet selection in red-tails and red colobus monkeys. In Hohmann, G. Robbins, M.M. & Boesch, C. (Eds), *Feeding Ecology in Apes and Other Primates: Ecological, Physical and Behavioral Aspects*. Cambridge University Press.

Davis, S. (2002). "*Lophocebus albigena*" (On-line), Animal Diversity Web. Accessed September 16, 2005 at http://animaldiversity.ummz.umich.edu/site/accounts/information/*Lophocebus_albigena*.html.

De merode, E. & Cowlishaw, G. (2006). Species Protection, the Changing Informal Economy, and the Politics of Access to the Bushmeat Trade in the Democratic Republic of Congo. *Conser. Biol.*, **20** (4), 1262–1271.

Fearnside P.M. (2005). Deforestation in Brazilian Amazonia: History, Rates, and Consequences. *Conservation Biology* **19**(3), 680-688.

Felton, A.M., Felton, A., Lindenmayer, D.B. & Foley, W.J. (2009). Nutritional goals of wild primates. *Functional Ecology* **23**(1), 70-78

Fisher, M. (2004). Household welfare and forest dependence in Southern Malawi. *Environment and Development Economics*, **9**(02), 135-154.

Freeland, W.J. (1979). Mangabey (*Cercocebus albigena*) social organization and population density in relation to food use and availability. *Folia primatologica.*, **32**(1-2), 108-124.

Ganzhorn, J.U. (1986). The influence of plant chemistry on food-selection by *Lemur catta* and *Lemur fulvus*. In Else, J.G. (Ed), *Primate Ecology and Conservation*. Selected Proceedings of the 10th Congress of the International Primatological society held in Nairobi, Kenya. July 1984.

Glew, L. & Hudson, M.D. (2007). Gorillas in the mist: the impact of armed conflict on the conservation of protected areas in sub-Saharan Africa. *Oryx, the International Journal of Conservation*,**41**(2), 140-150.

Groves, C. P. (2007). The endemic Uganda mangabey, *Lophocebus ugandae*, and other members of the albigena-group (*Lophocebus*). *Primate Conservation* **22**(1), 123-128.

Hamilton, C.A. (1984). *Deforestation in Uganda*. Oxford University Press, Nairobi.

Hanya, G. & Chapman, C.A. (2013). Linking feeding ecology and population abundance: a review of food resource limitation on primates. *Primate Conservation* **28**(2), 183-190.

Harris, T. R., & Chapman, C. A. (2007). Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates*, **48**(3), 208-221.

Houle, A., Chapman, C. A., & Vickery, W. L. (2007). Intratree variation in fruit production and implication for primate foraging. *International Journal of Primatology* **28**(6), 1197-1271.

Howard, P.C. (1991). Nature Conservation in Uganda's Tropical Forest Reserves. IUCN, Gland, Switzerland and Cambridge, UK. xvii + 313 pp.

Isabirye-Basuta, G.M. & Lwanga, J.S. (2008). Primate populations and their interactions with changing habitats. *International Journal of Primatology* **29**(1), 35-48.

Janson, C.H. & Chapman, C.A. (1999). Resources and primate community structure. In Fleagle, J.G., Janson, C.H. and Reed, K.E. (Eds), *Primate Communities* (pp. 237-267). Cambridge University Press. Cambridge.

Kaplin, B.A., Munyaligoga, V. & Moermond, T.C. (1998). The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). *Biotropica*, **30**(1), 56-71.

Kayanja, F.I.B. & Byarugaba, D. (2001). Disappearing forests of Uganda: The way forward. *Current. Science.*, **81**(8), 936-947

Knott, C.D. (1998). Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology* **19**(6), 1061-1079.

Lambert, J.E., Chapman, C.A., Wrangham, R.W. & Conklin-Brittain, N.L. (2004). Hardness of cercopithecine foods: Implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology* **125**(4), 363–368.

Livi-Bacci, M. (2012). *A concise history of World population*, 5th Edition. John Wiley and Sons Ltd, United Kingdom.

MAFF, 1995). Manual of nutrition. Published for the Ministry of Agriculture, Fisheries and Food by Her Majesty's Stationery Office. ISBN 0 11 242991 2

Marshall, A.J., Boyko, C.M., Feilen K.L., Boyko, R.H. & Leighton, M. (2009). Defining Fallback Foods and Assessing Their Importance in Primate Ecology and Evolution. *American Journal of Physical Anthropology* **140**(4), 603–614.

Marshall, A.J. & Wrangham, R.W. (2007). Evolutionary Consequences of Fallback Foods. *International Journal of Primatology* **28**(6), 1219-1235.

McCabe, G.M., Fernández, D. & Ehardt, C.L. (2013), Ecology of reproduction in Sanje mangabeys (*Cercocebus sanjei*): Dietary strategies and energetic condition during a high fruit period. *American Journal of Physical Anthropology* **75**(12), 1196-1208.

McNeely, J.A. (2003). Conserving forest biodiversity in times of violent conflict. *The international Journal of Conservation Oryx*, **37**(2), 142-152.

Milton, K. (1998). Physiological ecology of howlers (Alouatta): energetic and digestive considerations and comparison with the Colobinae. *International Journal of Primatology* **19**(3), 513-548.

Milton, K. (1984). The role of food-processing factors in primate food choice. In P. Rodman and J. Cant (Eds), *Adaptations for foraging in nonhuman primates*, (pp 249-279). Columbia University Press, New York.

MWLE (Ministry of Water, Lands and Environment) (2002). Uganda Forest Nature: Conservation MASTER PLAN

Nabihamba, E. (1996). Factors determining dietary choices among arboreal frugivores in Kibale forest in Western Uganda. Msc. Thesis, Makerere University, Kampala.

NFA-National Forestry Authority (2008). *Strategic action plan for the period 2008/9 to 2012/13 with priorities for the first five years*. Government of Uganda, Kampala.

NEMA. (2010). State of the Environment Report for Uganda 2010. National Environment Management Authority (NEMA), Kampala.

NEMA. (2008). State of environment report for Uganda 2006/7. National Environment Management Authority, Kampala.

NEMA. (2006). State of environment report for Uganda 2004/5. National Environment Management Authority, Kampala.

Obua, J., Agea, J.G. & Ogwal, J.J. (2010). Status of forests in Uganda. *African Journal of Ecology* **48**(4), 853-859.

Obua, J. & Agea, J.G. (2010). Forests and Forestry in Uganda. In Bongers, F. and Tennigkeit, T. (Eds), *Degraded forests in Eastern Africa: management and restoration* (pp. 65-88). Earthscan Ltd, London.

Okello, M.M. & Kiringe, W.J. (2004). Threats to Biodiversity and their Implications in Protected and Adjacent Dispersal Areas of Kenya. *Journal of Sustainable Tourism*, **12**(1), 55-69.

Olupot, W. (2000). Mass differences among male Mangabey monkeys inhabiting logged and unlogged forest compartments. *Conservation Biology* **14**(3), 833-843.

Olupot, W. (1999). Mangabey dispersal and conservation in Kibale National Park, Uganda. PhD Thesis. Purdue University.

Olupot, W., Chapman, C.A., Waser, P.M. & Isabirye-Basuta, G. (1997). Mangabey (*Cercocebus albigena*) Ranging Patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *Am. J. Primat.*, **43**(1), 65-78.

Olupot, W., Chapman, C.A., Brown, C.H. & Waser, P.M. (1994). Mangabey (*Cercocebus albigena*) population density, group size, and ranging: A twenty-year comparison. *American Journal of Primatology*, **32**(3), 197-205.

Onderdonk, D.A. & Chapman, C.A. (2000). Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *International Journal of Primatology* **21**(4), 587-611.

Peres, C.A. (1994). Primate responses to phenological changes in an Amazonian Terra Firme forest. *Biotropica*, **26**(1), 98-112.

Poulsen, F.E., Clark, C.J. & Smith, T.B. (2001). Seasonal variation in the feeding ecology of the grey-cheeked Mangabey (*Lophocebus albigena*) in Cameroon. *American Journal of Primatology*, **54**(2), 91-105.

Remis M.J. (1997). Ranging and grouping patterns of a western lowland gorilla group at Bai Hokou, Central African Republic. *American Journal of Primatology* **43**(2), 111-133.

Rode, K.D., Chapman, C.A., McDowell, L.R. & Stickler, C. (2006), Nutritional Correlates of Population Density across Habitats and Logging Intensities in Redtail Monkeys (*Cercopithecus ascanius*). *Biotropica*, **38**(5), 625–634.

Rode, K. D., Chapman, C. A., Chapman, L. J., & McDowell, L. R. (2003). Mineral resource availability and consumption by colobus in Kibale National Park, Uganda. *International Journal of Primatology* 24(3), 541-573.

Rothman, J. M., Chapman, C. A. & Van Soest, P. J. (2012) Methods in primate nutritional ecology: A user's guide. *International Journal of Primatology* **33,** 542-566.

Stickler, C.M. (2004). *The effects of logging on primate-habitat interactions: a case study of redtail monkeys (Cercopithecus ascanius) in Kibale National Park, Uganda.* Doctoral dissertation, University of Florida.

Struhsaker, T.T. (1997). *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation.* Florida University Press, Gainesville.

UBOS (2014) National Population and Housing Census (NPHC) conducted by Uganda Bureau of Statistics. Published by Uganda Government (GoU)

Waser, P.M. (1977). Feeding, Ranging and Group size in the Mangabey *Cercocebus albigena.* In Clutton-Brocks, T.H. (Ed), *Primate Ecology* (pp. 183-222). Academic Press, London.

Waser, P.M. (1975). Monthly variations in feeding and activity patterns of the mangabey, *Cercocebus albigena* (Lydekker). *East African Wildlife Journal* **13**(3-4), 249-264.

Wasserman, M. D. & Chapman, C. A. (2003). Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content. *Journal of Animal Ecology* **72**(4), 650-659.

Worman, C.O.D. & Chapman, C.A. (2006). Densities of two frugivorous primates with respect to forest and fragment tree species composition and fruit availability. *International Journal of Primatology* **27**(1), 203-225.

Worman, C.O. & Chapman, C.A. (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *Journal of Tropical Ecology* **21**(6), 689-697.

Worman, C.O.D. (2004). Forest, fragments, and fruit: Spatial and temporal variation in habitat quality for two species of frugivorous primates *(Cercopithecus mitis and Lophocebus albigena) in Kibale National Park, Uganda.* Doctoral dissertation, University of Florida.

Wrangham, R.W., Conklin-Brittain, N.L. & Hunt, K.D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I Antifeedants. . *International Journal of Primatology*, **19**(6), 949–970.

Wrangham, R.W., Conklin, N.L., Etot, G., Obua, J., Hunt, K.D., Hauser, M.D. & Clark, A.P. (1993). The value of figs to chimpanzees. . *International Journal of Primatology*, **14**(2),243-256.

CHAPTER TWO

2 LITERATURE REVIEW

2.1 Introduction

This chapter reviews work done by other researchers on the nutritional ecology of non-human primates and factors influencing choice of food consumed and related studies. The introduction covers the systematic classification of Grey-cheeked mangabeys, their ecological characteristic features related to food acquisition and their geographical spread across the African Continent. Then it divulges into habitat alterations, causes and effects on forest fauna including mangabeys. In addition, management histories and strategies of the study forest reserves have been cited and related to environmental degradation in respective habitats. Coping mechanisms to habitat disturbance by primates has also been outlined. The rest of the chapter focuses on Mangabey feeding habits, food selection, food availability, nutrition and functionality of anti-feedants or secondary compounds with particular emphasis on tannins.

2.2 Systematics and geographical spread of mangabeys

The Grey-cheeked Mangabey belongs to Family: Cercopithecidae, Sub-family: Cercopithecinae and Genius: *Lophocebus* which has six species. The most recently identified species *Lophocebus ugandae*, Groves (Olupot and Waser, 2013; Groves, 2007) pictured in Fig 2.1 was prior to 2007 lumped together with other populations of *Lophocebus albigena*, Lydikker.

Figure 2.1 Grey-cheeked Mangabey with long prehensile tail resting in *Ficus. mucuso* tree in Lwamunda forest reserve, Uganda.

The difference between *L. ugandae* and *L. albigena* according to Groves (2007) is that the former is bigger in size and restricted to Ugandan and Northern Tanzanian forests while the latter is much smaller and spread across the rest of tropical African forests (Kindon, 2013; Olupot and Waser, 2013). According to Davis (2002), each species exhibits different behaviours and occupies different niches with occasional home range overlaps. In this case, *L. ugandae* and *L. albigena* occupy completely different geographical areas without the remotest chance of home range overlap. When the Sanje Mangabey (*C. sanjei*) was discovered in 1989 in Tanzania's Uzungwa Mountains (Annon, 2005), there was premonition that other species would be uncovered and unsurprisingly *L. ugandae* was differentiated from *L. albigena* about two decades later. It is therefore probable that other *Lophocebus* species may be lurking somewhere and they will be discovered in due course.

Mangabeys are primarily lowland primate species. They can be found up to 1,600 m above sea level in strictly equatorial zones where they occupy both primary and secondary forests hence their presence in Mabira and Lwamunda forest reserves in Uganda. Their spatial spread includes mostly the lowland rain forests of central Africa, from the Cross River, Nigeria, through Central Africa to the Nile, north of the Congo River and the Lualaba River in the Democratic Republic of Congo. Their range encompasses south-east Nigeria, Cameroon, Congo, Gabon, mainland Equatorial Guinea, south-western Central African Republic and Democratic Republic of Congo (Chalmers, 1968). In Eastern Africa, they are found in Burundi, north-western Tanzania, and along Tana River in Kenya (Kingdon, 1974; Waser, 1975). In Uganda, *L. ugandae* inhabits scattered forests located in the west of the country where most of them are relatively undisturbed for instance Kibale and Bwamba forest reserves (Basuta, *unpublished data*). Within the Lake Victoria Basin (LVB) they are found in small pockets of Mabira and Lwamunda forest reserves (Waser, 1975).

2.3 Criteria for selection of Mabira and Lwamunda forest reserves

Mabira and Lwamunda (M&L) forest reserves were chosen for the present study because they have many contrasting habitats and corresponding different management histories.

These scenarios may have had impact on availability and quality of food resources for forest fauna including mangabeys. Primates therefore faced different environmental pressures and anthropogenic disturbances which may have presumably altered the nutritional ecology of mangabeys inhabiting both forest reserves. In addition, the dietary composition and/or balanced food intake may have also been altered owing to the reduction in the availability of potential food resources. The quality and quantity of food resources may have improved or declined depending on the prevailing conditions which may have presumably impacted on their group size, composition and ultimate Mangabey populations. As such, M&L present ideal forests for comparative studies. In spite of these glaring comparative scenarios, none of these presumptions have been exhaustively investigated. In both cases, the presumptions have remained speculative due to lack of information hence the need to conduct comparattive studies between the two forest reserves.

Besides, several other studies have been conducted in these same forests. Chalmers (1968) studied population dynamics, ecology and daily life of two groups of mangabeys, *Cercocebus albigena, johnstonii* in many Ugandan forests including Mabira and Lwamunda. Baldwin *et al.*, (1976) studied the ecology of colobus, guenon and mangabeys in Mabira. Although Waser (1975) did not conduct his studies in M&L, he focussed on ranging patterns, feeding activity, and time budgets of a group of gray-cheeked mangabeys albeit in the Kibale Forest, western Uganda. Spuhler and Jorde (1975) assessed the importance of phylogenetic and environmental determinants of the relationships among nineteen demographic, ecological and social behavioural variables observed in twenty one primate species. Of recent, other studies have engaged in crop-raiding phenomenon among mangabeys (Fungo *et al.*, 2013; Ogango, 2006). Studies on other primates have been conducted in the same forests for example Baranga (2004) investigated the ecology and survival of the red-tail monkey, *Cercopithecus ascanius schmidti* in Mabira fragmented forest patches outside the protected area system. In 2007, Baranga again undertook another study to assess resource use and impacts of human activities within Mabira forest.

2.4 Mabira and Lwamunda forest management histories

Hamilton (1984) detailed the management histories of most forests in Uganda which were subverted by the recent political upheavals and instability of 1970s and 80s. The management histories of Mabira and Lwamunda forest reserves are quite different. Whereas Mabira forest reserve was protected from encroachers by the 1993 UNESCO management strategy, it was not rigorously enforced in Lwamunda. Consequently, it has been transformed into agricultural land at time of reviewing this thesis (2016). The failure to restrain encroachers from forest reserves has been attributed to lack of participation by local communities in decision-making with regard to monitoring and enforcement of harvesting regulations (Banana and Gombya-Ssembajjwe, 2000). Secondly, the inadequate financial as well as human resources available at local government level appears to have hindered the establishment of an effective local forest management system (Gibson *et al.*, 2000)

2.5 Monitoring of forest health using biological indicators

There have been several studies conducted to monitor the health of forests (Drichi, 2003; MWLE, 2002; Hamilton, 1984). Some have used butterflies while others have used birds (MWLE, 2002) as indicator species. The criterion for choice of an indicator species or taxa is based on the indicator's dependence and linkage to natural forest habitats for survival. Mangabeys with their heavy reliance on trees for food and habitation reinforce their status as a potential indicator species. However, it has not been proven whether destruction of their habitats for timber harvest (Stickler, 2004) and agricultural purposes (Davis, 2002) invariably diminishes their potential as indicator species. Although the relationships between potential indicator species and total biodiversity are not well established (Lindenmeyer *et al.*, 2000), there is a need to test the relationships between the presence and abundance of potential indicator species and other taxa vis-a-vis the maintenance of critical ecosystem processes in forests. The relationship indices can be used as a forest management tool to judge the health of a forest against a background of degradation (Stickler, 2004).

2.6 Mangabey nutritional adaptations to alterations in M&L forest reserves

In response to incessant habitat degradation, mangabeys inhabiting M&L forest reserves have devised skills and various food acquisition mechanisms to cope with limited food resources and to wade off a myriad of competitors. Although there is limited documentation on the acquired skills and food manipulation mechanisms employed by mangabeys in M&L, several studies on mangabeys or other primates in other African forests have been conducted (Marshall, 2006; Worman and Chapman, 2005; Olupot *et al.*, 1994) and similar adaptations to habitat alterations on their feeding ecology were observed. Fundamental adaptations seem to have been centred on changes in population dynamics, home range, food availability, food selection, and food processing, dietary shifts, crop-raiding and food trade-offs.

As a consequence to habitat disturbance, Marshall (2006) reported a reduction of group and population size of *Procolobus gordonorum* inhabiting the poor habitats of Udzungwa Mountains of Tanzania. Rode *et al.* (2006) also reported that the redtails (*Cercopithecus ascanius*) supported in heavily logged habitat in Kibale National Park were 3.5 times less than in unlogged habitat as food availability became a limiting factor. Consequently, the redtails in that study exhibited reduced group sizes, fewer poly-specific associations and increased home range overlap. Furthermore, the food quantity and quality interacted significantly to reduce the nutritional value of redtail diets in the heavily logged area. Olupot *et al,* 1994) also observed that habitat disturbance led to extension of Mangabey home range in Kibale National Park hence increasing travel costs.

Deforestation tends to break the continuity of the tree canopy which increases travel costs and inevitably forces arboreal mangabeys to climb down to forage in undergrowth/forest floor. Food items normally found on the forest floor for instance mushrooms and herbaceous fruits are known to have low nutrient quality. It is generally perceived that herbaceous plants which characterize the undergrowth in a degraded and regenerating forest contain high levels of toxic secondary compounds like phenols. The extension of the home range as a result of food scarcity and the prohibitive travel costs coupled with the inevitable change in available food causes dietary shifts among primates (Stickler,

2004). Scarcity of minerals in fruit and seed causes a dietary shift among Mangabeys (Janson and Chapman, 1999). According to Worman and Chapman (2005), food scarcity imposes a dietary shift on frugivores. One of the dietary shifts observed among frugivores during spells of food scarcity is the consumption of other plant parts like leaves, flower buds, pith and seeds. Although leaves and seeds generally contain high amounts of proteins and lipids respectively, they also contain high levels of tannins which reduce the digestibility of proteins (DeGabriel *et al.*, 2009). As such, most primates would rather trade-off the deterrents with high nutrients food item than starve. Dietary shifts are usually associated with nutritional trade-off as a strategy to increase energy or protein intake (Schaefer *et al.*, 2003). In most cases, food items with high fibre and tannin are negatively correlated with food selection (Matsumoto-Oda and Hayashi, 1999) thereby limiting food choice and corresponding nutritional benefits. Consequently, during periods of food scarcity primates including mangabeys tend to have dietary shifts from predominantly frugivory to omnivory/folivory (Conklin-Brittain *et al.*, 2002; Poulsen *et al.*, 2001). Insufficient protein intake as a result of degradation compels mangabeys to supplement their diet through consumption of unpalatable plant parts like unripe fruit and mature leaves (Stickler, 2004; Chalmers, 1968). Scarcity of minerals in fruit and seed also compels mangabeys to consume leaves and clay like-soils (Janson and Chapman, 1999). Frugivores are known to respond to variation in fruit abundance and nutritional quality by changing metabolism and energy balance (Knott, 1998), ranging behaviour (Remis, 1997; Olupot *et al.*, 1997), and food selection (Peres, 1994; Wrangham *et al.*, 1998). Prior to this study, none of these responses had been established in mangabeys inhabiting forest reserves within Mabira and Lwamunda forest reserves.

Increased human population growth and conversion of forest habitats into agricultural land, (especially in Lwamunda) have resulted in greater proximity between humans and nonhuman primates. Consequently, there has been increased competition between the two kinds of primates for the declining natural resource. On the other hand, nonhuman primates have become more familiar to cultivated foods because of their superior nutritional content and properties. These two factors have induced crop-raiding (Hockings *et al.*, 2009) at the interface between the forest and farming communities.

Forest reserves surrounded by human communities are usually encroached for agricultural purposes. Proximity of gardens with domesticated crops to forest fauna and particularly primates is usually an enticement for crop-raiding (Strum, 2010; Hill, 2000) by forest fauna in response to reduced food availability within the forest environment (Naughton-Treves *et al.*, 1998; Tweheyo *et al.*, 2005). According to Rode *et al.* (2006) mineral nutrition was the likely driving factor influencing crop-raiding behaviour among some forest fauna and yet Saj *et al.* (2003) and Pienkowski *et al.* (1998) observed that in some incidences it was the type of crops grown and preventative measures used that influenced susceptibility to crop-raiding.

2.7 Mangabey conservation status

There are six species of mangabeys in East African forests with different conservation status. According to Oates *et al.* (2008), *L. albigena* is listed as "Least Concern" by International Union for Conservation of Nature (IUCN) and it remains a relatively widespread and common species. The conservation status of *L.ugandae* is yet to be determined. However, the Convention on International Trade in Endangered Species (CITES) of Wild Fauna and Flora has enlisted all mangabeys as threatened by habitat loss due to logging and agricultural activities. In addition, mangabeys are also hunted for bush meat especially in West and Central Africa (Davis 2002) resulting in population decline. The most endangered species is the Tana River Mangabey (*C. galeritus*) of Kenya (Kinnaird and O'brien, 1991) with status 1 on the CITES list, where only 1,200 are left in their narrow habitat of 60 km along the Tana River. They are threatened by deforestation, hydroelectric dam and irrigation projects (Hamerlynk *et al.*, 2012). With continued habitat alteration in M&L forest reserves, Ugandan Mangabey may also become an endangered species. Its status as a flagship species for conservation of its habitat will be enhanced.

2.8 Mangabey social group and home range

Mangabeys are arboreal primates that live in multimale/multifemale social groups of about 14 individuals (Waser, 1974) but sometimes they number up to 20 (Chalmers, 1968). The group is made up of several females with one or more adult males that may

associate with the group. Most Mangabey species are peaceful and rarely display dominance behaviour. As they forage, the group may break up into smaller groups depending on food availability. When food is plentiful, groups may merge into large temporary associations of up to 50 individuals (Waser, 1974). All Mangabey species associate freely with other primates especially guenons. They are found in a wide range of dense forest habitats like rainforests, mangroves, swamp forests and sometimes agricultural areas (Chalmers, 1968). They are rarely found in areas far removed from water sources (Nowak, 1999). In the context of Uganda, the population density of mangabeys in Bujuko forest reserve, which included the present Lwamunda forest reserve, was about 124 per km^2 in the late 1960s (Chalmers, 1968). However, due to increased demand for agricultural land and forest products from the Mabira and Lwamunda forest reserves (NEMA, 2006), their population density has declined drastically due to habitat alteration.

2.9 Roles of mangabeys in forest environments

Mangabeys like other primates play an important role in tropical forests as seed dispersers (Kimuyu *et al.*, 2012; Janson and Chapman, 1999; Waser, 1975) because they consume a wide range of fruits (Chapman, 1995; Garber and Lambert, 1998; Chapman and Onderdonk, 1998). In addition, their feeding and foraging habits inadvertently provides food for other organisms in the food web (Horn, 1987a) thus preservation of biodiversity through prey-predator relationships (Kingdon, 1974). Mangabeys also take part in many multi-species associations among *Cercopithecus* species such as *C. ascanius* or redtail monkeys and *C. Wolfi*. Forming associations with other *Cercopithecus* species appear to reduce predation and increase foraging success. In some people's cultures, mangabeys are utilized as an important protein source (food) for people living at the forest-agriculture interface (Davis, 2002).

2.10 Habitat disturbance in relation to Uganda Mangabey populations

Essentially, forest disturbance or alteration refers to inability of a forest to perform its cardinal roles of maintaining soil fertility and moist climate, soil erosion prevention, provision of reliable water supply and overall environmental protection (Hamilton, 1984;

Kayanja and Byarugaba, 2001). Once this happens, the impacts are reflected in the level of abundance and quality of forest fauna and flora. Specifically, forest disturbance contributes to habitat loss with consequential negative impacts on biodiversity, water cycling and rainfall patterns (Fearnside, 2005).

In Uganda, the greatest direct impact of forest loss has been the reduction in the quality, quantity and connectivity of natural habitats of forest fauna (Hamilton, 1984). Forest alterations in Uganda has been largely driven by human population growth, inequitable land, income distribution and development policies (Winterbottom and Eilu, 2006). These factors have led to rapid conversion of forested land for agriculture to increase food production in order to meet the demands of an incessant human population increase (Kayanja and Byarugaba, 2001). Despite the high incidence of disease, including HIV/AIDS, Uganda's population growth rate of 3.2% per year (UBOS, 2014) is almost three times the average world population growth rate of 1.3%. This translates into a human density estimate of 102 people/km^2 compared to the world's average of 42 people/km^2. In 2014 population census, Buikwe district where Mabira forest reserve is located had a population density of 345.1inhabitants /km^2 and Mpigi district where Lwamunda belongs had increased from 141.5 inhabitants /km^2 in 2006 (Banana *et al.*, 2007) to 208.2 inhabitants /km^2 in 2014 (UBOS, *unpublished data*). Both districts are some of the most densely populated districts in the country. Considering that over 84% of Ugandans live in rural areas (UBOS, 2012), supplies of firewood and forestry products for daily use exerts immense pressure on forest resources.

According to NEMA's 2004/5 State of Environment Report (NEMA, 2006), the human population at the forest interface had equally increased substantially in the last three decades. This increase is proportionally related to increase in the level of forest encroachment for agricultural purposes, industrial inputs and human settlements. Compared to 5 centuries ago, when 43% of the country was covered by closed forest (Grove, 1998), but by 1900, the per capita forest cover had fallen to about 12.5% (Obua *et al.*, 2010; Banana *et al.* 2007) and in 2014 it had declined to probably less than 2% (NaFORRI, *unpublished data*). In other words, 95% of the forest area was lost over the period of 500 years but according to Hamilton (1984) two thirds were lost in the last 20th

Century. Grove (1998) had predicted that only 4. 000 km^2 of the forest cover would remain by then. Based on habitat change from 1990-1995, the deforestation rate in Uganda has been estimated at 55,000 ha per year although other estimates push the figure to between 1.1% and 3.15% per year (Winterbottom and Eilu, 2006). In 1992, the Uganda National Environmental Action Plan (NEAP) estimated that deforestation in Uganda was occurring at a rate of 500 km^2 per year. Banana and Gombya-Ssembajjwe. (2000) quoting FAO report put it at 650 km^2 per year and NEMA (2010) reported an annual rate decline of 1.86 %. Ditiro *et al.* (2008) also reported a steady decline of forest cover at a rate of 55,000 ha/year. However, with the current rate loss estimate of 200 km^2 per year (Adrua, *unpublished data*), the forest cover may be currently far less than 2,000 km^2.

According to the National Biomass Study (NBSP, 1995), approximately 25 million tons of wood were consumed annually which translated to about 1.1 ton per capita per year. Most of the wood is used as household firewood (65%), charcoal (16%) and commercial / industrial firewood (14%) for brick burning and/or in bakeries. The study also projected that per capita forest area will decline from 0.3 hectare in 1991 to 0.1 hectare in 2025 (Fig. 2.2) in the absence of concerted efforts to invest in forestry and /or implementation of sustainable management strategies.

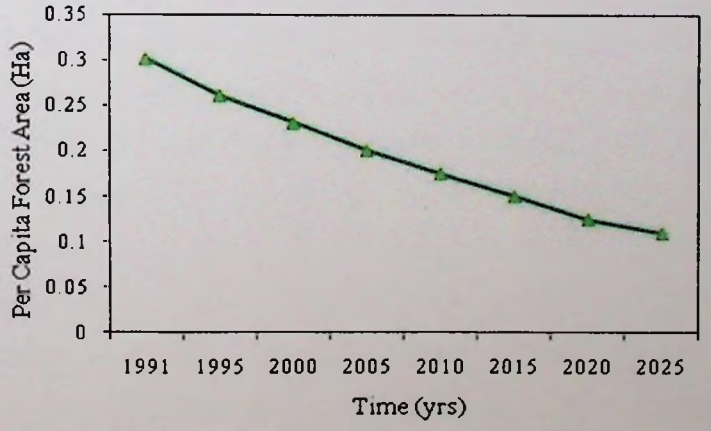


Figure 2.2 Projected per capita forest area for Uganda. (*Adapted*: Winterbottom and Eilu, 2006)

Failure to conserve the national forest cover will affect the seasonal weather patterns and

it will definitely contribute to loss of habitat for M&L forest fauna including mangabeys. Primates are known to be more sensitive to habitat disturbances (Olupot, 2000) than other forest fauna with the exception of butterflies (Akite, 2008) and birds Plumptre *et al.*, 2001). Several studies (Martínez-Mota *et al.*, 2007; Worman and Chapman, 2005; Poulsen *et al.*, 2001; Olupot, 2000; Chapman and Lambert, 2000; Medley, 1993) have been conducted to determine the magnitude, mode and variations of sensitivity of mangabeys to forest degradation.

2.11 Forest alterations in relation to Mangabey ecology

Considering that forests provide a suitable habitat for various forms of fauna including primates, their disturbance by logging or conversion into agricultural land has multifaceted consequences on the survival of primates and other forest fauna. Deforestation disrupts seed dispersal (Clark *et al.*, 2001), reduces resource abundance, diversity and forest tree densities (Stickler, 2004). The severity of the disturbance has varying implications for different fauna. In the case of primates, different species respond to habitat changes differently. In most cases, primates are forced to shift to another habitat in search of food. Most authors single out habitat loss as the principal outcome of forest disturbance (Mbora and McPeek, 2009; Fearnside, 2005; Kayanja and Byarugaba, 2001 Olupot, 1999; Johns and Skorupa, 1987).

The inter-related consequences of forest disturbance on the mangabeys also include habitat loss (Olupot, 1999; Stickler and Chapman, *unpublished data*), increased travel costs (Olupot, 1999), significant reduced food availability in terms of quantity and quality (Worman and Chapman, 2005) dietary shifts (Hemingway and Bynum, 2005; Jordano, 2000; Waser, 1975) and nutritional trade-off (Schaefer *et al.*, 2003). Food quality is known to affect inter-birth intervals, mean age of first conception, lifetime fitness, infant survival and ultimately population size (Rode *et al.*, 2006). According to Olupot *et al.* (1997) and Waser (1975), food availability which is a function of habitat degradation or seasonality, influences Mangabey ranging patterns. Besides, Kasenene (1987) asserts that logging lowers tree densities which in turn lessen food availability for primates. Homewood (1978) also observed that foraging increased when food was scarce, as did the total distance travelled and area searched for food. With prolonged habitat

disturbance, Mangabey populations tended to decline (Chapman and Lambert, 2000). The restriction imposed by deforestation, limits their access to other available food resources or suitable habitats (Cannon and Leighton, 1994; Putz *et al.*, 2001). Generally, environmental degradation as a result of logging, lessens productivity of remaining trees as they fruit less and become nutritionally poor (Stickler, 2004).

Several studies have speculated on inter-related factors which have ostensibly contributed to population declines. Milton (1981) cited increased risk to predation. Chapman *et al.* (2007) identified risk to parasitism and disease while Worman and Chapman (2005) observed a decline in food availability and quality which in turn led to extension of home range. Lee and Priston (2005) cited conflicts between humans and non-human primates over habitats. According to Freeland (1979) and Olupot (1999), foraging over large expanses of home range increases travel costs which in turn contributes to the onset of stress. When a primate is stressed its body systems succumb to parasitism and disease (Mbora and McPeek, 2009; Chapman *et al.*, 2005). Once stress sets in, the body condition deteriorates and the nutritional status declines accordingly. Ultimately, it may lead to local population extinction (Martínez-Mota *et al.*, 2007).

In a comparative study spanning several years (Chapman *et al.*, 2000), observed that among the five primates studied in Kibale National Park, 4 of them exhibited population declines while black and white colobus monkeys showed population increase. The population declines were partly attributed to food availability which has salient bearing on primate nutrition. In that with incessant tree felling, tree densities decline which results into large sized and number of gaps within a given forest (Skorupa, 1988). Foraging in such habitats inevitably increases travel costs for primates which certainly impinges on their nutritional status. Undernourishment of the primate tends to have a bearing on its reproduction and ultimately on its population densities.

2.12 Extrinsic factors influencing mangabey nutrition and conservation

Forests are the natural habitats of primates including mangabeys. Nonetheless, some extrinsic factors may contribute to the loss of these habitats. NEMA (2006) listed six factors that have contributed to forest cover decline. They included policy deficiencies, weak institutional structures at local level, high rate of human population growth and

migration, poverty and lack of alternative livelihood options. With regard to Mabira and Lwamunda forest reserves, forest clearance for agro-economic purposes exacerbated by rural poverty among the surrounding communities (MWLE, 2002; Turyahabwe and Banana, 2008) has contributed immensely to habitat loss. Both forest reserves are currently surrounded by a high human population density. These six factors have inadvertently influenced food and nutritional security of mangabeys inhabiting M&L forest reserves. With deficient policies, weak institutional structures at grassroots and biting poverty in Uganda, conservation of mangabeys may not be a possibility at the moment or in the near future (Isabirye-Basuta and Lwanga, 2008).

2.13 Characteristic physical features of mangabeys in relation to food acquisition

Mangabeys have large cheek pouches where food material is temporarily stored prior to processing (Waser, 1977) and simple stomachs typical of frugivores (Davis, 2002). The molars are quadrate, relatively long and bilophodont while incisors are thick and powerful compared to other related species (Flannery, 2000) and used for cracking hard fruit, nuts and seeds (Vogel *et al.*, 2014; Marshall and Wrangham, 2007; Lambert *et al.*, 2004; Chalmers, 1968). They are extremely agile climbers and excellent jumpers which allows them to pick fruit or seed from thin branches at the peripheral parts of the tree or underside of large branches (Davis, 2002: Waser, 1977). Unlike the red-capped and crested mangabeys that spend a lot of time foraging on the ground, the Grey-cheeked mangabeys stay mainly in the middle and upper tree canopies and rarely descend to the forest floor (Horn, 1987). However, when the habitat is altered, *L. ugandae* is compelled to forage on the forest floor where the quality of food may be poor and the risk of being killed by humans or other natural enemies may be high.

2.14 Mangabey feeding habits, food selection, availability and nutrition

Although mangabeys are predominatly frugivorous, they exhibit omnivorous feeding pattern to meet their nutritional requirements. In arid or deforested regions with unpredictable food distribution, some primates change their feeding patterns to adapt to the prevailing environment (Ganzhorn, 1986). When any of the basic componets (carbohydrates, proteins, fats, minerals and vitamins) become limiting in the available

food resources, mangabeys usually supplement their frugivorous diet with an item known to have adequate amounts of the desired component. For example, protein inadequacy in a Mangabey diet compels them to consume young leaves, flowers, (Olupot *et al.*, 1997) invetebrates and anthropods (Waser, 1975) while lack of minerals drives them to salt links (Hanya and Chapman, 2013).

2.14.1 Feeding habits

Although mangabeys may be classified as omnivorous, they are primarily frugivorous. Janson and Chapman (1999) categorized their wide range of food choice into three major components namely insect, fruit and leaves. They are quite catholic in their feeding habits that range from eating orchids to snakes (Oates *et al.*, 1980; Waser, 1977). The type and availability of food item influences their feeding habits (Janson and Chapman, 1999). However, during food scarcity mangabeys tend to consume other food items for example, young leaves (Baranga, 1984), flower buds (Olupot *et al.* (1997) and Waser (1975) other animals (Janson and Chapman, 1999). Many other primates are known to choose foods from more than one category of food resources to get the balanced essential nutrients and required energy (Milton, 1984) on a daily basis. Most primates prefer a protein and carbohydrate rich diet with minimal fibre content (Janson and Chapman, 1999). Frugivores may be limited by food quality since fruits, unlike leaves, are typically low in protein and minerals (Rode *et al.*, 2006). However, in times of food scarcity, nutrient trade-off among frugivores is quite common (Schaefer *et al.*, 2003). It is possible that mangabeys in both Mabira and Lwamunda forest reserves have similar feeding behaviour.

Mangabeys exhibit diurnal feeding patterns alternated with resting periods or other activities, which appear to be dictated by the distribution and availability of food (Waser, 1977). The feeding sequence includes reaching for, picking, manipulating or placing a food item in the mouth. The agility of their limbs allows them to hang upside down. They rip bark from certain tree species and break off dead branches to reach the insects and spiders that are hiding in the crevices. All mangabeys prefer ripe fruits but during periods of scarcity unripe fruit is also consumed. Generally, fruits form the bulk of their diet

constituting about 59% (Olupot *et al.*, 1997; Waser, 1975). When fleshy fruit are scarce, they often eat a lot of nectar (Chalmers, 1968). Usually this diet is supplemented by other vegetation and animal protein from invertebrates found on broad leaves of epiphytic plants that grow on many of the big branches high in the canopy (Davis, 2002).

2.14.2 Food selection

Primates generally select a diet that is rich in protein, carbohydrates and low in fibre (Janson and Chapman, 1999). Food choice has been correlated with digestive morphology of primates (Milton, 1981). Other authors have attributed choice to nutrient content (Matsumoto-Oda and Hayashi, 1999; Wrangham *et al.*, 1993; Oates *et al.*, 1980; Waser, 1977). Like other primates, mangabeys appear to have a wide range of food choice that may be typically divided into three major categories namely: insect, fruit and leaves (Janson and Chapman, 1999). In the first major study of this species, Chalmers (1968) observed that in central Uganda, mangabeys ate fruits, shoots, buds and flowers. However, there was specificity in that only 6 species (*Maesopsis eminii*, *Treculia africana*, *Phoenix reclinata* and several *Ficus* species) were utilized for fruits, (*Pygeum africanum, Sapium allipticum, Celtis durandii, Albizia grandebracteata, Pyenanthus angolensis* and *Ficus* species for shoots and *Sapium ellipticum* for flowers. In Bwamba forest reserve located in western Uganda, Waser (1977) noted that mangabeys ate seeds or fruits of *Pancovia turbinata*, *Plerandrus rosa* and young leaves of *Ficus* species and *Monodora* as well as *Crematogaster* ants. In his previous publication Waser (1975), had listed over 50 species of trees and parts that were utilized as food. The choice of fruit ranged from the tiny capsules of *Acanthopale* spp to the basket ball-sized fruits of *Monodora myristica*. Most of the fruits were figs or drupes of medium size diameter (0.5 –2.0 cm) with a fleshy pericarp surrounding the seed.

There are several factors that influence food selection among primates. They include position of fruit and taste (Chalmers, 1968), energetics (Chivers, 1986), availability (Olupot *et al.*, 1997), availability of other foods and seasonality Ganzhorn (1986). Presence of undesirable secondary compounds (Danish *et al.*, 2006) is also a food selection factor. Owing to the evolutionary purpose of attracting seed dispersers, fruit

pulp are generally easier to find, easier to ingest and digest than other types of food. However, frugivores have to cope with the fruit defensive mechanisms which include restrictive presentation or morphology or taste/ defensive chemicals and location of ripe fruit in the canopy that are often sparsely distributed in tropical forests (Janson and Chapman, 1999).

Selection of fruit parts based on taste seems to be inherent among primates. Frugivores select fruit pulps or accasional seed because of sweet taste. Fruits vary widely in their taste as exemplied by *Millettia laurentii* seeds which are mildly bitter while fruits of *Diospyros abyssinica / Celtis durandii* are intensely bitter and leave a burning aftertaste. However, in order of preference, mangabeys prefer fruits of *Diospyros abyssinica* which they eat at all stages of ripeness even when very small and secondly ripe *Celtis durandii* when in abundance (Stickler, 2004).

According to Ganzhorn (1986), presence of secondary metabolites especially tannins and alkaloids determines food selection among primates. Foods with high levels of secondary metabolites are rejected while foods with low levels are consumed (Chievers and Raemaekers, 1986). The undergrowth in degraded and regenerating forests usually consists of herbaceous plants which contain high levels of toxic secondary compounds like phenols. These secondary compounds protect the plant from pests including herbivores and frugivores. They are generally toxic to organisms as they interfere with enzyme systems, act as allergens or blood anticoagulants and therefore detrimental to frugivores food digestion system (Rattan, 2010). Phenols and carboxylic acids enhance toxicity which reduces palatability of the fruit. In a disturbed habitat, there is a tendency for some potentially edible plant food materials to exhibit high levels of secondary compounds depending on its physiological purpose and level of development. Secondary compounds are deterrent mechanisms plants employ to fend off pests, folivorous and frugivorous consumers (Howe and Jander, 2008; Bennett and Wallsgrove, 1994) prior to the intended use. However, at times primates can consumes parts with high levels of secondary compunds because they also contain high protein content. For example, Chievers and Raemaekers (1986) observed that *Lemur fulvus* ate leaves of clover (*Trifolium repens*) with an alkaloid content of 4.8µg but had high protein content thus

overriding the effect of alkaloids. Consumption of leaves, fruits, pith, barks laden with high levels of secondary compounds is less nutritive and requires specialized gastrointestinal adaptation to facilitate food digestion for optimal nutrient benefits. Presence of high level of secondary compounds like tannins in seed or leaf (Wrangham *et al.*, 1993) may require detoxification process which is not cost-effective among mangabeys (Nabihamba, 1996).

2.14.3 Food availability

Food availability and quality varies with seasons (Worman and Chapman, 2005) which induce differences in diet composition, activity budgets and travel patterns among primates (Kaplin *et al.*, 1998; Poulsen *et al.*, 2001). Habitat alteration and especially logging leads to reduction in potential food resources, availability and tree densities, which has a bearing on group size, food consumption rates and travel costs of primates (Chapman, 1988). Eventually, it may cause a change in diet and/or balanced food intake, which may have disastrous consequences on the already declining animal populations especially among lactating mothers and infants (Stickler, 2004). The location in the canopy may also influence food availability (Chalmers, 1968). According to Chalmers (*Ibid*) food (fruit and shoots) was more available at the tops of trees than it was at lower levels hence mangabeys' preference for upper canopies (Horn, 1987). Due to intense inter-specific competition, most fruits are eaten whilst still unripe or barely so. For example, *Cyphomandra belaceae* "bush tomato" relished by both humans and non-human primates is eaten while still green (Stickler, 2004). Conklin and Wrangham (1994) reported that figs are consumed by a variety of mammals and birds. As such, the quantities of fruit available for each frugivore will depend on their feeding behaviour. It also appears that the geographical location, type and availability of fruit trees influence Mangabey preference. Whereas *Diospyros abyssinica* was preferred in Kanyawara, it was ranked 23 among the 32 frequently used fruit trees in Ngogo area where *Uvariopsis congensis* was most preferred (Waser, 1977).

Most tropical forests exhibit seasonal variation in food availability. Olupot *et al.* (1997) noted that fruit abundance was higher during the wet season than during the dry season.

As a result, fruit scarcity forced mangabeys to travel longer distances in search of food. Freeland (1980) concluded that during the wet season, fruit availability influenced range use such that mangabeys hardly left an area with high fruit density. The author partly attributed this response to the rainwater that washed off faecal contamination on leaves and other vegetation. On the contrary, during the dry weather, the ranging patterns were highly influenced by faecal contamination on vegetation and the associated risk of parasite infection forced the mangabeys to abandon areas of high fruit density.

2.14.4 Food nutrition

Nutrition is a vital aspect of primate life and a major determinant in the selection of a habitat. So whatever changes that may take place in the selected habitat, they have dietary implications for the non-human primate inhabitants (Olupot *et al.*, 1994; Hamilton, 1984; Waser, 1977). The type and composition of food resources within the home range augmented by their quality and availability also contribute to habitat selection. The nutritive value gained from a particular food resource varies with season, locality and in different parts of the same plant. In a study conducted in Kibale National Park, Houle *et al.* (2007) found that fruit quantity and quality varied vertically within tree canopies. The fruit production was 3-4 times more in the upper than in lower canopies while the nutritional quality was 41.9% more sugar, 8.4% more crude proteins, and 1.8 times less of the potentially toxic saponin than lower crown ripe fruit of *Diospyros abyssinica*. Frugivores are known to respond to variation in fruit abundance and nutritional quality by changing metabolism and energy balance (Knott, 1998), ranging behaviour (Remis, 1997; Olupot *et al.*, 1997), and food selection (Peres, 1994; Wrangham *et al.*, 1998).

In a forest environment, there are several factors that may determine the nutritional requirements of primates including mangabeys. They include habitat disturbance (Olupot, 1999) seasonality (Poulsen *et al.*, 2001) competition (Struhsaker, 1997), type of food ingested (Wrangham *et al.*, 1993), level of leaf or fruit maturity (Stickler, 2004; Baranga, 1983) and location in the canopy (Houle *et al.*, 2007). In Kibale national park, Olupot (1999) reported that habitat disturbance had direct impacts on the nutritional ecology of mangabeys while Chapman (1988) specifically noted that it reduced potential food

resources and availability. As a result, group size reduced considerably and composition changed (Freeland, 1979). It is probable that all these factors may be at play in both Mabira and Lwamunda forest reserves and yet their interactions with regard to Mangabey nutrition have not been established.

Most frugivores prefer ripe fruit pulp because it provides readily available energy (Jordan, 2000; Chivers and Raemaekers, 1986) to meet their activity budgets (Wrangham *et al.*, 1993). As such, pulp is a superior source of calories which explains the high number of interspecific competitors for pulp including squirrels, bats, birds and other primates (Waser, 1977). In the absence of ripe fruit, there is a dietary shift to unripe fruit; known to have high levels of condensed tannins and fibre (Poulsen *et al.*, 2001). These two fruit constituents compromise the nutrient intake of primates in terms of quantity and quality. Although the nutritional requirements of primates and their energetics have not been exhaustively investigated (Milton, 2003; Chivers, 1986), there is a traditional view that fruits in tropical forests tend to offer better nutrient options than leaves (Danish *et al.*, 2006). This is because fruits tend to provide high quality and easily digestible forms of carbohydrates but low in fibres and secondary compounds. Fruit pulp has high concentration of water-soluble carbohydrates, complex carbohydrates and minerals compared to seed which has high levels of condensed tannins, lipid and fibre (Wrangham *et al.*, 1993). The protein content of pulp and seed of the same tree does not vary as much as between species (Conklin and Wrangham, 1994).

However, in the event of insufficient available protein, mangabeys like other frugivorious primates are compelled to supplement their protein intake through consumption of other animals or leaves (Janson and Chapman, 1999). Scarcity of minerals in fruit and seed compels mangabeys to consume leaves and clay-like soils (Janson and Chapman, 1999). The consumption of leaves is limited to young ones because of their high protein; low fibre and low toxic secondary compounds (Baranga, 1983). Generally, mature leaves offer more protein, higher levels of fibre, little energy and they are likely to have undesirable secondary compounds. Almost all authors cited in this study have acknowledged the significance of fruit and seed in the diet of mangabeys as opposed to leaves. Waser (1977) noted that a large proportion of Mangabey feeding observations

involved the advanced stages of reproductive rather than vegetative plant parts for their nutritional requirements. Although seeds are often lumped together with fruit when considering primate diet, they are a distinct category of food item. This is because they contain a complete set of nutritional components required by the germinating seed and subsequent growing seedling (Parolin *et al.*, 2010). Typically, seeds contain high amounts of fats, proteins and minerals especially phosphorous, which is a limiting nutrient in most animal diets (Wrangham *et al.*, 1998). Certain tree species are known to have higher amounts of specific nutrient components than others. For example, minerals are scarce in most fruits but figs are known to have larger amounts of calcium than other fruit trees in the same forest (O'Brien *et al.*, 1998).

2.15 The role of importance of fall-back fruits in mangabey diet

Fallback foods are defined as resources of relatively low preference that are used seasonally when preferred foods are unavailable (Marshall, *et al.*, 2009; Marshall and Wrangham, 2007; Lambert *et al.*, 2004). Alternatively, they may be defined as foods whose use is negatively correlated with the availability of preferred foods (Conklin-Brittain *et al.*, 1998). On the other hand Furuichi *et al.* (2001) defined FBFs as those fruits that play a prominent role in sustaining animals during periods of general food scarcity. Essentially, definitions of FBFs imply that there is a distinction between preference and importance. Whereas preference is a matter of dietary choice, importance is a measure of dietary composition (Marshall and Wrangham, 2007). FBFs can be classified into two classes namely staples and fillers. The former were available all year round and may constitute up to 100% of the diet while the latter constituted < 100% and could be completely avoided for long periods of time (Marshall, *et al.*, 2009; Furuichi *et al.*, 2001). FBFs are regarded as significant components in primate diets because of their contribution to the sustainability role (Chapman *et al.*, 2012). Most primates have evolved specific masticatory and digestive adaptations to consume fallback foods when preferred foods are scarce (Porter *et al.*, 2009). Fallback foods can be categorized into nuts, seeds, fruits and root vegetables (Lucas *et al.*, 2009). Fall-back fruits (FBFs) are important in the diet of frugivores especially during periods of low food availability that is often exacerbated by climatic changes and anthropogenic activities.

When foraging for seasonal or preferred foods, primates employ different foraging patterns depending on severity of habitat disturbance (Olupot, 1999; Freeland, 1979; Waser, 1975). According to Worman and Chapman (2005) when food resources become severely compromised in terms of quantity and quality, mangabeys tend to have dietary shifts (Waser, 1975) and nutritional trade-off (Schaefer *et al.*, 2003). There are divergent dietary switches that have been observed in other primates regarding fall-back foods (Vogel *et al.*, 2009) during periods of low fruit availability. Knowledge of FBFs is necessary for evaluation of Mangabey's ability to response to food scarcity caused by anthropogenic habitat alteration (Chapman *et al.*, 2012).

Several fruits have been identified as fall-back items in the nutritional ecology of mangabeys or indeed other primates but *Ficus* species appear to be the commonest FBF (Krishnadas *et al.*, 2011; Felton *et al.*, 2010; Vogel *et al.*, 2009; Kagoro-Rugunda and Baranga, 2009; Naughton-Treves *et al.*, 1998). However, figs are nutritionally deficient (Wrangham *et al.*, 1993) although some species like *Ficus insipida* contains high concentrations of almost all amino acids, minerals and proteins (Wendeln *et al.*, 2000). Other food items have also been regarded as FBFs for instance; tree stem piths, seed and unripe fruit (Wrangham *et al.*, 1998), terrestrial herbaceous vegetation (THV) (Inogwabini and Matungila, 2009; Wrangham *et al.*, 1996) and fruit of *Musaga leo-errerae* (Furuichi *et al.*, 2001). According to Marshall and Wrangham (2007), FBFs tend to be foods of low preference but with high seasonal importance and tend to be eaten all year round. Essentially, there are five major characteristics of FBFs fruits. They include abundance and availability over time, hardness of the protective structures especially the seed coat, nutritional attributes and their proportion to the overall primate diet.

FBFs tend to have high abundance but spatiotemporally dispersed and thrive in patchy sized habitats (Saito 1996). They also tend to bear fruit all year round as exemplified by many fig species (Marshall *et al.*, 2009; Naughton-Treves *et al.*, 1998; Wrangham *et al.*, 1996; Milton *et al.*, 1982). They bear large quantities of fruits (Chapman *et al.*, 1992) and can be found in many rainforest ecosystems as source of food for many frugivores including mangabeys. Figs were listed as one of the most important 50 species utilized as food by mangabeys in Central Uganda four and a half decades ago (Waser, 1975).

Most FBFs show distinct patterns of availability; particularly in tropical rainforests (Krishnadas *et al.*, 2011; Milton *et al.*, 2005). The seasonal fluctuations of preferred fruits obtaining therein create periods of resource scarcity for frugivores and readily available FBFs assume priority significance in their diets. Habitat alteration has a direct effect on food availability which compels mangabeys to consume FBFs in the absence of preferred fruits. Apart from human population increases and resultant encroachment for agricultural purposes, there are other contributory factors that may lower food availability. They include bushfires, poor agricultural practices, mining/drilling, construction, skewed policies and legislation pertaining to the forestry sector and civil strife (Hamilton, 1984). These and other related factors synergistically impose quantitative as well as qualitative changes in food nutrition and availability with direct effect on forest fauna populations. Primates are known to be more sensitive to habitat disturbances (Olupot, 2000) than other forest fauna with the exception of butterflies (Akite, 2008) and birds (Plumptre *et al.*, 2001).

Most FBFs are characterized by hardness of fruit structures especially the lignified exocarp or endocarp which plays the protective role against fungi, bacteria and other environmental stress elements (Seidel *et al.*, 2010). To access the desired edible part, frugivores have to devise processing techniques to overcome the hardness. For example, Hohmann (2009) observed that chimpanzees used stones to crack-open the hard nuts. According to Kinzey and Norconk (1990), hardness is an important physical fruit and seed property which determines food choice, processing method and influences feeding behaviour among primates. Besides dietary choice, hardness of some FBFs could have also contributed to the evolutionary development of *L. albigena -ugandae* thick enamel (Lambert *et al.*, 2004) and in great apes (Constantino *et al.*, 2009).

During periods of food scarcity brought about by seasonality and degradation, mangabeys tend to consume whatever is available including food items known to have high levels of condensed tannins and fibre (Poulsen *et al.*, 2001). They also tend to forage over a large area in the quest to meet their energetic and nutritional requirements (Chapman and Chapman, 2000). In the process, they encounter intra and interspecific stiff competition

within a home range which forces low ranking individuals to switch to inferior low quality food items (Saito, 1996). Such inferior low quality food items were regarded as FBFs according to Marshall and Wrangham (2007).

2.16 Impact of plant secondary compounds on primate feeding behaviour

Primates are known to select specific plant or insect species and parts based on their nutrient and secondary compound content variations (Glander, 1982). Most plant secondary compounds or metabolites can be classified into three major groups: terpenoids, alkaloids and phenolic compounds (Croteau *et al.*, 2000). Whereas, terpenoids are toxins and deterrents to herbivores, they are attractants to dispersers. Alkaloids on the other hand are synthesized principally from amino acids to protect plants from a variety of herbivores. Phenolic compounds consist of tannins, lignins, flavonoids and some simple phenolic compounds used as defences against herbivores and pathogens (Harborne, 2014). In addition, lignins strengthen cell walls mechanically, and many flavonoid pigments are important attractants for pollinators and seed dispersers. Conklin-Brittain *et al.* (1998), describes secondary compounds as ante-feedants with antinutritional properties.

There are over eight thousand different phenolic compounds (Balasundram *et al.*, 2006) but tannins were singled out in the present study because they are the most abundant secondary metabolites of plants (Dai and Mumper, 2010) and occur in high concentrations in the diets of cercopithecines than other primates (Milton, 1984). Essentially, tannins are water-soluble and complex polyphenolic secondary metabolites (Kraus *et al.*, 2003) with anti-nutritional properties. According to Hernes and Hedges (2000), tannins are the fourth most abundant biochemical terrestrial biomass produced by vascular plant tissues after cellulose, hemicellulose and lignin. Owing to their complex chemical structure, synthesis of tannin molecules by the plant is energetically costly and therefore their production can only be counterbalanced by the plants investing less in other production (Coley, 1986; Sagers and Coley, 1995) depending on their significance in the forest ecosystems. Phenolics are known to be toxic to some insects but harmless to vertebrates (Harbone, 1988) and residual saponnins may disrupt fungal cells without affecting the would-be-seed dispersers (Roddick and Rijnenberg, 1987). Foraging

primates encounter a diverse range of plant secondary metabolites (PSMs) in the majority of foods consumed including tannins. PSMs play a significant role in diet selection of mammalian herbivores (Berger *et al.*, 1977; Foley *et al.*, 1999; Reichardt *et al.*, 1990). The complete avoidance of PSMs in the diet is not likely to be a realistic strategy especially during periods of food scarcity. The vast majority of PSMs that primates ingest are not so acutely toxic that a single bite would be lethal or severely detrimental, but large amounts of even low potency compounds can be harmful. Consequently, mangabeys must have mechanisms that allow them to detect and regulate their intake of PSMs to ensure that low potency toxins do not cause damage. Understanding the sort of mechanisms that mangabeys use to regulate toxin intake augments the criteria used for their food selection and broader feeding ecology. One of the strategies applied to regulate toxin intake is the development of salivary proline-rich proteins (PRPs). When the Mangabey ingests foods with tannins, PRPs forms complexes with tannins which prevent the interaction of tannins with other biological compounds and absorption from the intestinal canal. The consequences of binding tannins with salivary proteins are two-fold. Tannins are inactivated as toxins, enabling the animal to eat tannin-rich browse and permeability of glycoprotein and cytochrome P4503A regulated absorption of PSMs by gut cells (Sorensen and Dearing, 2003; Sorensen *et al.*, 2004). Another mechanism used by mangabeys to regulate PSMs intake is by trade-offs between macro- nutrients and PSMs.

Pre-ingestive mechanisms where taste and trigeminal stimulation are applied can also be used to regulate intake of PSMs. Foods can be repellent to animals by irritating trigeminal nerves in the mouth and causing a burning sensation. If it is too intense, food consumption is reduced. Animals use trigeminal feedback to regulate their intakes of these irritant PSMs for example, Jakubas *et al.* (1993) showed that coniferyl benzoate (CB) a secondary metabolite, was a trigeminal irritant in birds and that ruffed grouse could regulate their intake of CB in aspen. Compounds that are intensely bitter like phenolic glycoside may also be effective deterrents at high concentrations and lead to thresholds in the ingestion of the PSM and can constrain feeding rates of mammalian herbivores. PSMs can be eliminated from the body by biotransformation of lipophilic

PSMs (Boyle *et al.*, 2000) prior to excretion through urine. Terrestrial animals have evolved a powerful suite of biotransformation enzymes to convert lipophilic PSMs into more polar metabolites readily excreted in urine or bile. These enzymes are considered to have evolved in part as a response to dietary plant toxins (Gonzalez and Gelboin, 1994; Gonzalez and Nebert, 1990).

2.17 Dietary fruit selection in relation to nutrition

The concept of linking nutritional aspects to ecology of primates and particularly mangabeys is a recent development. Many studies have been conducted on the ecology, feeding, seed dispersal and many other aspects but the present study casts the net wider to underscore the nutritional criteria used by mangabeys to select fruit/fruit parts for consumption. The present study seeks to answer pertinent questions regarding nutritional ecology of frugivores with emphasis on mangabeys. To what extent does relative fruit abundance and availability influence dietary selection? How about the influence of fruit quality (macro-nutrient and tannins) on fruit selection? In view of the declining food resources attributed to anthropogenic or human activities within habitat, how do mangabeys respond to the changing habitat to meet their dietary requirements? What is the role of fall-back fruits in the Mangabey diet in the absence of preferred fruits?

2.18 References

Akite, P. (2008). The effects of anthropogenic disturbances on the diversity and composition of the butterfly fauna of sites in the Sango Bay and Iriri areas, Uganda: Implications for conservation. *African Journal of Ecology* **46**(1), 3–13.

Alpert, P. (1996). Integrated conservation and developmental projects. Examples from Africa. *BioScience*, **46** (11), 845-855.

Balasundram, N., Sundram, K. & Samman, S. (2006). Phenolic compounds in plants and agri-industrial by-products: Antioxidant activity, occurrence, and potential uses. *Food chemistry* **99**(1), 191-203.

Banana, A.Y., Vogt, N.D., Bahati, J. & Gombya-Ssembajjwe, W. (2007). Decentralized governance and ecological health: why local institutions fail to moderate

deforestation in Mpigi district of Uganda. *Academic Journals Scientific Research and Essay* **2**(10), 434-445.

Banana, A.Y. & Gombya-Ssembajjwe, W. (2000). Successful Forest Management: The importance of security of tenure and rule enforcement in Ugandan forests. In Gibson, C.C., McKean, M.A. and Ostrom, E. (Eds), *People and Forests: Communities, Institutions, and Governance* (pp. 87-97), 1 Review. The MIT Press, Science.

Baranga, D. (2007). Observations on resource use in Mabira forest reserve, Uganda. *African Journal of Ecology*, 45(s1), 2-6.

Baranga, D. (2004). Red-tail monkey groups in forest patches outside the protected area system in the 'Kampala area'. *African Journal of Ecology* 42(s1), 78-83.

Baranga, D. (1983). Changes in chemical composition of food parts in the diet of colobus monkeys. *Ecology,* **64**(4), 668-673.

Bennett, R.N. & Wallsgrove, R.M. (1994), Secondary metabolites in plant defence mechanisms. *New Phytologist*, **127**(4): 617-633.

Berger, P.J., Sanders, E.H., Gardner, P.D. & Negus, N.C. (1977). Phenolic plant compounds functioning as reproductive inhibitors in *Microtus montanus*. *Science*, **195**(4278), 575-577.

Boyle, R., McLean, S., Foley, W.J., Moore, B.D., Davies, N.W. & Brandon, S. (2000). Fate of the dietary terpene, p-cymene, in the male koala. *Journal of Chemical Ecology* **26**(5), 1095-1111.

Cannon, C.H. & Leighton, M. (1994). Comparative locomotor ecology of gibbons and macaques: selection of canopy elements of crossing gaps. *American Journal of physical Anthropology*, **93**(4), 505-524.

Chalmers, N.R. (1968). The visual and vocal communication of free inhabiting Mangabeys in Uganda. *Folia Primatologica,* **9**(3-4), 258-280.

Chapman, C.A., Rothman, J.M. & Lambert, J.E. (2012). Food as a selective force in primates. In Mitani, J.C., Call, J., Kappeler, P.M., Palombit, R.A. and Silk, J.B. (Eds), *The Evolution of Primate Societies,* (pp. 149-168). University of Chicago Press.

Chapman, C.A., Saj, T.L. & Snaith, T.V. (2007). Temporal dynamics of nutrition, parasitism, and stress in colobus monkeys: Implications for population regulation and conservation. *American Journal of Physical Anthropology* **134**(2), 240–250.

Chapman, C.A., Chapman, L.J., Rode, K.D., Hauck, E.M. & McDowell, L.R. (2003). Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal of Primatology*, **24**(2), 317-333.

Chapman, C.A. & Lambert, J.E. (2000). Habitat alteration and the conservation of African primates: Case study of Kibale National Park, Uganda. *American Journal of Physical Anthropology* **50**(3), 169-185.

Chapman, C.A. & Chapman, L.J. (2000). Determinants of group size in primates: the importance of travel costs. In Boinski, S. and Garber, P.A. (Eds), *On the move: How and why animals travel in groups* (pp. 24-42). University of Chicago press.

Chapman, C. A., Balcomb, S. R., Gillespie, T. R., Skorupa, J. P., & Struhsaker, T. T. (2000). Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conservation. Biology*, **14**(1), 207-217.

Chapman, C.A., & Onderdonk, D.A. (1998). Forests without primates: primate/plant co-dependency. *American Journal of Physical Anthropology* **45**(1), 127-141.

Chapman, C.A. (1995). Primate seed dispersal: co-evolution and conservation implications. *Evolutionary Anthropology* **4**(3), 74-82.

Chapman, C.A., Chapman, L.J., Wangham, R., Hunt, K., Gebo, D. & Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica*, **24**(4), 527-531.

Chapman, C.A. (1988). Patterns of foraging and range use by three species of neotropical primates. *Primates*, **29**(1), 177-194.

Chivers, D.J. (1986). Nutrition, Diet and Feeding Adaptations. In Else, J.G. (Ed). *Primate ecology and conservation*. Selected Proceedings of the 10th Congress of the International Primatological society held in Nairobi, Kenya. July 1984.

Chivers, D.J. & Raemaekers, J.I. (1986). Natural and synthetic diets of Malayan gibbons. In Else, J.G. (Ed). *Primate ecology and conservation*. Selected Proceedings of the

10th Congress of the International Primatological society held in Nairobi, Kenya. July 1984.

Clark, C.J., Poulsen, J.R. & Parker, V.T. (2001). The role of arboreal seed dispersal groups on the seed rain of lowland tropical forest. *Biotropica*, **33**(4), 606-620.

Coley, P.D. (1986). Costs and benefits of defence by tannins in a Neotropical tree. *Oecologia*, **70**(2), 238-241.

Conklin-Brittain, N.L., Wrangham, R.W. & Smith, C.C. (2002). A two-stage model of increased dietary quality in early hominid evolution: the role of fiber. In Unger, P. and Teaford, M. (Eds). *Human Diet: Its Origin and Evolution* (pp. 61-76). Bergin & Garvey, Westport.

Conklin-Brittain, N.L., Wrangham, R.W. & Hunt, K.D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *International Journal of Primatology* **19**(6), 971-998.

Conklin, N.L. & Wrangham, R.W. (1994). The Value of Figs to a Hind-gut Fermenting Frugivore: a Nutritional analysis. *Biochemical Systematic & Ecology* **22**(2), 137-151.

Constantino, P.J., Lucas, P.W., Lee, J.J.W. & Lawn, B.R. (2009). The influence of fallback foods on great ape tooth enamel. *American Journal of Physical Anthropology*,**140**(4), 653-660.

Croteau, R., Kutchan, T.M. & Lewis, N.G. (2000). Natural products (secondary metabolites). In Buchanan, B., Gruissem, W. and Jones, R. (Eds), *Biochemistry and molecular biology of plants,* Chapter 24 (pp. 1316). American Society of Plant Physiologists.

Dai, J. & Mumper, R.J. (2010). Plant phenolics: extraction, analysis and their antioxidant and anticancer properties. *Molecules*, **15**(10), 7313-7352.

Danish, L., Chapman, C.A., Hall, M.B., Rode, K.D. & Worman, C.O. (2006). The role of sugar in diet selection in red-tails and red colobus monkeys. In Hohmann, G. Robbins, M.M. and Boesch, C. (Eds), *Feeding Ecology in Apes and Other Primates: Ecological, Physical and Behavioral Aspects*. Cambridge University Press.

Davis, S. (2002). "*Lophocebus albigena*" (On-line), Animal Diversity Web. http://animaldiversity.ummz.umich.edu/site/accounts/information/ *Lophocebus_albigena*.html. Accessed September 16, 2005

DeGabriel, J.L., Moore, B.D., Foley, W.J. & Johnson, C.N. (2009). The effects of plant defensive chemistry on nutrient availability predict reproductive success in a mammal. *Ecology*, **90**(3), 711-719.

Ditiro, G., Vedeld, P., & Gombya-Ssembajjwe, W. (2008). From forest reserve to national park: change in legal status and impacts on livelihoods and biodiversity resources, Mt. Elgon, Uganda. *NORAGRIC working paper*.

Drichi, P. (2003). National Biomass Study: Technical Report of 1996-2002. Forest Department, Ministry of Water Lands and Environment.

Fearnside P.M. (2005). Deforestation in Brazilian Amazonia: History, Rates, and Consequences. *Conservation Biology* **19**(3), 680-688.

Flannery, S. (2000). "*Lophocebus albigena*" (On-line). Primate Info Net Fact Sheets. At http://animaldiversity.ummz.umich.edu/local/redirect.php/http://www.gisbau.uniroma1.it/amd/amd004.html. Accessed September 16, 2005

Felton, A.M., Felton, A., Foley, W.J. & Lindenmayer, D.B. (2010). The role of timber tree species in the nutritional ecology of spider monkeys in a certified logging concession, Bolivia. *Forest Ecology and Management* **259**(8), 1642-1649.

Foley, W.J., Iason, G.R. & McArthur, C. (1999). Role of plant secondary metabolites in the nutritional ecology of mammalian herbivores: how far have we come in 25 years? In *vth International Symposium on the Nutrition of Herbivores* (pp. 130-209).

Freeland, W.J. (1979). Mangabey (*Cercocebus albigena*) social organization and population density in relation to food use and availability. *Folia primatology*. **32**(1-2), 108-124

Freeland, W.J. (1980). Mangabey (*Cercocebus albigena*) movement patterns in relation to food availability and faecal contamination. *Ecology.*, **61**(6), 1297-1303.

Freeland, W. J. (1979). Primate social groups as biological islands. *Ecol.* 60(4), 719-728.

Fungo, B., Eilu, G., Tweheyo, M. & Baranga, D. (2013). Forest disturbance and cropping mixtures influence crop raiding by red-tailed monkey and grey-checked

mangabey around Mabira Forest Reserve, Uganda. *Journal of Ecology and the Natural Environment* **5**(2), 14-23.

Furuichi, T., Hashimoto, C. & Tashiro, Y. (2001). Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: examination of fallback foods. *International Journal of Primatology.*, **22**(6), 929-945.

Ganzhorn, J.U. (1986). The influence of plant chemistry on food selection by *Lemur catta* and *Lemur fulvus*. In Else, J.G. (Ed), *Primate Ecology and Conservation.* Selected Proceedings of the 10th Congress of the International Primatological society held in Nairobi, Kenya. July 1984.

Garber, P.A. & Lambert, J.E. (1998). Primates as seed dispersers: ecological processes and directions for future research. *American Journal Physical Anthropology* **45**(1), 3-8.

Gibson, C. C., McKean, M. A., & Ostrom, E. (2000). Explaining deforestation: the role of local institutions. *People and forests: Communities, institutions, and governance*, 1-26.

Glander, K.E. (1982). The impact of plant secondary compounds on primate feeding behaviour. *American Journal Physical Anthropology* **25**(3) 1–18.

Gonzalez, F.J. and Gelboin, H.V. (1994). Role of human cytochromes P450 in the metabolic activation of chemical carcinogens and toxins. *Drug metabolism reviews* **26**(1-2), 165.

Gonzalez, F.J. and Nebert, D.W. (1990). Evolution of the P450 gene super family: animal-plant 'warfare', molecular drive and human genetic differences in drug oxidation. *Trends in Genetics*, **6**(6), 182-186.

Groves, C.P. (2007). The Endemic Uganda Mangabey, *Lophocebus ugandae,* and other members of the albigena –group (*Lophocebus*). *Primate Conser.* **22**(1), 123-128

Grove, S. (1998). *A nature conservation source – Book for forest professional.* Commonwealth Secretariat.

Hanya, G., & Chapman, C. A. (2013). Linking feeding ecology and population abundance: a review of food resource limitation on primates. *Ecological research* **28**(2), 183-190.

Hamerlynk, O., Luke, Q., Nyange, T.M., Duvail, S. and Leauthaud, C. (2012). Range Extension, Imminent Threats and Conservation Options for Two Endangered Primates: The Tana River Red Colobus *Procolobus rufomitratus rufomitratus* and the Tana River Mangabey *Cercocebus galeritus* in the Lower Tana Floodplain and Delta, Kenya. *African Primates*, 7(2), 211-217

Hamilton, C.A. (1984). *Deforestation in Uganda*. Oxford University Press, Nairobi.

Harbone, J. B. (1988). Short book reviews. *Phytochemistry*, **27**(5), 1570.

Hemingway, C.A. & Bynum, N. (2005). The influence of seasonality on primate diet and ranging. In Brockman, D.A. and van Schaik, C.P. (Eds). *Seasonality in primates* (pp. 57-104). Cambridge University Press, New York.

Hernes, P.J. & Hedges, J.I. (2000). Determination of condensed tannin monomers in environmental samples by capillary gas chromatography of acid depolymerisation extracts. *Analytical Chemistry* **72**(20), 5115-5124.

Hill, C.M. (2000). Conflict of interest between people and baboons: Crop-raiding in Uganda. *International Journal of Primatology* **21**(2), 209-315.

Hockings, K.J., Anderson, J.R. & Matsuzawa, T. (2009), Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced environment. *American Journal Primatol*ogy **71**(8): 636-646.

Hohmann, G. (2009). The diets of non-human primates: frugivory, food processing, and food sharing. In Hublin, J-J. and Richards, M.P. (Eds) *The Evolution of Hominin Diets* (pp. 1-14). Springer, Netherlands.

Homewood, K.M. (1978). Feeding strategy of the Tana mangabey (*Cercocebus galeritus galeritus*) (Mammalia: Primates) *Journal of Zoology* **186**(3), 375–391.

Horn, D. J. (1987a). Vegetational background and parasitism of larval diamond-back moth on collards. *Entomologia experimentalis et applicata*, **43**(3), 300-303.

Horn, A.D. (1987b). The Socioecology of the Black Mangabey near Lake Tumba, Zaire. *American Journal Primatol*ogy **12**(2), 165-180.

Houle, A., Chapman, C.A. & Vickery, W.L. (2007). Intra-tree variation in fruit production and implication for primate foraging. . *International Journal of Primatology* **28**(6), 1197-1271.

Howe, G.A. and Jander, G. (2008). Plant immunity to insect herbivores. *Annual Review of Plant Biology*, **59**(1), 41-66.

Inogwabini, B.I. & Matungila, B. (2009). Bonobo food items, food availability and bonobo distribution in the Lake Tumba Swampy forests, Democratic Republic of Congo. *The Open Conservation Biology Journal* **3**(1), 14-23.

Isabirye-Basuta, G.M. & Lwanga, J.S. (2008). Primate populations and their interactions with changing habitats. *International Journal of Primatology* **29**(1), 35-48.

Jakubas, W.J., Karasov, W.H. & Guglielmo, C.G. (1993). Ruffed grouse tolerance and biotransformation of the plant secondary metabolite coniferyl benzoate. *Condor*, **95**(3), 625-640.

Janson, C.H. & Chapman, C.A. (1999). Resources and primate community structure. In Fleagle, J.G., Janson, C.H. and Reed, K.E. (Eds), *Primate Communities* (pp. 237-267). Cambridge University Press, Cambridge.

John, A.D. & Skorupa, J.P. (1987). Responses of rain forest primates to habitat disturbance: A Review. *International Journal of Primatology* **8**(2), 157-191.

Jordano, P. (2000). Fruits and frugivory. In Fenner, M. (Ed). *Seeds: the ecology of regeneration in plant communities,* 2 Ed (pp. 125-166). CABI Publishers. Wallingford, UK.

Kagoro-Rugunda, G. and Baranga, J. (2009). The fruit phenology of Musanga leo-errerae and its importance for chimpanzee diet in Kalinzu Forest Uganda. *African Journal of Ecology*, **47**(1), 14-19.

Kasenene, J.M. (1987). The influence of mechanized selective logging, felling intensity and gap-size on the regeneration of a tropical moist forest in the Kibale Forest Reserve, Uganda (Doctoral dissertation, Michigan State University. Department of Botany and Plant Pathology).

Kaplin, B.A., Munyaligoga, V. & Moermond, T.C. (1998). The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*), *Biotropica*, **30**(1), 56-71

Kayanja, F.I.B. & Byarugaba, D. (2001). Disappearing forests of Uganda: The way forward. *Current Science*. **81**(8), 936-947

Kimuyu, D.M., Wahungu, G.M. & Otieno, D.O. (2012). Seed dispersal by Tana River mangabeys in fragmented gallery forests. *Open Journal of Ecology* **2**(1), 12-20

Kingdon, J. (2013). *The Kingdon field guide to African mammals*. A&C Black.

Kingdon, J. (1974). *East African Mammals: An Atlas of Evolution in Africa* (Vol. I). University of Chicago Press, Chicago, II.

Kinnaird, M.F. & O'brien, T.G. (1991). Viable Populations for an Endangered Forest Primate, the Tana River Crested Mangabey (*Cercocebus galeritus galeritus*). *Conservation Biology* **5**(2), 203–213.

Kinzey, W.G. & Norconk, M.A. (1990). Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology* **81**(1), 5–15.

Knott, C.D. (1998). Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology* **19**(6), 1061-1079.

Kraus, T.E., Dahlgren, R.A. & Zasoski, R.J. (2003). Tannins in nutrient dynamics of forest ecosystems-a review. *Plant and Soil*, **256**(1), 41-66.

Krishnadas, M., Chandrasekhara, K. & Kumar, A. (2011). The response of the frugivorous lion-tailed macaque (*Macaca silenus*) to a period of fruit scarcity. *American Journal of Primatology*, **73**(12), 1250-1260.

Lambert, J.E., Chapman, C.A., Wrangham, R.W. & Conklin-Brittain, N.L. (2004), Hardness of cercopithecine foods: Implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology*, **125**(4), 363–368.

Lee, P.C. & Priston, N.E.C. (2005). Human attitudes to primates: perceptions of pests, conflict and consequences for primate conservation. Commensalism and conflict: *The human-primate interface*, Oklahoma: *American Society of Primatologists*. 1-23.

Lindenmayer, D.B., Margules, C.R. & Botkin, D.B. (2000). Indicators of biodiversity for ecologically sustainable forest management. *Conservation biology*, **14**(4), 941-950.

Lucas, P.W., Constantino, P.J., Chalk, J., Ziscovici, C., Wright, B.W., Fragaszy, D.M., Hill, D.A., Lee, J.J.-W., Chai, H., Darvell, B.W., Lee, P.K.D. & Yuen, T.D.B.

(2009). Indentation as a technique to assess the mechanical properties of fallback foods. *American Journal of Physical Anthropology*, **140**(4), 643-652.

Marshall, A.J., Boyko, C.M., Feilen, K.L., Boyko, R.H. & Leighton, M. (2009). Defining fallback foods and assessing their importance in primate ecology and evolution. *American Journal of Physical Anthropology*, **140**(4), 603-614.

Marshall, A.J. & Wrangham, R.W. (2007). Evolutionary Consequences of Fallback Foods. *International Journal of Primatology*, **28**(6), 1219-1235

Marshall, A.R. (2006). Primate responses to habitat variation: A case study in the Udzungwa Mountains of Tanzania. A paper presented at the 21st Congress of the International Primatological Society, convened at Imperial Resort Beach Hotel, Entebbe-Uganda. *International Journal of Primatology* **27**(1), 112-130

Martínez-Mota, R., Valdespino, C., Sánchez-Ramosm M.A. & Serio-Silva, J.C. (2007). Effects of forest fragmentation on the physiological stress response of black howler monkeys. *Journal of Animal Conservation*, **10**(3), 374-379

Matsumoto-Oda, A. & Hayashi, Y. (1999). Nutritional aspects of fruit choice by chimpanzees. *Folia Primatology,* **70**(3), 154-162.

Mbora, D.N.M. & McPeek, M.A. (2009). Host density and human activities mediate increased parasite prevalence and richness in primates threatened by habitat loss and fragmentation. *Journal of Animal Ecology*, **78**(1), 210-218.

Medley, K.E. (1993). Primate conservation along the Tana River, Kenya: an examination of the forest habitat. *Conservation Biology*, **7**(1), 109-121.

Milton, K., Giacalone, J., Wright, S.J. & Stockmayer, G. (2005). Do frugivore population fluctuations reflect fruit production? Evidence from Panama. In Dew, L.J. and Bouli, J.P. (Eds), *Tropical Fruits and Frugivores* (pp. 5-35). Springer Netherlands.

Milton, K. (2003). The critical role played by animal source foods in human (Homo) evolution. *The Journal of nutrition*, **133**(11), 3886S-3892S.

Milton, K. (1984). The role of food-processing factors in primate food choice. In Rodman, P. and Cant, J. (Eds), *Adaptations for foraging in nonhuman primates,* (pp. 249-279). Columbia University Press, New York.

Milton, K., Windsor, D.M., Morrison, D.W. & Estribi, M.A. (1982). Fruiting phenologies of two Neotropical Ficus species. *Ecology*, **63**(3), 752-763.

Milton, K. (1981). Food choice and digestive strategies of two sympatric primate species. *The American Naturalist*, **117**(4), 496-505.

MWLE (Ministry of Water, Lands and Environment). (2002). Uganda Forest Nature: Conservation MASTER PLAN. Published by Government of Uganda (GoU).

Nabihamba, E. (1996). Factors determining dietary choices among arboreal frugivores in Kibale forest in Western Uganda. Msc Thesis, Makerere University, Kampala.

Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R. (1998). Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, **35**(4), 596-606.

NBSP (National Biomass Study Project). (1995). *Technical Report: National Biomass Study*. Forestry Department, Ministry of Natural Resources, Kampala, Uganda.

NEMA (2010). *State of the Environment Report for Uganda 2010*. National Environment Management Authority (NEMA), Kampala.

NEMA. (2006). *State of Environment Report for Uganda 2004/5*. National Environment Management Authority, Kampala.

Nowak, R. (1999). *Walker's Mammals of the World.* (6 Ed., Vol I). Baltimore, Md: The John Hopkins University Press.

Oates, J.F., Groves, C.P. & Ehardt, C. (2008). *Lophocebus albigena.* In: IUCN 2012. *IUCN Red List of Threatened Species.* Version 2012.2.

Oates, J.F., Waterman P.G. & Choo, G.M. (1980). Food selection by the South Indian Leaf-monkey, *Presbytis johnii* in relation to leaf chemistry. *Oecologia (berl)*, **45**(1), 45-46.

Obua, J., Agea, J. G., & Ogwal, J. J. (2010). Status of forests in Uganda. *African Journal of Ecology*, 48(4), 853-859.

O'Brien, T.G., Kinnaird, M.F., Dierenfeld, E.S., Conklin-Brittain, N.L., Wrangham, R.W. & Silver, S.C. (1998). What's so special about figs? *Nature*, **392** (6677), 668

Ogango, A. (2006). Crop Raiding by Mangabeys in Lwamunda forest reserve, Uganda. A Research Project Submitted to the Zoology Department in Partial Fulfilment of the Requirements for a Degree in Bachelor of Science, Makerere University.

Olupot W & Waser P. M (2013) *Lophocebus albigena* Grey -cheeked Mangabey. In Mammals of Africa. Eds Butynski T. M, Kingdon J and Kalina J. Vol II Primates. Bloomsbury Publishing, London. pp 2006-2009 I

Olupot, W. (2000). Mass differences among male Mangabey monkeys inhabiting logged and unlogged forest compartments. *Conservation Biology*, **14**(3), 833-843.

Olupot, W. (1999). Mangabey dispersal and conservation in Kibale National Park, Uganda. PhD Thesis. Purdue University.

Olupot, W., Chapman, C.A., Waser, P.M., & Isabirye-Basuta, G. (1997). Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *American Journal of Primatology*, **43**(1), 65-78

Olupot, W., Chapman, C.A., Brown, C.H. & Waser, P.M. (1994). Mangabey (*Cercocebus albigena*) population density, group size, and ranging: A twenty-year comparison. *American Journal of Primatology*, **32**(3), 197-205.

Parolin, P., Waldhoff, D. & Piedade, M.T.F. (2010). Fruit and seed chemistry, biomass and dispersal. In Junk, W.J., Piedade, M.T.F., Wittmann, F., Schongart, J. and Parolin, P. (Eds), *Amazonian floodplain forests* (pp. 243–258). Springer, Dordrecht.

Peres C.A. (1994). Primate responses to phenological changes in an Amazonian Terra Firme forest. *Biotropica*, **26**(1), 98-112.

Pienkowski, M.W., Watkinson, A.R., Kerby, G., Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R. (1998). Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, **35**(4), 596–606.

Plumptre, A., Dranzoa, C. & Owiunji, I. (2001). Bird communities in logged and unlogged African forests. Lessons from Uganda and Beyond. In Fimbel, R.A., Grajal, A. and Robinson, J.G. (Eds), *The Cutting Edge: Conserving Wildlife in Logged Tropical Forests.* Columbia University Press.

Porter, L.M., Garber, P.A. & Nacimento, E. (2009). Exudates as a fallback food for Callimico goeldii. *American Journal of Primatology*, **71**(2), 120-129.

Poulsen, F.E., Clark, C.J. & Smith, T.B. (2001). Seasonal variation in the feeding ecology of the grey-cheeked Mangabey (*Lophocebus albigena*) in Cameroon. *American Journal of Primatology*, **54**(2), 91-105.

Putz, F.E., Sirot, L.K. & Pinard M.A. (2001). Tropical forest management and wildlife: silvicultural effects on forest structure, fruit production and locomotion of arboreal mammals. In Fimbel, R.A. Robinson, J.G. and Grajal, A. (Eds). *The cutting Edge: Conserving Wildlife in Logged Tropical forests* (pp. 11-35). Columbia University Press, New York.

Rattan, R.S. (2010). Mechanism of action of insecticidal secondary metabolites of plant origin. *Crop protection*, **29**(9), 913-920.

Reichardt, P. B., Bryant, J. P., Mattes, B. R., Clausen, T. P., Chapin III, F. S., & Meyer, M. (1990). Winter chemical defense of Alaskan balsam poplar against snowshoe hares. *Journal of Chemical Ecology*, **16**(6), 1941-1959.

Remis, M.J. (1997). Ranging and grouping patterns of a western lowland gorilla group at Bai Hokou, Central African Republic. *American Journal of Primatology*, **43**(2), 111-133.

Rode, K.D., Chapman, C.A., McDowell, L.R. & Stickler, C. (2006), Nutritional Correlates of Population Density across Habitats and Logging Intensities in Redtail Monkeys (*Cercopithecus ascanius*). *Biotropica*, **38**(5), 625–634.

Roddick, J.G. & Rijnenberg, A.L. (1987). Synergistic interaction between the potato glycoalkaloids α-solanine and α-chaconine in relation to lysis of phospholipid/sterol liposomes. *Phytochemistry*, **26**(5), 1325-1328.

Sagers, C.L. & Coley, P.D. (1995). Benefits and costs of defence in a Neotropical shrub. *Ecology*, **76**(6), 1835-1843.

Saito, C. (1996). Dominance and feeding success in female Japanese macaques: effects of food patch size and inter-patch distance. *Animal Behaviour*, **51**(5), 967-980.

Saj, T.L., Sicotte, P. & Peterson, J.D. (2003). The conflict between vevert monkeys and farmers at the forest edge in Entebbe, Uganda. *African Journal of Ecology*, **39**(2), 195-199.

CHAPTER THREE

3 GENERAL MATERIALS AND METHODS

3.1 Study area

The study was conducted in Lwamunda and Mabira forest reserves, Uganda. (Figures 3.1 and 3.2) from June 2004 to March 2007. Several researchers (Groves, 2007; Ogango, 2006; Baranga, 2004; Obua, 1994; Baldwin *et al.*, 1976; Waser, 1975; Spuhler and Jorde, 1975; Chalmers, 1968) have conducted studies on Mangabey (*Lophocebus ugandae* in Mabira and Lwamunda (ML) forest reserves for the last five decades. Being in the same LVB, both forest reserves have bimodal rainfall patterns varying between 1200-1500 mm annually and distributed between two rainy distinct seasons April-May and October-November (Kizza, *et al.*, 2009). The former is located 54 km from Kampala along Jinja road and between 0° 24`and 0° 35`North latitudes and 32° 52` and 33° 07`East longitudes). It covers an area of 306 km^2 with a total boundary length of 347.4 Km on undulating hills and valleys at an elevation of 1070–1340 m above sea level (Howard *et al.*, 1991). On the other hand, Lwamunda is a riverine forest reserve surrounded by isolated flat-topped hills with steep slopes and stands at an average elevation of 1200 m above sea level. It is located 27 km along Kampala-Mityana road between 0° 15′ and 0° 23′ North latitudes and 32° 30′ and 32° 43′ East longitudes) with a relatively small area of only 67 km^2.

As stated above, several researchers have conducted related studies in both forest reserves prior to the present study. Chalmers (1968) studied the ranging behaviour of grey-checked mangabeys while Waser (1975) conducted monthly variations in feeding and activity patterns of the same species. Other researchers concentrated on ecology and social behaviour of primates (Baldwin *et al.*, 1976; Spuhler and Jorde, 1975). Baranga (2004 & 2007) studied resource use in Mabira forest reserve at the same time with the present study. After almost 30 years since Waser's 1975 study was conducted, and after two decades of observable deforestation (Hamilton, 1984) the present study focused on

nutritional ecology of Grey-checked Mangabey (*Lophocebus ugandae*) and its adaptations to low food availability.

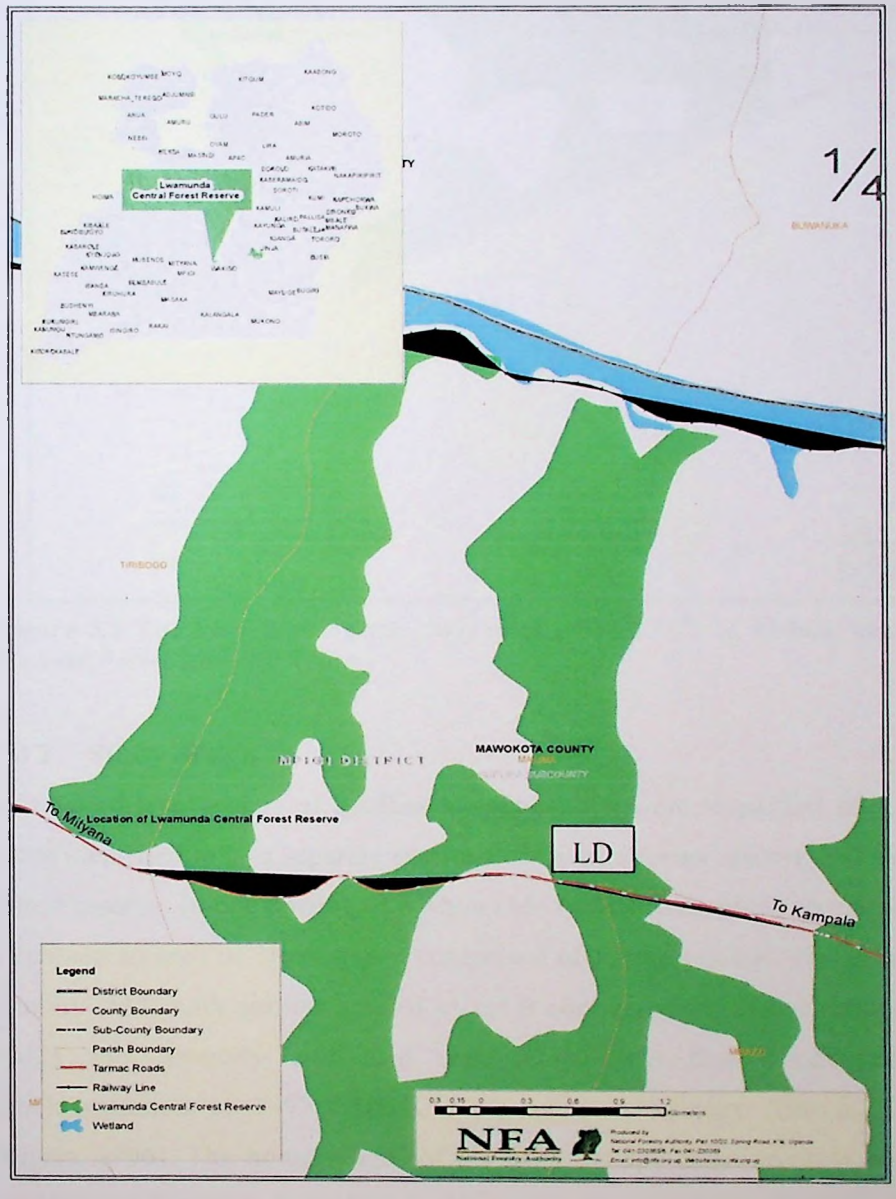


Figure 3.1 The Map showing the study site (LD) in Lwamunda forest reserve (*Source*: National Forest Authority (NFA)

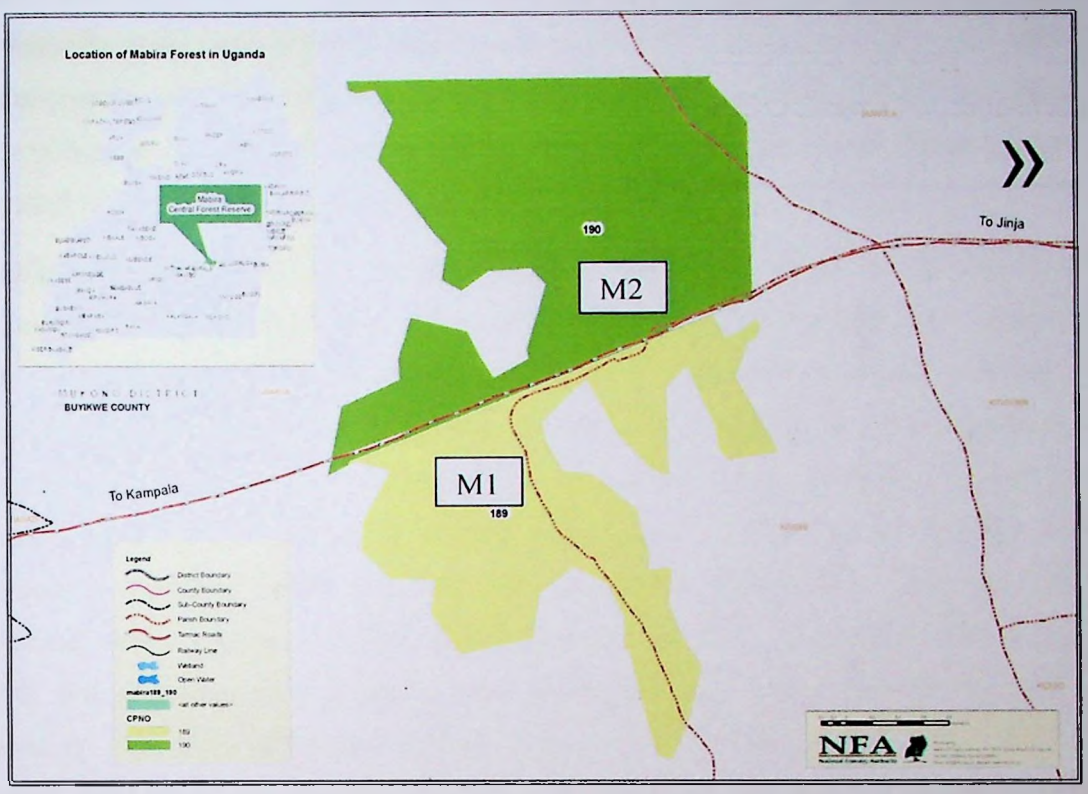


Figure 3.2 The Map showing the study sites (M1 & M2) in Mabira forest reserve. *Source*: National Forest Authority (NFA)

3.2 Study design

A total of five groups of habituated mangabeys were identified under the study. Two were identified in two separate portions of Mabira forest reserve and three in Lwamunda forest reserve. In one portion of Mabira (M1) which was relatively undisturbed one group occupied an area of $1Km^2$ and it comprised of 12 individuals. The other group occupied Mabira (M2) with similar area of $1Km^2$ it comprised of 13 individuals. Mabira portion (M2) was formerly cultivated area which was then abandoned owing to the implementation of 1993 UNESCO management strategy (Basuta, *unpublished data*; Alpert, 1996). The home ranges of the three groups in Lwamunda overlapped after six months due to severe degradation and particularly illegal pit-sawing and agricultural crop production. The overlap of home ranges had serious implications on the study design but a decision was made to concentrate on the large group that comprised of 14 individuals. This group occupied the western portion of Lwamunda although the three groups had

initially occupied different and distinct home ranges before the overlap. In essence, the study area comprised of three sites with different levels of degradation namely: Lwamunda which was severely degraded; Mabira (M1) which was fairly undisturbed by anthropogenic activities and Mabira (M2) which was regenerating after three decades of encroachment. M1 and M2 were sections of the same Mabira Central forest reserve but exposed to different management histories.

Each group was observed and trailed for 5 consecutive days in each month from Jan 2004 to June 2007. During the first one year, time was spent observing the type of fruit trees that were frequently visited by mangabeys. Based on 5 minutes systematic scan sampling method, the activity patterns (feeding, resting and socialising) of mangabeys were determined. The activity of "feeding" was considered only when the Mangabey was actively choosing a food item or holding it in its hand. An individual chewing was not considered "feeding" (Harcourt and Stewart, 1984). Observation data on diet was collected over a period of 2 consecutive days per group in a month starting from July 2005. For purposes of this study, only fruits and seeds were considered since they constitute over 50% of Mangabey diet (Waser, 1975; Olupot *et al.*, 1997). The top 10 priority fruit tree species most utilized by mangabeys in each study area were identified (Table 3.1) and marked with a well-labelled 20 x 15 cm metal plate and their location noted using Garmin Channel XL GPS

Table 3.1. Priority fruit trees in three study sites with designated data use *where* 1= Phenology; 2 = Nutrient composition; 3 = Ripeness trend

Fairly undisturbed (M1) and regenerated (M2) sections of Mabira forest reserve		*Severely degraded Lwamunda forest reserve*	
Priority fruit tree species	Data use	Priority fruit tree species	Data use
Ficus mucuso	1, 2, 3	*Blighia unijugata*	1, 2, 3
Measopsis eminii	1, 2, 3	*Ficus mucuso*	1, 2, 3
Celtis durandii	1,2,3	*Maesopsis eminii*	1, 2, 3
Celtis africana	1,2	*Myrianthus arboreus*	1, 2, 3
Celtis mildbraedii	1, 2,	*Blighia unijugata*	1, 2, 3
Canarium indicum	1, 2, 3	*Ficus sur*	1, 2, 3
Antiaris toxicaria	1,2	*Canarium indicum*	1, 2, 3
Albizia grandibracteata	1,2	*Ficus exasperata*	1, 2, 3
Ficus exasperata	1, 2, 3	*Rheedia edulis*	1, 2
Treculia africana	1,2	*Albizia grandibracteata*	1,2

For each fruit tree species identified, a total of 10 individuals were similarly identified and marked. Some fruit tree species with respective individuals across the three study sites had been designated for compositional data collection, during the course of the study, a decision was made to sample all trees in fruit because of their differing phenology. Fruit tree species whose fruits exhibited distinct stages of ripeness were sampled once every month for size and weight measurements at each stage of development. Apart from analysis of fruit macro-nutrients, tannin content for each stage of ripeness was also determined. Other ecological studies namely phenology, feeding and fruit processing patterns used by mangabeys to access desired fruit parts for consumption was conducted in both study sites over a period of 24 months. The phenology data for the priority tree species was correlated with chemical analyses. Parallel studies were undertaken to determine food tree densities for comparison to the proportion of fruiting trees, Mangabey group sizes and compositions.

3.3 Field observations

In each forest type, the habituated mangabeys were observed for 5 consecutive days in a month for over a period of 12 months to establish fruit trees utilized, mechanisms of fruit processing prior to consumption, trends of fruit ripening, abundance in relation to other food sources and other factors influencing food availability. During the tracking of the respective three groups of mangabeys, 1-2 hours was spent under tagged fruiting trees where they were feeding to examine the remains of fruit or seed. The parts of fruit/seed consumed were noted and the remains photographed. The manner in which the fruit or seed were being processed prior to consumption was recorded to develop a story. The different processing methods and manipulation skills varied with stages of ripeness or development. They were identified and photographed using a digital camera Model Pentax 3.1 pixel. The level of maturity and ripeness based on colour changes was recorded. As the fruit matured, the colour changed from different shades of green to red, orange and other bright colours depending on fruit species or type. The level of fruit ripeness varied from the yellowish green colour of a mature fruit to a tint of red which was indicative of a very ripe fruit that varied with type fruit. Similarly, the level of seed maturity varied with tree species and it was determined by weight, width and length

measurements. Size and sometimes colour changes were a function of fruit/seed maturity.

3.3.1 Phenological data collection

From July 2005, the abundance of fruit on 10 individuals of priority 10 fruit trees species in each study site was recorded on a monthly basis using a visual abundance score (VAS: 0-4) according to Chapman *et al.* (1992); where *score 0* denoted total absence of fruit; *score 1* represented 25% fruit abundance; *score 2* represented 50% fruit abundance; *score 3* represented 75% fruit abundance and *score 4* represented maximum fruit abundance. The level of fruit ripeness on the same trees was similarly recorded and scored. Although most fruits exhibited several stages of ripening during their development, it was only any semblance of ripeness that was evaluated and scored using the VAS method. *Score 0* denoted total absence of ripe fruit while *scores 1, 2, 3* and *4* represented 25%, 50%, 75% and > 75% respectively of total fruits on tagged trees were ripe albeit at different stages of ripeness. However, there were some fruits whose ripeness could not be deciphered by hue change at a distance for example *Celtis, Albizia, Blighia, Rheedia* and *Myrianthus* species. In such instances, clusters were harvested and assessed from the forest floor. Thereafter each fruit was monitored on weekly basis for stages of fruit development to establish time duration between respective stages of maturity.

3.3.2 Diet in relation to fruit abundance

From data generated in Sub-section 3.3.1, the proportion of individual fruit trees for each priority fruit trees that were in fruit were scored on the relative scale of 0-4 with respect to fruit abundance and ripeness. This was done on a monthly basis. The number of trees with edible fruit parts and number of trees with inedible fruit parts were identified and scored every month for each priority fruit tree species. The proportion of fruit in the diet of mangabeys was calculated from the score and phenological data.

3.3.3 Feeding ecology

The technique mangabeys utilized food resources available in study sites, varied with stage of ripeness for each fruit. Essentially, there was an average of 5 ripening stages per fruit that were agreed upon by the supervisor, researcher and field assistant and

numerically coded. For each ripening stage, the exact part of the fruit (seed or pulp) eaten was noted and scored accordingly. In incidences where seed was eaten, efforts were made to find out whether the seed coat was removed prior to consumption or it was eaten together with the seed.

3.4 Fruit sample collection for nutritional chemical analysis

3.4.1 Sampling method

Fruit or fruit part or seed were picked from the selected fruit tree using a hooked long pole for reachable trees. However, picking samples from high trees was a challenge especially in Mabira M1 and therefore some samples from inaccessible trees were picked from the forest floor provided they were fresh. Scoring for abundance and ripeness or availability from the forest floor in a forest with tall trees with a closed canopy was also a challenge.

3.4.2 Sample size

Samples consisting of fruits and/or seeds from the 10 priority tree species that were fruiting were collected monthly, over a period of 18 months. When distinguishing between fallback and seasonal or preferred fruit trees, a quadratic equation (Cochran, 1977): $n = (Z_{\alpha/2})pq/E^2$ was used to determine the minimal number of months the fruit tree was fruiting; w*hereby n* is the sample size; Z is the tabulated values from the normal Z table ($z = 1.96$); α = level of significance ($\alpha = 0.05$); p = probability that a priority fruit tree was fruiting throughout the 24 months of the study; q = probability that a priority fruit tree was not fruiting and E represents the sampling error that may be due to mis-identification of fruiting tree species. Depending on the fruit size and actual edible portion of the fruit observed being consumed by mangabeys, 1-2 kg of fruit were picked from each of the 10 individual trees of the priority fruiting tree species. The weight, width and length of each fruit or seed sample were measured according to Houle *et al.* (2007). Each sample was photographed using a digital camera Model Pentax 3.1 pixel, sealed in plastic bag and transported to the Department of Animal Science- Makerere University on the same day. The 1-2 kg of the collected sample was stabilized by drying

in an air oven at 45°C, ground into a powder and then stored in an airtight vial to await respective subsequent analyses. Samples were analysed for their nutritional composition using standard analytical methods (Sub-sections 3.5.1 and 3.5.2).

3.5 Sample preparation for chemical analysis

At Animal nutrition laboratory of Department of Agricultural Production Makerere University, weight and size measurements were determined before splitting the fruit to access the consumable part e.g. seed and aril for *Blighia* spp. For purposes of this study, only seeds and aril have been considered since fruit constitute over 50% of mangabeys diet (Waser, 1975; Olupot *et al.*, 1997). The 1-2 kg of the collected sample was stabilized by drying in an air oven at 45°C to a constant weight for 1-2 days depending on level of fruit part succulence. Dried samples were ground into a powder through a 1-mm mesh screen using FOSS Cyclotec^{TM} 1093 sample mill made in Sweden and then stored in an airtight vial to await respective subsequent analyses.. Since the *Blighia* aril samples were always less than the minimum quantities for the FOSS Cyclotec, milling was done using a mortar and pestle. The milled or powdered sample was packed in Ziploc bags, labelled and stored at room temperature until ready for use. Samples were analysed for their nutritional composition using standard analytical methods (Sub-sections 3.5.1 and 3.5.2).

3.5.1 Chemical analyses

In the absence of the hi-tech Near-Infrared Reflectance Spectroscopy (NIRS) that offers rapid and cost-effective means of analysis (Rothman *et al.*, 2009), the traditional nutritional analytical methods (paragraph below) were used to quantify protein, crude fibre, gross energy and soluble carbohydrates (sugars) in fruit and seed samples consumed at various stages of maturity by mangabeys. In addition, one of the secondary compounds namely condensed tannins was analysed in the same samples.

All collected samples were subjected to macro-nutrient analysis using various methods. Micro-Kjeldahl method (Rothman *et al.*, 2012; AOAC 1991) was used to quantify protein; Van Soest *et al.* (1991) method was used to determine crude fibre while AOAC (1995) method was used to determine gross energy using a Bomb Calorimeter SG96/02/536, Gallenkamp England UK. Fat or lipid component was determined by

soxhlet method for ether extract (Harris, 1970); and the Anthrone method (Hansen and Møller, 1975) was used to determine soluble carbohydrates (sugar).

3.5.2 Analysis of secondary compounds/metabolites

Since tannins occurred in high concentrations in the diets of cercopithecines than other seconday metabolites (Milton, 1984), a choice was made to use them as a measure of fruit selection criterion by mangabeys in LVB forest reserves. Other researchers (Rode *et al.*, 2006; Krief *et al.*, 2005; Chapman and Chapman, 2002; Cipollini and Levey, 1997; Herrera, 1982) have used a whole spectrum of secondary metabolites to assess the nutritional quality of non-human diets but financial constraint limited this study to only tannins. Their levels were determined by Broadhurst and Jones (1978) vanillin assay. Due to limited quantity of *B.unijugata* aril samples, only analyses fat and tannins were conducted. The actual nutritional quality of the diet was calculated from the amount of macro-nutrients in the fruit part consumed by mangabeys.

3.6 Data analysis

Descriptive statistics (mean, SD and SE) were used on raw fruit abundance scores for each fruiting tree over the study period. A one way ANOVA using SPSS version 17 was used to compare the mean monthly phenological fruit availability and abundance scores in the 3 forest types. A t-test was done using Stata version 12.1 to check if there is a difference in the mean weights among fruits common in both forests. Further still, a linear regression was done to find the relationship between the edible, inedible and fruitless trees among the 3 forests. The spatial and temporal patterns of fruit variability between forests were also analysed using the same package. However, fruit availability was determined by expressing the proportion of fruiting trees as percentage of all tagged trees regardless of species on a monthly basis. Using Sigma plot version 11, the number of fruiting trees per forest were plotted against time to establish fruiting seasons in both forests in terms of duration and variability. The number of fruit types that were manipulated by mangabeys in different habitats (Mabira 1&2 and Lwamunda were analysed using Stata version 12. The two-way ANOVA using Sigma plot Stata version 12 was used to establish the relationship between fruit abundance or fruit cover and forest

type or with stage of fruit development. To compare nutrient content (sugar, protein and fat) between fall-back fruits (FBFs) and seasonal (SFs) or preferred fruits (PFs) occurring in the three study sites, one way ANOVA was also used.

Parametric procedures on nutrition data including tannin levels were used to test for differences between fruit species, fruit development stages and study sites (habitats) using Student's independent sample t- tests and Pearson regression correlations that involved descriptive and inferential packages. Samples from multiple species or more than two study sites were analysed using one-way ANOVA (SPSS 17.0). Bonferroni post hoc tests were employed in cases where ANOVA was significant. The ANOVA entailed comparison between species, stages of fruit development or levels of fruit ripeness and forest types to establish relationship between independent and primary variables. The one way ANOVA was used to compare between different parts consumed and parts rejected by mangabeys and differences in study sites.

3.7 References

Alpert, P. (1996). Integrated conservation and developmental projects. Examples from Africa. *BioScience*, **46** (11), 845-855.

AOAC. (1995). *Official methods of analysis* Chapter 4. Animal Feed. Official methods of analysis'. 16thedition. AOAC International, Arlington, VI, USA. 30 pp.

AOAC. (1991). *Official Methods of Analysis,* 15th Edition. Association of Official Analytical Chemists, AOAC Inc., Arlington ,VA. 22201 USA

Baldwin, L.A., Teleki, G. & Kavanagh, M. (1976). Field research on colobus, guenon, mangabey and patas monkeys: a historical, geographical and bibliographical listing. *Primates,* **17**(2), 233-251.

Baranga, D. (2004). Forest fragmentation and primate survival status in non-reserved forests of the Kampala area, Uganda. *African Journal of Ecology,* **42**(1), 70-77.

Baranga, D. (2007). Observations on resource use in Mabira Forest Reserve, Uganda *African Journal of Ecology*, **45**(1), 2-6.

Broadhurst, R.B. & Jones, W.T. (1978). Analysis of condensed tannins using acidified vanillin. *Journal of the Science of Food and Agriculture*, **29**(9), 788-794.

Chalmers, N.R. (1968). The visual and vocal communication of free inhabiting Mangabeys in Uganda. *Folia Primatologica,* **9**(3-4), 258-280.

Chapman, C.A. & Chapman, L.J. (2002). Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. *Comparative Biochemistry and Physiology-Part A: Molecular & Integrative Physiology*, **133**(3), 861-875.

Chapman, C.A., Chapman, L.J., Wrangham, R., Hunt, K., Gebo. D. and Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica*, **24**(4), 527-531.

Cipollini, M.L. & Levey, D.J. (1997). Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *The American Naturalist*, **150**(3), 346-372.

Cochran, W. G. (1977). Sampling techniques (3rd ed.). New York: John Wiley & Sons.

Groves, C. P. (2007). The endemic Uganda mangabey, *Lophocebus ugandae*, and other members of the albigena-group (*Lophocebus*). *Primate Conservation*, **22**(1), 123-128.

Hamilton, C.A. (1984). *Deforestation in Uganda*. Oxford University Press, Nairobi.

Hansen, J. & Møller, I.B. (1975). Percolation of starch and soluble carbohydrates from plant tissue for quantitative determination with anthrone. *Analytical biochemistry*, **68**(1), 87-94.

Harcourt A.H. & Stewart, K.J. (1984). Gorillas' time feeding: aspects of methodology, body size, competition and diet. *African Journal of Ecology*, **22**(3), 207-215.

Harris, L.E. (1970). *Nutrition Research Techniques for Domestic and Wild Animals*. Animal Science Department, Utah State University, Logan Utah, USA.

Herrera, C.M. (1982). Defence of ripe fruit from pests: its significance in relation to plant-dispersers interactions. *The American Naturalist*, **120**(2), 218-241.

Houle, A., Chapman, C.A. & Vickery, W.L. (2007). Intratree variation in fruit production and implication for primate foraging. *International Journal of Primatology*, **28**(6), 1197-1217.

Howard, P. C., Butler, J., & Howard, P. (1991). Nature conservation in Uganda's tropical forest reserves. IUCN, Gland, Switzerland and Cambridge, UK with the financial support of WWF-International.

Kizza, M., Rodhe, A., Xu, C. Y., Ntale, H. K., & Halldin, S. (2009). Temporal rainfall variability in the Mabira and Lwamunda in East Africa during the twentieth century. *Theoretical and applied climatology*, **98**(1-2), 119-135.

Krief, S., Hladik, C.M. & Haxaire, C. (2005). Ethnomedicinal and bioactive properties of plants ingested by wild chimpanzees in Uganda. *Journal of ethnopharmacology*, **101**(1), 1-15.

Milton, K. (1984). The role of food-processing factors in primate food choice. In Rodman, P. and Cant, J. (Eds), *Adaptations for foraging in nonhuman primates,* (pp. 249-279). Columbia University Press, New York.

Ogango, A. (2006). Crop Raiding by Mangabeys in Lwamunda forest reserve, Uganda. A Research Project Submitted to the Zoology Department in Partial Fulfilment of the Requirements for a Degree in Bachelor of Science, Makerere University.

Olupot, W., Chapman, C.A., Waser, P.M. & Isabirye-Basuta, G. (1997). Mangabey (*Cercocebus albigena*) Ranging Patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *American Journal of Primatology*, **43**(1), 65-78.

Obua, J. (1994). Integrating Indigenous Knowledge in Conservation and Development of Forest Ecotourism in Mabira, Uganda. Department of Forestry, Makerere University.

Rode, K.D., Chiyo, P.I., Chapman, C.A. & McDowell, L.R. (2006). Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behaviour. *Journal of Tropical Ecology,* **22**(4), 441-449.

Rothman, J.M., Chapman, C.A. & Van Soest, P.J. (2012). Methods in primate nutritional ecology: A user's guide. *International Journal of Primatology*, **33**(3), 542-566.

Rothman, J.M., Chapman, C.A., Hansen, J.L., Cherney, D.J.R. & Pell, A.N. (2009). Rapid assessment of the Nutritional Value of Foods eaten by Mountain Gorillas: Applying Near-Infrared Reflectance Spectroscopy to Primatology. *International Journal of Primatology,* **30**(5), 729-742.

Spuhler, J.N. & Jorde, L.B. (1975). Primate phylogeny, ecology and social behaviour. *Journal of Anthropological Research,* **31**(4), 376-405.

Van Soest, P.J., Robertson, J.B. & Lewis, B.A. (1991). Methods for dietary fiber, neutral detergent fiber, and non-starch polysaccharides in relation to animal nutrition. *Journal of Dairy Science,* **74**(10), 3583-3597.

Waser, P. M. (1975). Monthly variations in feeding and activity patterns of the Mangabey, *Cercocebus albigena* (Lydekker). *East African Wildlife Journal*, **13**(3-4), 249-264

CHAPTER FOUR

4 Patterns of fruit processing by Grey-cheeked mangabeys (*Lophocebus ugandae* Groves) in Mabira and Lwamunda forest reserves, Uganda

M. Masette, G. Isabirye-Basuta and D. Baranga.

Department of Biological Sciences, Makerere University, P.O. Box 7062, Kampala, Uganda

Abstract

Mangabey diet is believed to be influenced by fruit availability and quality. However, the relationship between the two variables and the level to which fruit is processed prior to ingestion is not well understood. We investigated this relationship by examining fruit abundance, quality and processing of fruits belonging to 10 tree species commonly utilized by mangabeys (*Lophocebus ugandae*) inhabiting Mabira and Lwamunda forest reserves as source of food. The number of trees in fruit and phenological scores were documented on a monthly basis; these were used as indices of fruit abundance while fruit ripeness, fruit weight and parts of fruit consumed or rejected at respective fruit development stages were used as indices of fruit quality. This was done in three habitats with different management histories from June 2005 to March 2007. Our results showed that the mean number of trees in fruit varied with habitat type. They were 5.75±1.8 in fairly undisturbed Mabira (M1), 5.13±1.78 in regenerating Mabira (M2) and 3.88±1.9 in Lwamunda. Edible fruits in M1 were significantly higher than in Lwamunda ($P<0.001$ using one-way ANOVA). Fruit abundance expressed in terms of fruit cover per tree did not exceed 25% in Lwamunda but it was always above 50% in M2 and M1. Of the ten priority trees whose fruits were commonly consumed by mangabeys in Lwamunda, M2 and M1, about 60%, 20% and <1% respectively were processed to access endosperm or pulp. Mangabeys preferred ripe pulp of most fruits but unripe fruit pulp were consumed during periods of fruit scarcity. The stage of fruit development dictated the specific

part(s) of fruit to be consumed and the mode of ingestion. The pulp of ripe fruits was gnawed or fruit consumed whole and pulp peeled off in the mouth while intermediate ripening stages of most fruits were avoided except for a few genera. The level of fruit ripeness also determined the pattern of fruit processing. *Ficus* species (*sur* and *exasperata*) were consumed whole while unripe fruits of *Canarium indicum, Maesopsis eminii, Pseudospondias microcapa* were processed. Large-sized fruits like *Treculia africana* and *Myrianthus arboreus* were consumed in piece-meal portions, medium-sized fruits were gnawed at to access the desired part(s) and small-sized ones were invariably ingested whole. Immature fruits belonging to *Canarium indicum, Pseudospondias microcapa* and *Maesopsis eminii* and *Myrianthus arboreus* were processed to access endosperm. Generally, patterns of fruit processing increased with food scarcity exacerbated by prolonged dry spells.

Key words. Mangabey diet, fruit availability, quality and processing

4.1 Introduction

Fruit processing constitutes behavioural methods employed by primates to access a nutritive or energy-rich part of the fruit or seed (Lambert, 1999). The methods of access vary between species but also with fruit type, seed size, fruit ripeness, fruit availability, fruit morphology and foraging behaviour of individuals among other factors (Lambert, 2002). The daily foraging pattern of frugivorous primates is usually dictated by availability and quality of fruits as reflected in the nutritional content. The management history of the habitat has implications for Mangabey foraging behaviour. In severely degraded habitat, mangabeys may be forced to extend their home range because of poor food potential and quality while in a fairly undisturbed habitat where the quality of food may be relatively high and available, the mangabeys hardly extend their home range.

Several studies on mangabeys and other primates in forests across Africa have been conducted (Hohmann, 2009; Nowell and Fletcher, 2008) that showed influence of habitat alteration on feeding ecology. When Kunz and Linsenmair (2007) conducted studies on feeding behaviour and selectivity of olive baboons (*Papio anubis*) on the African locust

bean (*Parkia biglobosa*, Mimosaceae), they consumed different parts of the plant based on seed size during fruit development. The hardness of foods consumed by primate may also influence food choice and processing (Lambert *et al.*, 2004). In a severely degraded forest, it appears chemical composition and ease of food acquisition play a lesser role in the choice or selection of fruit/seed or portion for consumption than in fairly undisturbed forest reserves. This is because when food is plentiful, primates tend to be fastidious and food nutrient assumes a critical role. Lawes *et al.* (1990) noted that during a dry season when fruit was scarce, Samango monkeys (*Cercopithecus mitis labiatus*) in Ngoye forest in S. Africa, tended to be less selective in their choice of food species and ate available food regardless of their energy content. There was a shift towards less nutritious items such as leaves. During the wet season, when there was a wide choice, monkeys tended to select fruits with high energy values.

According to Janson and Chapman (1999), the majority of primates prefer a protein and carbohydrate rich diet with minimal fibre content although others have been observed to preferentially select and consume large volumes of fruit that are rich in lipids and soluble carbohydrates (Di Fiore *et al.*, 2008). Due to this apparent preference for energy-dense foodstuffs, coupled with the highly energetic lifestyles of these frugivores, energy has been suggested to be the primary driver behind their food choice (Di Fiore and Rodman, 2001; Strier, 1992; Rosenberger and Strier, 1989; Homewood, 1978).

Grey-cheeked mangabeys are omnivorous but tends towards frugivory. They are omnivorous as evidenced by their wide range of food choice (Kimuyu *et al.*, 2012; Poulsen *et al.*, 2001) but they are fundamently frugivorous. During periods of low food availability that may be exacerbated by incessant habitat alteration, nutrient trade-off is quite common among frugivores (Schaefer *et al.*, 2003). Like most primates, mangabeys turn to foods that are not used at other times of the year (Hohmann, 2009) when preferred food sources are scarce. Since over 50% of Mangabey diet is predominantly fruit (Hohmann, 2009; Waser, 1975) preference for ripe fruit is understandably high. According to Herrera (1982), most ripe fruits change colour, texture, taste, conspicuousness and scent to attract dispersers as a strategy for regeneration. Ripe fruit

provides readily available energy (Jordano, 2000) to meet activity budgets in primates (Wrangham and Waterman 1993). In the absence of ripe fruit, there is a dietary shift to food items known to have high levels of condensed tannins and fibre (Poulsen *et al.*, 2001) as a trade-off. This dietary shift compromises their nutrient intake in terms of quantity and quality. Additionally, it involves considerable amount of fruit processing which is time as well as energy consuming.

In this paper, we hypothesized that fruit processing and patterns of fruit manipulation were a function of fruit availability and quality as typified by fruit size, maturity and level of ripeness. Succinctly, in heavily degraded Lwamunda forest reserve, fruit processing was more intense than in fairly undisturbed Mabira forest reserve as a coping mechanism to meet the daily dietary intake. As such, mangabeys inhabiting severely degraded Lwamunda forest reserve were less choosy in their food selection than in Mabira (M1).

4.2 Materials and Methods

4.2.1 Study area

We studied Grey-checked mangabeys in Mabira (306 km^2, 0° 24`N and 0° 35`E and longitude 32° 52`N and 33° 07`E) and Lwamunda Forest Reserves, Uganda (67 $km^{2,}$ - 0° 15′ N and 0° 23′ N longitude 32° 30′ E and 32° 43′ E) from June 2004 to March 2007. Several researchers have conducted studies here since 1965 (Baldwin *et al.*, 1976; Chalmers, 1968; Spuhler and Jorde, 1975; Waser, 1975). Both forests being within the Lake Victoria Basin (LVB) have bimodal rainfall patterns varying between 1200-1500 mm annually and typically distributed between two rainy distinct seasons April-May and October-November (Kizza, *et al.*, 2009). Mabira is located on undulating hills and valleys at an elevation of 1070–1340 m above sea level while Lwamunda is a riverine forest reserve surrounded by isolated flat-topped hills with steep slopes and is at an elevation of 1200 m (Howard *et al.*, 1991). The two forests have different management histories. As such, the (3) selected study sites varied according to the level of degradation. In Mabira forest reserve, one site was a fairly undisturbed (M1) while the other (M2) was regenerating after two decades encroachment. The Lwamunda (LD) study site was severely degraded and encroached for agricultural purposes.

4.2.2 Study design

Three (3) groups of habituated mangabeys; one in each study areas (M1, M2 and LD) were observed for 5 consecutive days in each month during the 24 month study period. A systematic 5 minute-scan sampling (Waser, 1975) was supplemented with ad libitum observations when regular systematic sampling was difficult. Fruit remains under trees where mangabeys had been feeding were also carefully examined for identification of the exact parts they were feeding on. Mechanisms of fruit processing prior to consumption were noted and recorded. The phenology of individual 10 fruit trees of the top 10 priority fruit tree species utilized by mangabeys in each study area were identified (Table 4.1) and marked with their location noted using Garmin Channel XL GPS.

Table 4.1 Priority fruit trees in Mabira and Lwamunda forest reserves sampled for fruit phenology where *1 = Phenology data; 2= fruits showed colour change during ripening*

Fairly undisturbed (M1) and regenerated (M2) sections of Mabira forest reserve		*Severely degraded Lwamunda forest reserve*	
Priority fruit tree species	Data use	Priority fruit tree species	Data use
Ficus mucuso	1, 2	*Blighia unijugata*	1, 2
Measopsis eminii	1, 2	*Ficus mucuso*	1, 2
Celtis durandii	1,2	*Maesopsis eminii*	1, 2
Celtis africana	1,2	*Myrianthus arboreus*	1, 2
Celtis mildbraedii	1, 2	*Blighia unijugata*	1, 2
Canarium indicum	1, 2	*Ficus sur*	1, 2
Antiaris toxicaria	1,2	*Canarium indicum*	1, 2
Albizia grandibracteata	1	*Ficus exasperata*	1, 2
Ficus exasperata	1, 2	*Rheedia edulis*	1, 2
Treculia africana	1	*Albizia grandibracteata*	1

The presence of fruit on the marked fruit trees was recorded on a monthly basis using a visual abundance score (VAS: 0-4) according to Chapman *et al.* (1992).where 0 denoted total absence of fruit and 4 represented maximum fruit availability. The level of fruit availability was indexed by the percentage of trees with edible ripe fruits in comparison with inedible fruit stages and fruitless trees within the home range of each Mangabey group. Samples of each fruit type were collected based on stage of fruit maturity and ripeness. Each stage of fruit development were weighed using a digital sensitive balance.

The respective weights were entered in Microsoft Excel 2007 version sheet for generation of descriptive statistics. The parts of fruit/seed and the remains consumed by mangabeys were recorded. Fruit maturity were determined by age and level of ripeness was visually assessed by colour changes. In most cases, fruit maturity corresponded with level of fruit ripeness. Colours changed from apple green to bright red or maroon hue depending on fruit type. Immature green fruits were designated stages 1-3 of development with age variation of 2-12 weeks, yellowish hues were normally stages 3-5 with age variation of 12-36 weeks and bright red or maroon represented stages 5-7 with age above 36 weeks of development. The colour changes and age depended on type of fruit.

4.2.3 Data analysis

Using SPSS version 17, a one way ANOVA was used to compare the mean monthly phenological fruit availability and abundance scores in the 3 forest types. The spatial and temporal patterns of fruit variability between forests were also analysed using the same package. However, fruit availability was determined by expressing the proportion of fruiting trees as percentage of all tagged trees regardless of species on a monthly basis. Using Sigma plot version 11, the number of fruiting trees per forest were plotted against time to establish fruiting seasons in terms of duration and variability. The correlation coefficient was established between the amount of monthly rainfall (mm) and the number of fruiting trees in each habitat per month using Stata version 12.1. The number of fruit types that were processed by mangabeys in different habitats (Mabira 1&2 and Lwamunda) were analysed using Stata version 12.1. Microsoft Excel 2007 descriptive statistics were used for mean weights and standard deviations for fruits at various stages of development. Furthermore, a t-test was done using Stata version 12.1 to check if there is a difference in the mean weights among fruits common in both forests.

4.3 Results

4.3.1 Fruit abundance

Fruit abundance was assessed in terms of number of trees in fruit regardless of the proportion of fruits on each tree and phenological scores. The proportion of trees in fruit

in each study site declined throughout the study period. The monthly variations between sites were significant. Mabira (M1) and Mabira (M2) were significantly different from Lwamunda (t-test, $p < 0.05$; $p= 0.034$; $N= 97$) but not different from each other (t-test, $t = 0.215$ and $N = 90$ $p>0.05$). Using regression best fit-line with $R^2 = 0.0175$, Lwamunda had significantly less (2%) fruiting trees than in Mabira M2 with $R^2 = 0.206$ or 21% (Fig 4.1). Generally, food availability as represented by number of fruiting trees, declined gradually in the three study sites from 2005-2007. However, the number of fruiting trees from October to June were more than other months of the year though the gradient varied across study sites; Mabira –M2 (y= (-0.308) x + 7.893)) and Lwamunda (y= (-0.0804) x + 1.666)) than Mabira –M1 (y= (-0.040) x + 5.565)). Mabira (M1) was more stable with average number of six fruiting trees over study time than 4 and 1 for Mabira (M2) and Lwamunda respectively which was indicative of the level of degradation.

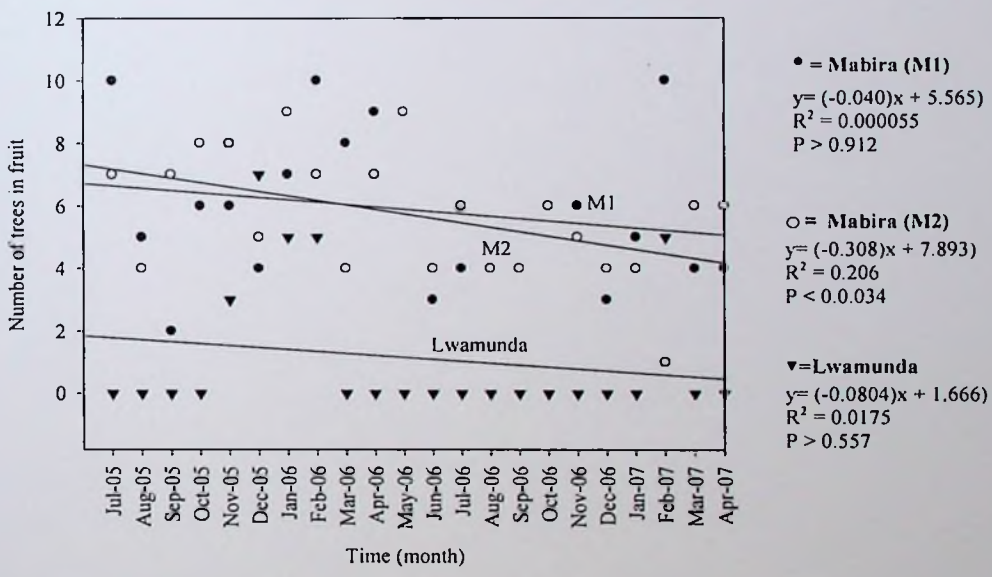


Figure 4.1 Number of trees fruiting over a period of 34 months in 3 study sites

4.3.2 Phenological scores

The fruit cover on individual trees as exemplified by the mean abundance score (Fig. 4.2a – 4.2d) varied with type of forest. Whereas it did not exceed 25% in Lwamunda, fruit

cover was always above 25% in the two Mabira study sites. The wide mean fruit cover variations between replicates that signified instability was more pronounced in Lwamunda than either in Mabira M1 or M2. Figs seemed to be available all year around albeit with varying abundance between species. Other fruit tree species like *Celtis* species, *C.indicum* and *M.eminii* were also regularly available though not throughout the year. However, *B.unijugata*, *A. toxicaria, R.edulis*, *T.africana* and *M.arboreus* seemed to bear fruit once in every 1-2 years. Consequently, food potential in the respective study sites varied spatiotemporally with different fruiting trees peaking seasonally. Generally, there were more trees in fruit at any one time in Mabira (M1) and (M2) than they were in Lwamunda.

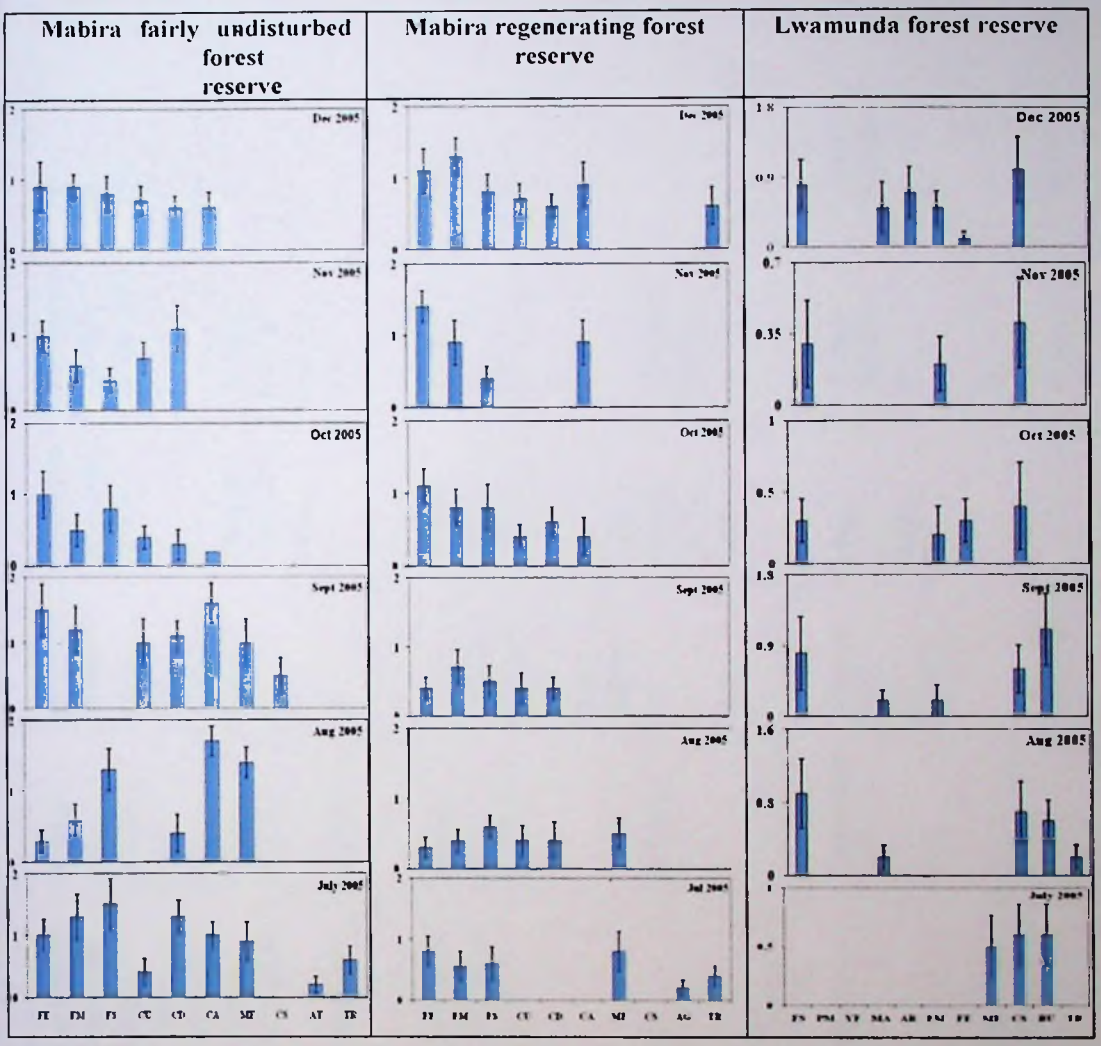


Figure 4.2a Mean variation with standard error (SE) of fruit abundance in Mabira (undisturbed and regenerating) and Lwamunda forest reserves from July-Dec 2005

(Key: **FE**- *Ficus exasperata*; **FM**- *Ficus mucuso;* **FS**- *Ficus sur;* **CU**- *Celtis mildbraedii;* **CD**- *Celtis durandaii;* **CA**- *Celtis Africana;* **ME**- *Maesopsis eminii;* **CS**- *Canarium indicum;* **AT**- *Antaliaris toxicaria;* **TR**- *Treculia africana;* **PM**- *Pseudospondias microcapa;* **MA**- *Myrianthus arboreus;* **BU** *Blighia unijugata;* **AG**-*Albizia grandibracteata* ; **YF**-*Rheedia edulis*)

The number of trees bearing fruits in Mabira forests (M1 and M2) was more than their counterparts in Lwamunda forest reserve (Fig. 4.2a). On average, at least 6 of the commonly utilized fruit trees were in fruit and they included figs (*F. sur; F. mucuso* and *F. exasperata*), *Celtis* species and *M.eminii*.

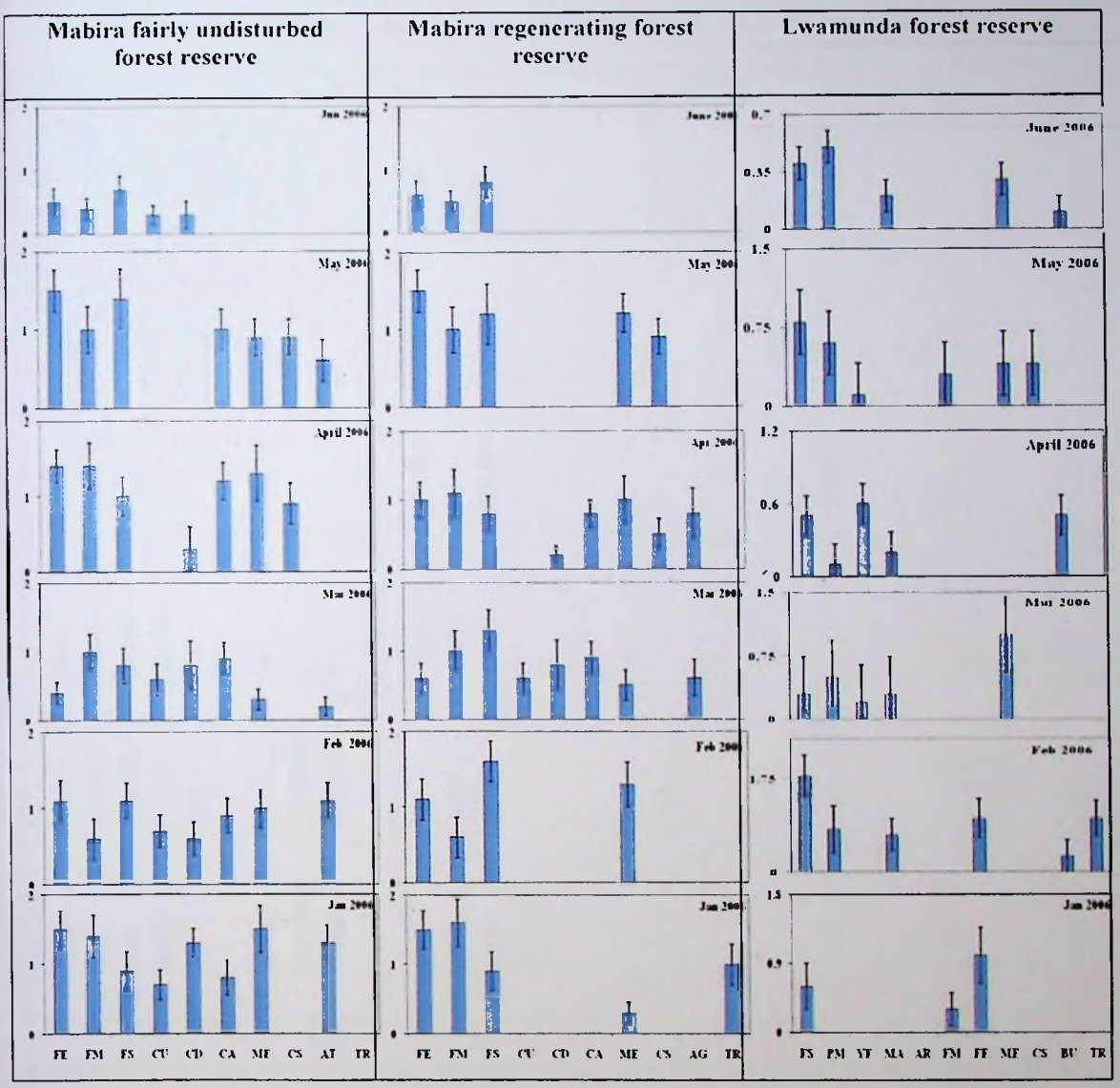


Figure 4.2b Mean variation with standard error (SE) of fruit abundance in Mabira (fairly undisturbed and regenerating) and Lwamunda forest reserves from Jan-June 2006

(Key: **FE-** *F.exasperata;* **FM-** *F. mucuso;* **FS-** *F. sur;***CU-** *C. mildbraedii*; **CD-** *C. durandaii*; **CA-** *C. africana;* **ME-** *M. emunii;* **CS-** *C. indicum;* **AT-** *A. toxicaria*; TR- *T.africana*; **PM-** *P. microcapa*; **MA-** *M. arboreus;* **BU** *B. unijugata*; **AG-***A. grandibracteata* ; **YF-***R. edulis*)

The number of fruiting trees increased to 7 during the first half of the following year (Fig 4.2b) but declined second half (Fig.4.2c) with only 5, 3 and 2 number of fruiting trees in M1, M2 and Lwamunda respectively.

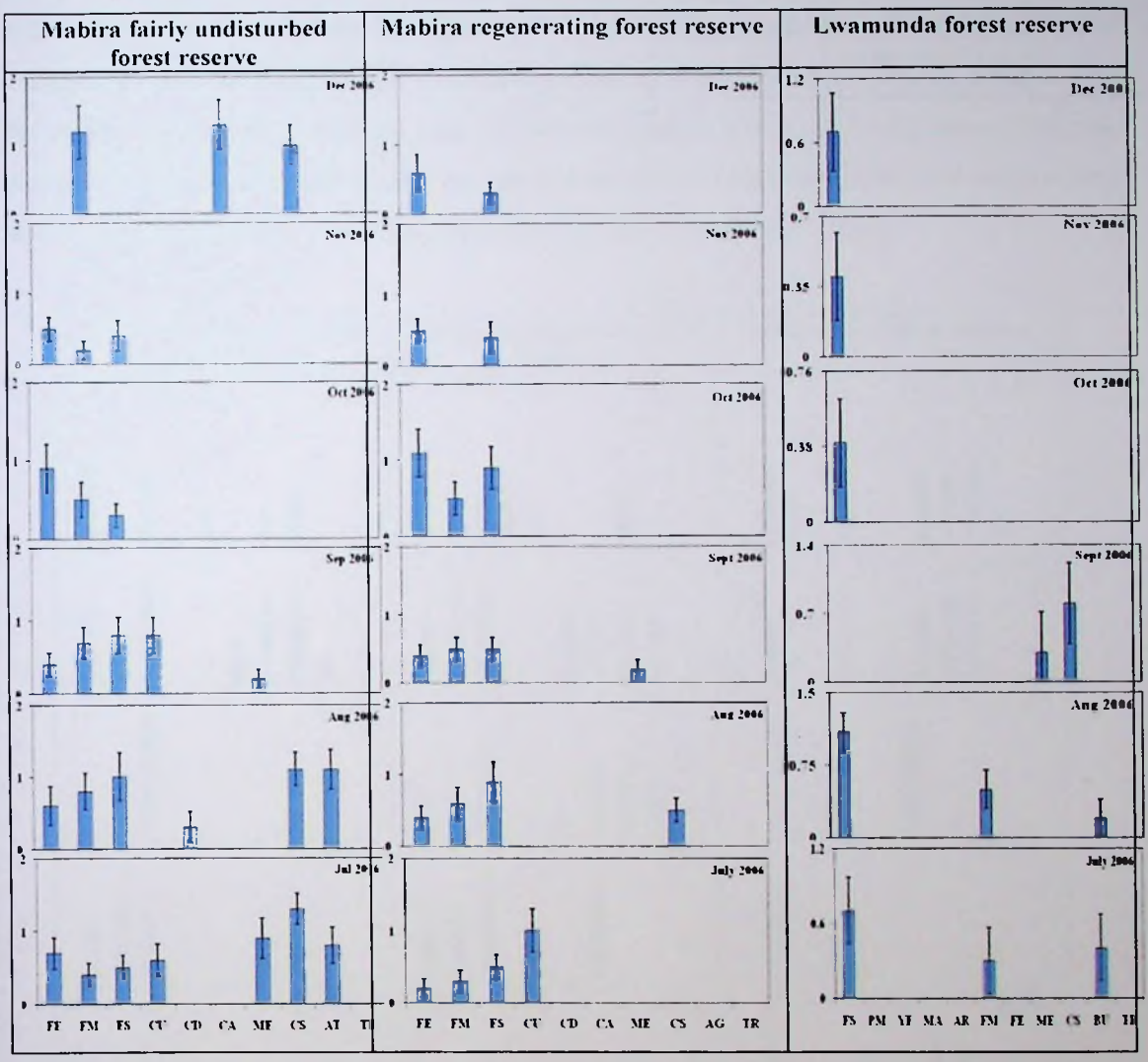


Figure 4.2c Mean variation with standard error (SE) of fruit abundance in Mabira (fairly undisturbed and regenerating) and Lwamunda forest reserves from July-Dec 2006.

(Key: **FE-** *F. exasperata;* **FM-** *F. mucuso;* **FS-** *F.sur;***CU-** *C. mildbraedii*; **CD-** *C.durandaii*; **CA-** *C.africana;* **ME-** *M. emunii;* **CS-** *C.indicum;* **AT-** *A. toxicaria*; TR- *T.africana*; **PM-** *P. microcapa*; **MA-** *M. arboreus*; **BU** *B. unijugata* ; **AG-***A. grandibracteata* ; **YF-***R. edulis*)

The month of November 2006 registered the lowest level of food availability.The only food available for mangabeys in the three study sites were figs although they were inedible in Lwamunda (Fig. 4.2d). On the contrary, the average number of trees bearing fruits in Lwamunda were only five (5) with a mean abundance score below 1. The

relatively low standard error (SE) in both M1 and M2 was indicative of reliable food for mangabeys and the wide SE for Lwamunda denoted unreliable food source. Despite the November 2006 rain at 400mm and 150 mm in Mabira and Lwamunda forest reserves respectively (Fig 4.3a and b), the dry spell from July to October 2006 had irreversibly affected food availability for subsequent months in all the 3 study sites.

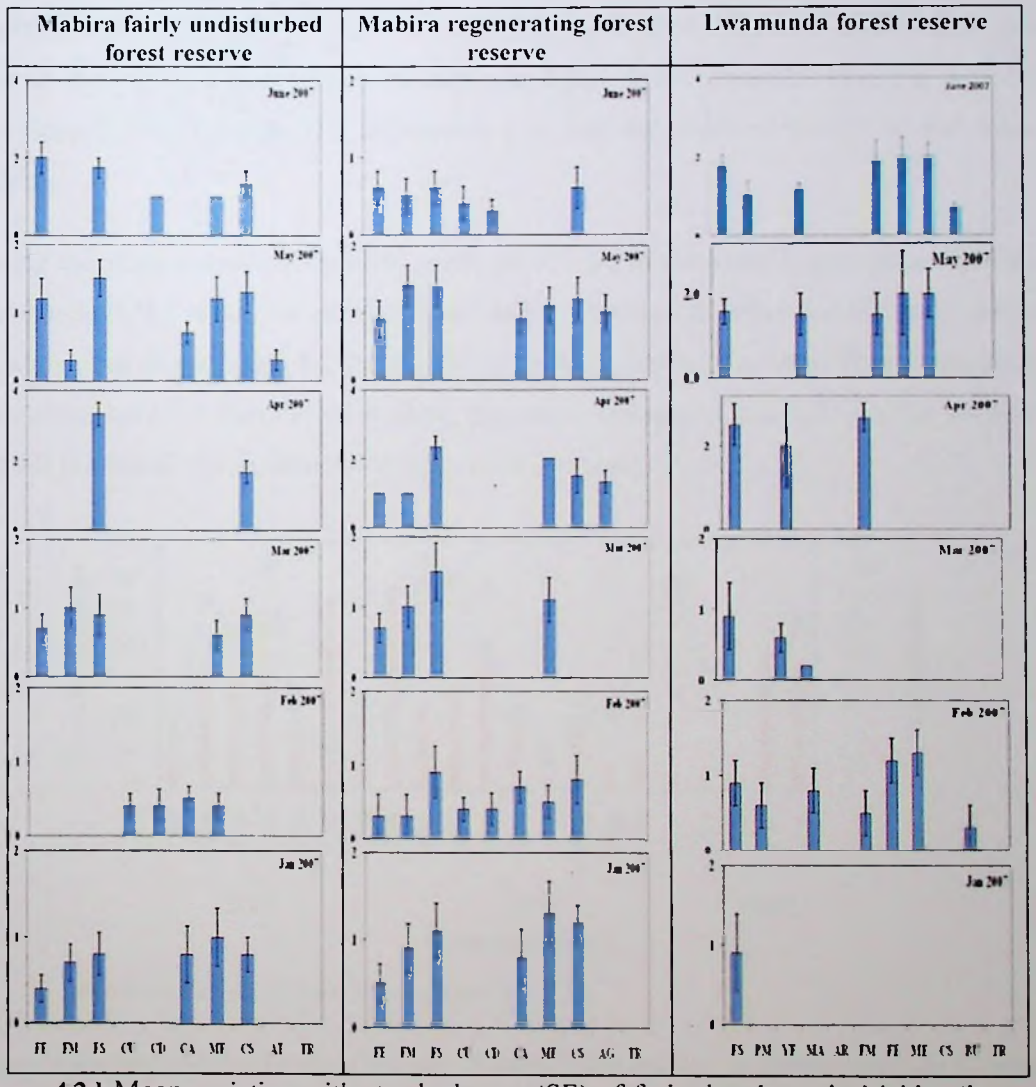


Figure 4.2d Mean variation with standard error (SE) of fruit abundance in Mabira (intact and regenerating) and Lwamunda forest reserves from Jan-June 2007.

(Key: **FE-** *F.exasperata;* **FM-** F. *mucuso;* **FS-** *F. sur;***CU-** *C. mildbraedii*; **CD-** *C. durandait*; **CA-** *C.africana;* **ME-** *M. emunii;* **CS-** *C.indicum;* **AT-** *A. toxicaria*; TR- *T.africana*; **PM-** *P.microcapa*; **MA-** *M. arboreus*; **BU** *B. unijugata* ; **AG-***A. grandibracteata* ; **YF-***R. Edulis*)

The variation in the amount of rainfall received per given period seemed to influence the availability of food sources in both study sites. During the wet season (February-June), fruit abundance was higher than during the beginning of the rainy season and throughout the dry season (July-September and December-January) depending on the study site. However, the dry spell of the later part of 2006 and early 2007 was so severe that most marked trees in the three study sites did not bear fruit. The impact of the November rainfall on level of tree fruiting was explicitly realized in February 2007 when over 5 trees in each forest reserve were in fruit (Fig 4.2d). It was probable that the dry season experienced between June and September also had an effect on flowering and later on fruiting

During the study period, the rainfall trend within the Mabira and Lwamunda Mabira and Lwamunda (ML) varied on monthly basis and it appeared to influence fruit abundance in all study sites as indicated by the number of trees in fruit per month. There was positive correlation between number of fruiting trees and amount of rainfall. As the amount of rainfall increased, the number of fruiting trees increased.

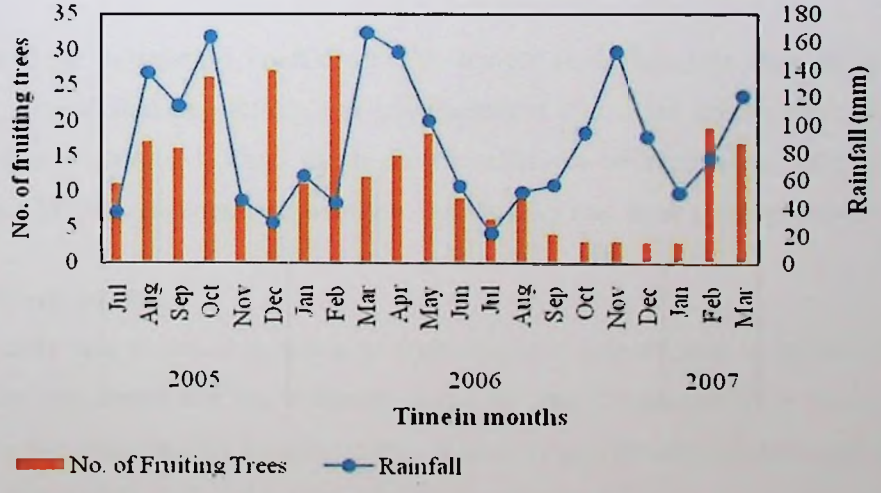


Figure 4.3a Relationship between amount of fainfall and number of fruiting trees in Lwamunda forest reserve during the study period from July 2005 to March 2007. (*Source for rainfall data:* Uganda Meteorological Department)

While the correlation coefficient in Lwamunda was 0.1031 (Fig 4.3(a), it was 0.3114 in Mabira (M1) and 0.1934 in Mabira (M2) (Fig 4.3 (b).

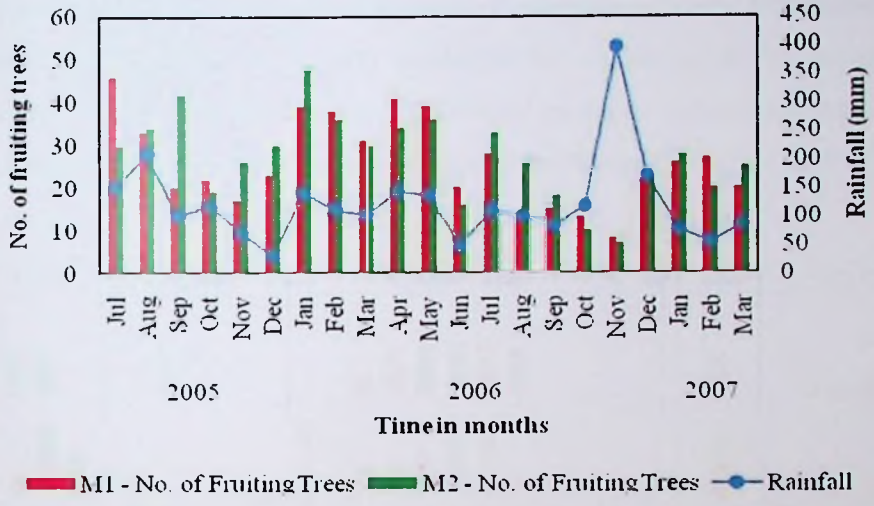


Figure 4.3b Relationship between amount of fainfall and number of fruiting trees in both Mabira (M1) and Mabira (M2) forest reserves during the study period from July 2005 to March 2007. (*Source for rainfall data:* Uganda Meteorological Department)

Evidently, the correlation coefficient was lowest in Lwamunda than in M1 and M2 because of incessant tree felling and encroachment by human communities living at the forest edge. Mabira (M1) had the highest coefficient because of its fairly undisturbed status and M2 was regenerating with low tree density and thick undergrowth.

4.3.3 Fruit quality

Fruit quality was assessed in terms of fruit ripeness, size of fruit as dictated by weight, fruit parts consumed and the different stages of fruit development at which they were available for consumption by mangabeys. These three variables varied with habitat type namely Mabira M1, M2 and Lwamunda forest reserves.

4.3.3.1 Fruit ripeness

It was observed that fruit abundance as represented by number of fruiting trees did not directly translate into food availability. This was because some trees aborted immediately

after fruiting due to stress or other factors which were beyond the scope of this study. In such cases, the fruits were not available as food for mangabeys. Other incidences that rendered some fruits unavailable for consumption by mangabeys were when some proportion of fruit was inedible on account of unripeness. Only the edible proportion constituted fruits or parts that were available for consumption by mangabeys. The inedible proportion contributed to the overall food potential within a habitat. The number of trees with edible fruits varied spatiotemporally as illustrated in Figs 4.4a to 4.4d.

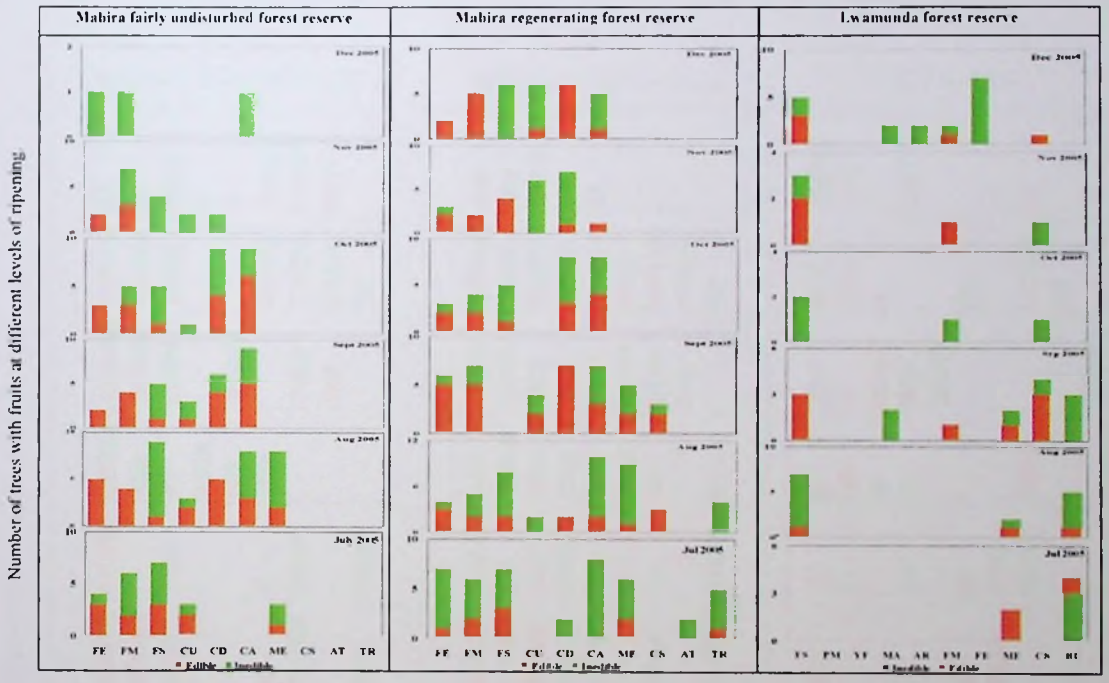


Figure 4.4a Number of edible and inedible fruits as indices of potential available food in Mabira and Lwamunda forest reserves from July-Dec 2005.

(Key: **FE-** *F. exasperata;* **FM-** *F. mucuso;* **FS-** *F. sur;***CU-** *C. mildbraedii*; **CD-** *C. durandaii*; **CA-** *C. africana;* **ME-** *M. emunii;* **CS-** *C. indicum;* **AT-** *A. toxicaria*; TR- *Treculia africana* **PM-** *P. microcapa*; **MA-** *M. arboreus*; **BU** *B. unijugata* ; **AG-***A. grandibracteata* ; **YF-***R. edulis*)

During 2006 in both Mabira and Lwamunda forest reserves (Fig 4.4b and 4.4c), the mean number of fruit that were edible was about 10, 9 and 4 with a standard deviation of 8, 6 and 3 respectively. Although the variance between M1 and M2 was not significant, it was

markedly different between them and Lwamunda. Whereas there was edible fruit of one type of the other in Mabira (M1) throughout the year albeit in different quantities, there was almost no edible fruit in Lwamunda during the months of October to December. Surprisingly in Mabira (M2), the edible fruit seemed more abundant from the months of January to June than it was in either M1 or Lwamunda. However, the potential for increased food availability as indicated by the inedible fruit was higher in M1 than in either M2 or Lwamunda. The mean number of trees with inedible fruits was 20, 24 and 5 with a standard deviation of 10, 15 and 4 respectively.

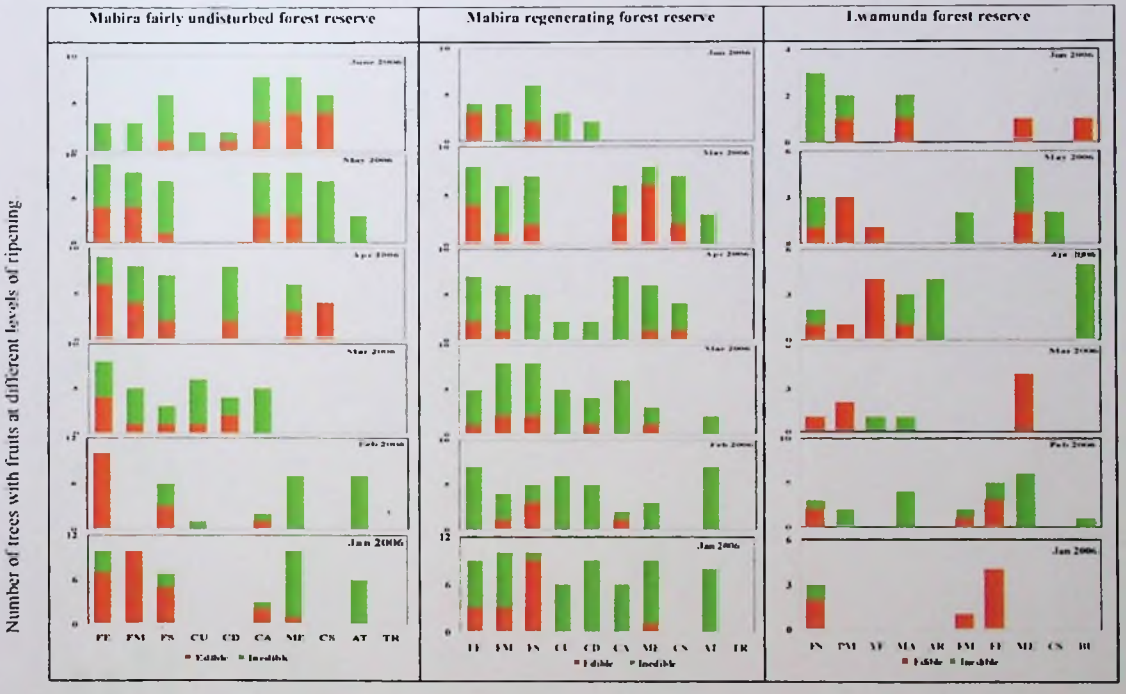


Figure 4.4b Number of edible and inedible fruits as indices of potential available food in Mabira and Lwamunda forest reserves from Jan-June 2006.

(Key: **FE-** *F. exasperata;* **FM-** F. *mucuso;* **FS-** *F. sur;* **CU-** *C. mildbraedii*; **CD-** *C. durandaii*; **CA-** *C.africana;* **ME-** *M. emunii;* **CS-** *C.indicum;* **AT-** *A. toxicaria*; TR- *T.africana*; **PM-** *P. microcapa*; **MA-** *M. arboreus*; **BU** *B.unijugata* ; **AG-***A.grandibracteata* ; **YF-***R. edulis*)

During the months of July, August and December, there was a limited number of trees with edible fruits in M2 although the potential in form of inedible fruits existed in the former two months than in December. In Lwamunda forest reserve, there was perpetually limited potential and edible fruit. It was only during the months of February that there was comparable number of 16 trees that were in fruiting but had inedible fruit. Overall, the annual mean number of fruitless individual trees in Lwamunda was 90 while in Mabira M1 it was 74 and 69 in M2 which implied that there was relatively more food in Mabira forests than in Lwamunda at any one time during 2006.

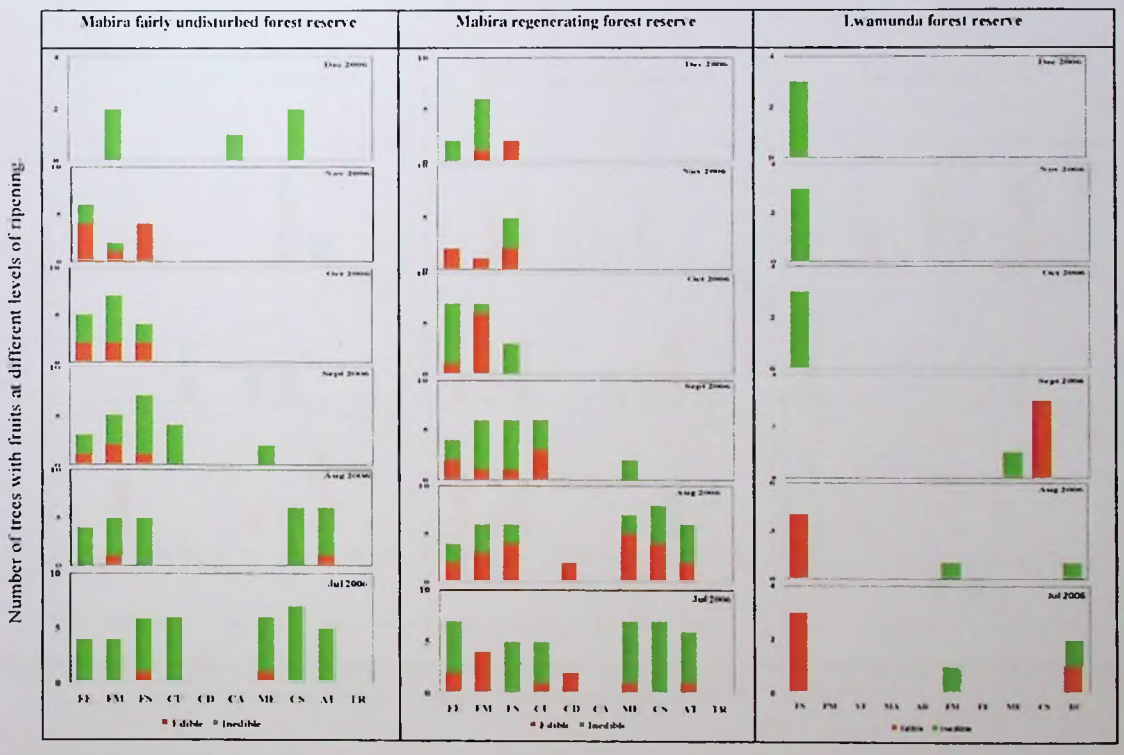


Figure 4.4c Number of edible and inedible fruits as indices of potential available food in Mabira and Lwamunda forest reserves from July-Dec 2006.

(Key: **FE-** *F. exasperata;* **FM-** F. *mucuso;* **FS-** *F. sur;* **CU-** *C. mildbraedii..*; **CD-** *C. durandaii*; **CA-** *C.africana;* **ME-** *M. emunii;* **CS-** *C.indicum;* **AT-** *A. toxicaria*; TR- *T.africana*; **PM-** *P. microcapa*; **MA-** *M. arboreus*; **BU** *B.unijugata* ; **AG-***A.grandibracteata* ; **YF-***R. edulis*)

From January to March 2007, the number of trees with edible fruit were fewer across the three habitats (Fig 4.4d) than during other months. Most of the trees in fruit were figs, *M.eminii* and *C.indicum*. From January to February, it was a nutritional challenge for the mangabeys inhabiting Lwamunda forest reserve because the only fruiting trees were *F.sur* and *F.mucuso* which unfortunately did not have edible fruit. In Mabira M1 and M2, the nutritional situation was manageable because of the comparatively more fruiting trees with edible fruits. However, most of these fruit trees belonged to a category of fall-back fruits known to be nutritionally deficient which implied that although they were available, they probably could not meet the dietary requirements of mangabeys.

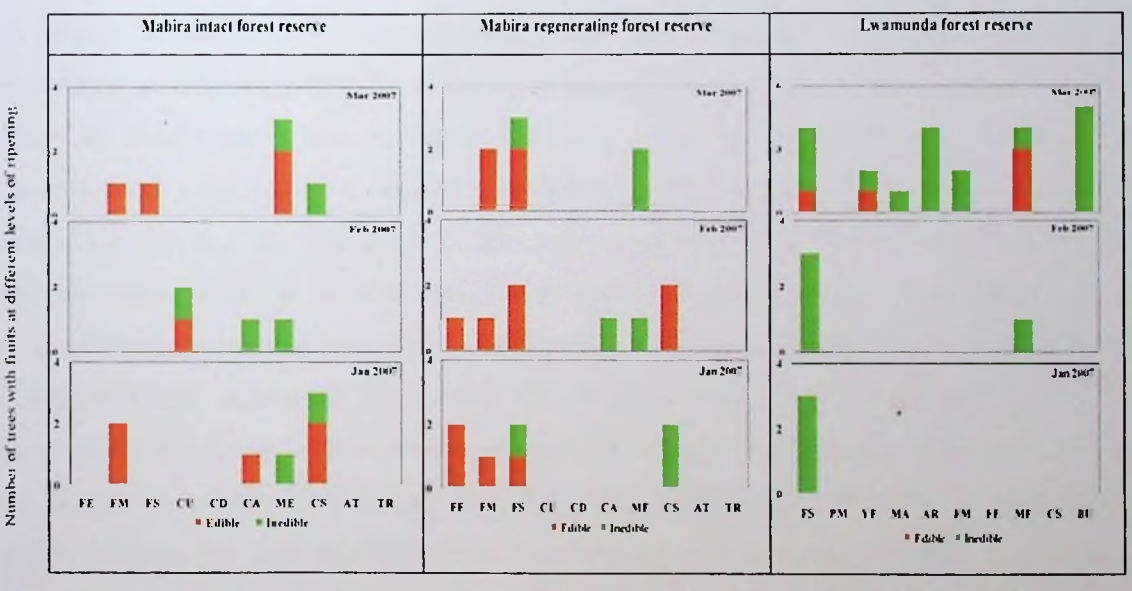


Figure 4.4d Number of edible and inedible fruits as indices of potential available food in Mabira and Lwamunda forest reserves from Jan-March 2007.

(Key: **FE-** *F. exasperata;* **FM-** F. *mucuso;* **FS-** *F. sur;* **CU-** *C. mildbraedii..*; **CD-** *C.durandaii*; **CA-** *C. africana;* **ME-** *M. emunii;* **CS-** *C.indicum;* **AT-** *A. toxicaria*; TR- *T.africana*; **PM-** *P. microcapa*; **MA-** *M. arboreus*; **BU** *B.unijugata*; **AG-***A. grandibracteata* ; **YF-***R.edulis*)

Generally, fruit abundance and availability depicted by ripeness occurred during wet as well as dry seasons. Most species showed a peak in fruiting during the second dry season

(December -January). A peak period in the production of mature fruit occurred during the latter part of the long dry season. When phenological patterns of fruit tree species that occurred in both forests were compared, there was no significant difference (one way Anova, $p>0.05$). They tended to follow the general trends of the respective forest ecosystems.

It was observed that fruit abundance did not directly translate into food availability because a proportion of fruit trees had unripe fruits and therefore inedible. To exemplify the status of tree fruitfulness over a period of time, year 2006 was chosen. During this year, the mean number of fruit that were edible in both Mabira and Lwamunda forest reserves was about 10, 9 and 4 with a standard deviation of 8, 6 and 3 respectively. Although the variance between M1 and M2 was not significant ($p= 0.231$ at 95%), it was markedly different between them and Lwamunda. Whereas there was edible fruit of one type of the other in Mabira (M1) throughout the year albeit in different quantities, there was almost no edible fruit in Lwamunda during the months of October to December. Surprisingly in Mabira (M2), the edible fruit seemed more abundant from the months of January to June than it was in either M1 or Lwamunda. However, the potential for increased food availability as indicated by the inedible fruit was higher in M1 than in either M2 or Lwamunda. The mean number of trees with inedible fruits was 20, 24 and 5 with a standard deviation of 10, 15 and 4 respectively. During the months of July, August and December, there were virtually no edible fruits in M2 although the potential in form of inedible fruits existed in the former two months than in the latter one month. In Lwamunda forest reserve, there was perpetually limited potential and edible fruit. It was only during the months of February that there was comparable number of 16 trees that were in fruiting but had inedible fruit. Overall, the annual mean number of fruitless replicates in Lwamunda was 91 while in Mabira M1 it was 70 and 67 in M2 which implied that there was relatively more food in Mabira forests than in Lwamunda at any one time during 2006. Generally, fruit availability was relatively more in Mabira forests than in Lwamunda as summarized in Fig 4.5.

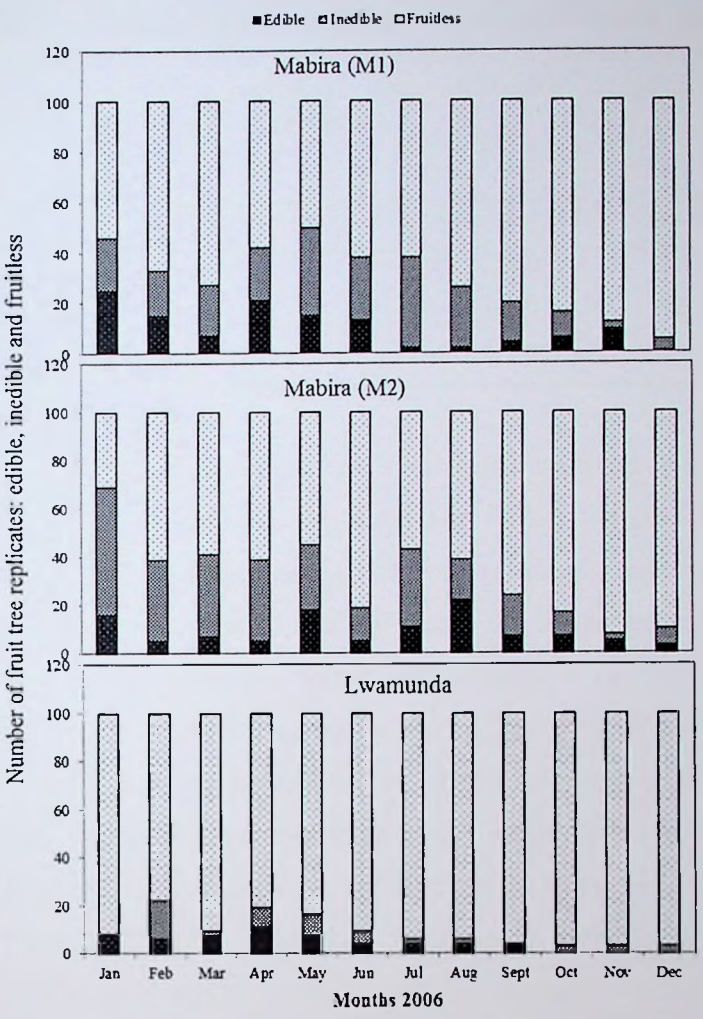


Figure 4.5 Seasonal variation of fruit availability for mangabeys in Mabira and Lwamunda forest reserves during 2006 study period

Table (4.2) shows the mean annual number of trees that had relatively ripe fruit and therefore could be eaten by mangabeys (edible) and those that fruited but fruits were still unripe (inedible) and as such could not be utilized as food for mangabeys. In addition, the table also shows the number of trees that were fruitless which was indicative of fruit availability as represented by 90 in Lwamunda, 74 in Mabira M1 and 69 in M2 during 2006.

Table 4.2 Comparative analysis of fruit availability indicated by mean number of priority fruit trees commonly utilized as food by mangabeys in Mabira (M1&M2) and Lwamunda forest reserves during period of study 2005-2007. (*Figures in brackets are the coefficients, M1 being the reference*)

Tree fruitfulness	Fairly undisturbed (M1)	Regenerating (M2)	Lwamunda	P=value
Edible fruits	10.15	10.20 (0.05)	3.85 (-6.3)	0.0011
Inedible fruits	15.7	20.7 (5)	6 (-9.7)	0.0001
Fruitless	74.15	69.1 (-5.05)	90.15 (16)	0.0000

Coefficience measured the variance of fruit availability between M2 or Lwamunda from Mabira M1 which was a reference or standard. The further the coefficient was from M1, the greater was the difference between the two forests being compared. When analysis of variance was performed to compare edibility across the three study sites (Table 4.2), the results showed that; there was no significant difference ($p>0.001$) between Mabira undisturbed (M1) and Mabira regenerating (M2) forests indicated by the small co-efficiency of 0.5 but there was significant difference between Mabira undisturbed and Lwamunda. When inedibility comparisons were made between forests, the results reflected that there was no significant ($p>0.05$) difference between the independent variables in M1 and M2 forests. However, there was a significant ($p<0.05$) difference between the variables; M2 and Lwamunda, then Lwamunda and M1. Fruitlessness was significantly different ($p<0.001$) between the variables M1 and Lwamunda. However, there was no significant ($p>0.001$) difference between the other comparisons (M1 and M2; M2 and Lwamunda).

4.3.3.2 Fruit weight

Although the width and length of fruits were measured, the inconsistency in their morphology rendered the collected data unusable. Hence only the weight parameter has been used to correlate with maturity (Table 4.3 and 4.4). As expected the mean weight of fruit increased exponentially up to week 15-24 depending on type of fruit and then it levelled off as the fruit matured and ripened.

Table 4.3 Weight (g) and standard deviation in *brackets* of fruit at respective development stages (expressed in weeks after fruiting) in Mabira forest reserve.

Fruit type	3-4wks	8-12 wks	10-18wks	15-24wks	20-28wks	22-28wks	24-32wks
C. africana	0.2(0.04)	0.3(0.02)	0.25(0.2)	1.43(0.05)			
C. durandii	0.1(0.03)	0.2(0.03)	0.5(0.21)	1.3(0.03)		-	
C. mildbraedii	0.3(0.03)	0.4(0.02)	0.7(0.25)	1.5(0.13)	1.5(0.03)		
F. exasperata	2.83(0.5)	5.87(0.15)	18.17(0.51)	16.0(0.24)	2.83(0.5)		
F. mucuso	1.72(0.1)	3.14(0.27)	11.75(0.45)	18.2(0.5)	20.12(0.25	21.72(0.1)	
F. sur	6.8(0.42)	9.11(0.71)	11.0(0.42)	10.8(0.71)	9.67(0.03)	11.23(0.01)	10.71(0.1)
M. eminii	2.14(0.3)	2.89(0.26)	4.33(0.33)	4.2(0.37)	4.5(0.03)	2.14(0.3)	
C. indicum	3.78(0.3)	4.25(0.16)	4.56(0.02)	6.23(0.2)	6.48(0.13)		
P. microcapa	2.83(0.5)	5.87(0.15)	8.17(0.51)	16.0(0.24)	17.8(0.27)		

Table 4.4 Weight (g) and standard deviation in (*brackets*) of fruit at respective development stages (expressed in weeks after fruiting) in Lwamunda forest reserve.

Fruit type	3-4wks	8-12 wks	10-18wks	15-24wks	20-28wks	22-28wks	24-32wks
B. unijugata	1.5(0.5)	2.13(0.82)	2.25(0.25)	3.5(0.5)	3.75(0.02)		
R. edulis	1.5(0.24)	2.3(0.16)	2.49(0.07)	2.42(0.21)	2.52(0.06)	2.61(0.03)	2.73(0.1)
M. arboreus	7.35(0.36)	13.45(0.11)	35.09(0.72)	114.23(0.09)	147.32(0.15)	150 02(0.45)	
F. exasperata	2. 3(0.1)	3. 7(0.1)	5. 7(0.51)	6.0(0.24)	2. 3(0.1)		
F. mucuso	2.2(0.1)	2.14(0. 7)	6.5(0.4)	8.2(0.1)	10.2(0.2)		
F. sur	3.4(0.08)	3.57(0.42)	4.2 (0.21)	4.75(0.48)	5.25(0.06)	4.8(0.03)	5.72(0.06)
M. eminii	3.25(0.04)	3.0(0.12)	3.0(0.03)	4.38(0.26)	3.9(0.09)		
C. indicum	3.2(0.24)	4.7(0.21)	6.3(0.25)	4.5(0.27)	8.1(0.22)	3.2(0.24)	
P. microcapa	3.2(0.1)	4.0(0.46)	4.11(0.39)	3.63(0.32)	3.88(0.30)		

When a t-test was performed to find out whether there was significant difference in weights of fruits of the same tree but growing in different study site, it was found not to be significant ($p > 0.05$; $p = 0.2630$) regardless of the stage of development.

4.3.3.3 Fruit parts consumed by mangabeys

It was observed that as fruit availability declined, mangabeys devised coping mechanisms against fruit scarcity. They manipulated or processed fruit to gain access to preferred parts. Consequently, there was elaborate fruit processing in the severely degraded Lwamunda forest reserve than there was in the fairly undisturbed portion of Mabira forest reserve (M1). Essentially, there were three parts of the fruit consumed during its

development namely pulp, endosperm and seed. The manipulation methods used by mangabeys to access them varied with fruit type and stage of maturity (Table 4.5).

Table 4.5 The different edible fruit parts consumed by mangabeys in Mabira and Lwamunda forest reserves (*Shaded cells indicate the fruit part consumed by mangabeys*)

	Edible part of fruit consumed											
Fruit species	**Mabira (M1)**				**Mabira (M2)**				**Lwamunda (LD)**			
	E	S	P	W	E	S	P	W	E	S	P	W
C. indicum			■		■		■		■		■	
M. eminii			▫				■		■		■	
P. microcapa			▫		■		■		■		■	
Afromomum africanum										■		
R. edulis											■	
F. sur				■				■				■
F. exasperata				■				■				■
F. mucuso				■				■				■
B. unijugata		■								■		
M. arboreus									■		■	
A. grandibracteata										■		
C. africanas		■				■						
C. durandii		■				■				■		
Turreanthus africanus												
Treculia africana										■	■	
Cola spp										■		
Domesticated fruits							■				■	

E= endosperm; S= seed; P= pulp; W= whole fruit; ▫ = Not observed but probably utilized

Pulp consumption was observed during consumption *Celtis* spp and *R. edulis*. Small sized fruits were shoved into the mouth, then either chewed or ingested or the ripe supple fruit pulp was sucked off the seed and the fruit skin was spat (Fig 4.6).

Figure 4.6 Fruit skins of *R. edulis*) spat out after consumption of the pulp fruit in Lwamunda forest reserve

Alternatively, mangabeys consumed whole figs (*F. sur, F. exasperata, F. mucuso*) and then passed out seeds in their faeces. Domesticated fruits that had been abandoned in

Mabira M2 after restriction on encroachment were consumed directly or in piece meal depending on fruit size. For example small ripe banana was peeled then ingested whole while pineapples were consumed in piece meal. The fruit peels or exo-carp of mature *Afromomum* or ripe domesticated fruits like passion fruits were split open by a single bite and the contents consumed directly. Owing to stiff competition with humans and other frugivores, mangabeys did not wait for them to ripen but consumed them at the earliest opportunity.

The consumption of endosperm by mangabeys involved elaborate manipulation of fruits especially in Lwamunda and to a certain extent in Mabira M2 forest reserves. It involved gnawing pulp off young fruit and biting through the endocarp to pick out the endosperm. The pulp was not eaten but spat probably due to bitterness or astringency. Although the technicalities of endosperm retrieval were similar in the two study sites, they distinctively varied with fruit species. Whereas mangabeys laboriously processed young *B. unijugata*, *C. indicum*, *P. microcapa*, *M. arboreus* and *M. eminii* fruit to access the seed or endosperm in Lwamunda, there were few observable incidences of fruit processing in fairly undisturbed Mabira forest reserve. When picking out endosperm from immature *C. indicum*, mangabeys bit the fruit longitudinally or vertically to remove the endosperm depending on habitat. Whereas mangabeys in Lwamunda split young fruits of *C. indicum*, *M. eminii* and *P. microcapa* longitudinally to access the endosperm during periods of scarcity in Mabira M2, the *C. indicum* fruit was split transversely across the fruit (Fig 4.7).

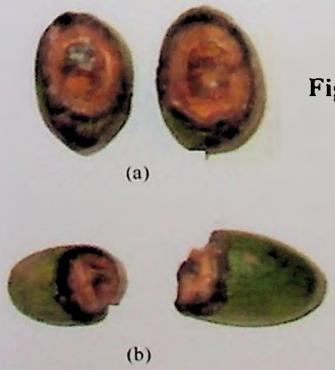


Figure 4.7 Different splitting adaptations for *C. indicum* in Lwamunda (a) and Mabira-M2 (b) forest reserves during periods of food scarcity.

As the seed matured and the seed coat hardened, it became progressively difficult to access the endosperm despite their strong jaws and molars. Instead, mangabeys gnawed the pulp (Fig. 4.8) and consumed it depending on the level of ripening. In this study, gnawing was only observed in severely degraded Lwamunda and Mabira regenerating (M2) forest reserves. The pulp was completely or partially gnawed depending on availability of other food items. For example in Lwamunda, when the food was scarce during the months of December to February, most of the *C. indicum* fruits were completely gnawed (Fig. 4.8 (b). When other foods were available during the months of March-June, *C. indicum* at the periphery of the forest was partially gnawed (Fig. 4.8 – a).

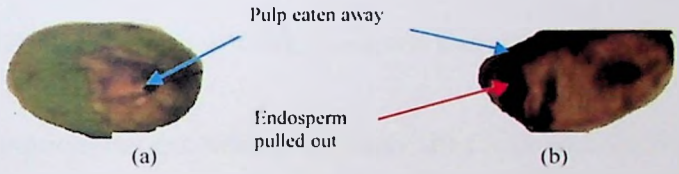


Figure 4.8 Partial or complete gnawing of *C. indicum* pulp by mangabeys in both Lwamunda and Mabira - M2 forest reserves

The *P. microcapa* fruit was bitten through longitudinally to access the endosperm just like *C. indicum* was consumed. The pulp of young fruit (Fig 4.9) was spat out in preference to the endosperm as a food source probably due to high levels of defensive secondary compounds in the immature pulp.

Figure 4.9 The chemically defended *Pseudospondias* pulp spat out by Mangabeys in preference for probably less defended endosperm

Mangabeys also consumed endosperm of young *M.arboreus* at stage 1 (about 4 months after fruiting. The composite fruit was green and immature but during food scarcity,

mangabeys bit through the fruit to pick out only the endosperm from fruit segment (Fig 4.10)

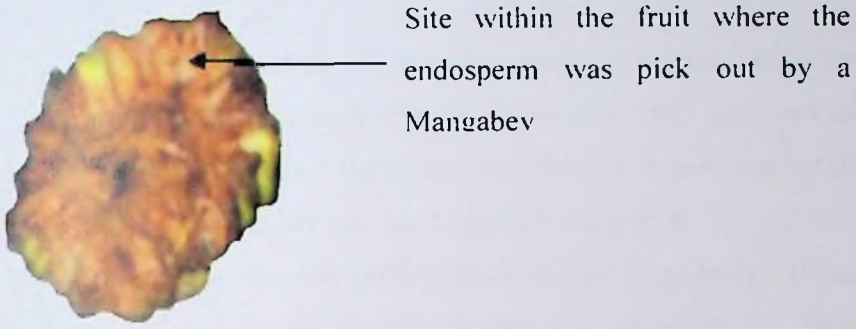


Figure 4.10 Fruit segment from which endosperm was picked out and consumed by mangabeys

Seed consumption was exhibited in all study sites with specific fruits; *A. grandibracteata*, *Celtis africana*, *C. durandii*, *Turreanthus africanus* and *Treculia* spp. These were the commonest sources of seed for mangabeys in Mabira and Lwamunda forest reserves (Fig. 4.11). Naturally, a mature seed contains all the high quality nutrients required by the subsequent germinating seedling but with high levels of antifeedants for protection against pests. However at the immature stage of fruit development, the endosperm appears to contain less antifeedants like tannins and therefore ideal as a food source for mangabeys.

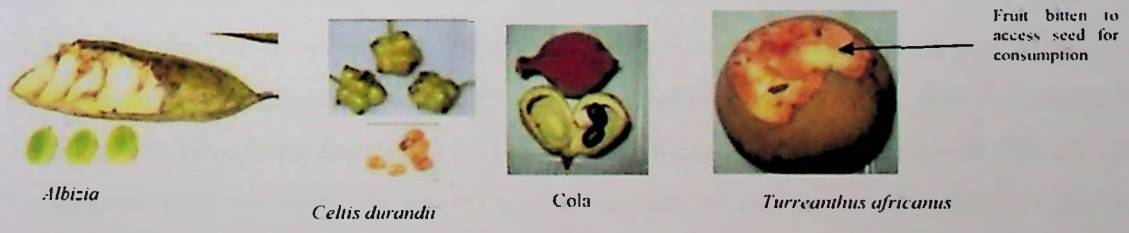


Figure 4.11 The different images of different fruits processed by mangabeys to access seed in Lwamunda forest reserve.

As the seed matures, the level of antifeedants tends to increase and with the lignifying seed coat, the endosperm becomes progressively more inaccessible to mangabeys. On the contrary, the tannins seem to decrease in fruit pulp as the fruit matures or ripens. This nutrient shift across the fruit parts during development or ripening seemed to determine food choice among mangabeys especially those inhabiting severely degraded forest reserves like Lwamunda.

There were different methods employed by mangabeys to access seeds from fruits or receptacles. They tended to vary with fruit type. Quite often, the fruit pod or endosperm was yanked out of the fruit by force using the forelimbs. For instance, at the immature stage of *Albizia*, mangabeys bit off the seed coat of the pod to access the young seed which was the only portion of the tree utilized as food. After maturity, *Albizia* seed were not accessible probably due to the hard seed coat and probably the high content of antifeedants also contributed to the inaccessibility. *C. durandii* and *C. africana* were similarly utilized at four (4) weeks after fruiting. Conversely, *Treculia*, cola species and *Turreanthus africanus* seeds were only consumed when the fruit was mature. Now, this was interesting because one would have expected the seeds of these fruits to be laden with anti-feedants at this stage of maturity which would render them unavailable for consumption. This observation may portray three scenarios; either not all seeds are highly defended by secondary compounds or the level of defence is low at maturity stage in these particular fruits. It was probable that it was a strategy for the plant to ensure that seeds were dispersed at the appropriate time of maturity.

4.3.3.4 Fruit development stages at consumption

It was observed that most fruits exhibited several stages of development or ripening and mangabeys utilized different parts at each of the stages depending on fruit type. The classic example was *B. unijugata* which has been exhaustively described in Chapter 5 of this thesis. For purposes of this paper only six fruiting tree species that exhibited the above pattern have been described in detail. They included three species of figs (*F. sur, F. exasperata, F. mucuso*) but since the ripening sequence was similar, only *F. sur* has

been exhaustively described in this Chapter. Others include *R. edulis*, *C. indicum*, *P. microcapa*, *M. eminii* and *M. arboreus*

Ficus sur was consumed whole between 20-32 weeks after fruiting. There were seven visually distinguishable stages of development and mangabeys started consuming them from stage 4 (20 wks) to stage 7 (32 wks) which were the edible stages of ripening (Fig 4.12).

Figure 4.12 Development and ripening stages (weeks after fruiting) of *F. sur* in Mabira and Lwamunda forest reserves

The first three stages of figs development (3-15 weeks after fruiting) were not utilized as food probably due to high levels of secondary compounds evidenced by substantial amounts of sticky sap. After the fourth month, the fruit matured and started to ripen sequentially. It appears that choice of stage for consumption was highly influenced by fruit abundance, level of competition exerted by other frugivores and availability of other food items within the home range. It was also probable that mature and ripe fruit with low secondary compounds was a strategy of the plant to ensure seed dispersal.

With regard to *R. edulis* or yellow fruit, mangabeys only utilized the pulp of the very ripe fruit as food although it exhibited seven stages of ripeness (Fig. 4.13).

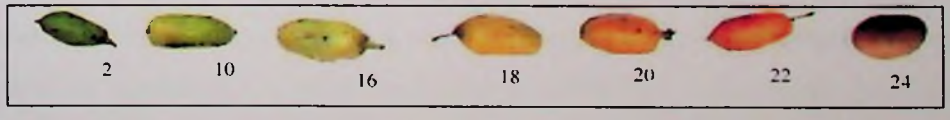


Figure 4.13 Development and ripening stages (weeks after fruiting) of *R. edulis* in Lwamunda forest reserve.

The fruit skin was peeled off by the front teeth and discarded then the fruit was shoved into the mouth where the pulp was sucked off the seed as shown in Fig. 4.6 (Sub-section 4.3.3.3). *R.edulis* was only present in Lwamunda and fruited in abundance during the months of February to May. Probably, the high level of abundance may explain why only the ripe fruit was consumed as opposed to other stages.

In both forest reserves, *C. indicum* was abundant and available for more than 18 months of the study period which qualified it to be a "fall back" fruit. There were five (5) distinct stages observed during its development (Fig 4.14). Different parts of the fruit were utilized as a food resource from week 3 to week 24 after fruiting.

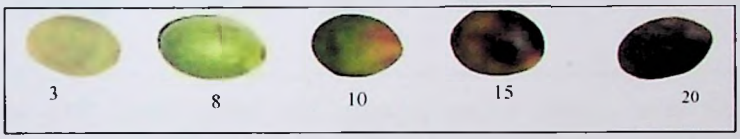


Figure 4.14 Development and ripening stages (weeks after fruiting) of *Canarium indicum* in Mabira and Lwamunda forest reserves

At *Stage 1* (3 weeks after fruiting), mangabeys split young fruits longitudinally or transversely to access the endosperm which was the only part of fruit eaten at this stage of development. The variation was attributed to localized foraging habits among mangabeys in Mabira. The pulp at week 3 was intensely rejected and avoided as a food source; probably due to high levels of tannins because mangabeys spat it when picking out the endosperms which were presumably less chemically defended with antifeedants than the pulp. At *Stage 2* (8 weeks after fruiting), mangabeys consumed the pulp in small quantities and predominantly consumed endosperms. It appears, the defensive mechanism in pulp declined slightly as the fruit matured and therefore it was available for consumption. Fruit processing to pick out the endosperm for consumption appeared to be dependent on availability of other food sources within the home range. At *Stage 3* (10 weeks after fruiting), the fruit started ripening from the petiole and it extended progressively to the posterior as evidenced by the colour change from green to brown-maroon. However, it was not ripe enough for the mangabeys to solely depend on the pulp as food source. They seemed to supplement pulp consumption with continued hacking

through the kernel to access the endosperms. After 15-20 weeks after fruiting, the pulp was ripe and ready for consumption. The pulp was more accessible to mangabeys than the endosperm because of the hardening seed coat. Although the matured endosperm or seed was nutritiously superior, it was highly defended with antifeedants and therefore unavailable as a food source.

Pseudospondias microcapa was a priority fruit for mangabeys in Lwamunda but scanty in Mabira forest reserve. It exhibited six visually distinct stages from fruiting to ripening based on colour hues (Fig 4.15).

Figure 4.15 Development and ripening stages (weeks after fruiting) of *P. microcapa* in Lwamunda forest reserves.

At stage 1 (3 weeks after fruiting), the fruits weighed 3g on average and they were still green in colour. However, its endosperm was a source of food for mangabeys during spells of food scarcity. The endosperm was presumably less chemically defended than the pulp. At maturity, when the fruit colour changed from apple green (10 weeks after fruiting) to maroon (15-24 weeks after fruiting), mangabeys changed their feeding habits from consuming endosperm to pulp eating. There were two probable and interrelated explanations namely; effortless access to readily available digestible energy source in the ripe fruit pulp and secondly accessibility to the endosperm was denied due to the hardened kernel. Besides, the endosperm that was developing into seed was probably being heavily defended with antifeedants which rendered it unavailable for consumption at this stage of development.

Maesopsis eminii occurred in all the three study forest habitats and it exhibited six distiquishable stages from fruiting to ripening (Fig. 4.16).

Figure 4.16 Development and ripening stages (weeks after fruiting) of *Maesopsis eminii* in Mabira and Lwamunda forest reserves.

Mangabeys consumed different portions of the fruit at different stages of development. At *stage 1* (3 weeks after fruiting), the fruit was fairly immature but its endosperm was utilised as a food source in both forest reserves by mangabeys. However, the regularity of utilization varied with habitat. Whereas mangabeys in Lwamunda consumed its endosperm regularly, the fruit was virtually ignored in Mabira. At *stage 2* (8 weeks after fruiting), the fruit pulp was still unpalatable but the endosperm could be picked out by splitting the fruit longitudinally. At *stage 3* (10 weeks after fruiting), fruit was partially ripe but it was consumed together with the endosperm. At *stage 4* (15 weeks after fruiting), mangabeys preferred pulp to endosperm probably due to its inaccessibility given the hardened seed coat. It was possible that as the endosperm matured into seed, the level of antifeedants increased appreciably and acted as deterrent to frugivores before it was ready for dispersal. At *stage 5* (20 weeks after fruiting), only the pulp was consumed and at *stage 6* (24 weeks after fruiting), the fruit pulp was so ripe that when it was shoved into the mouth, nothing remained on the spat out seed. Naturally, the level of competition for the ripe fruit was quite stiff at this stage. The main competitors were other frugivores like turracos, hornbills, red-tails and squirrels.

Myrianthus arboreus is a composite fruit which was more common in Lwamunda and the regenerating part of Mabira (M2) than in fairly undisturbed portion of Mabira (M1) forest reserves. There were probably 5 distinct developmental stages for *Myrianthus* fruit (Fig 4.17).

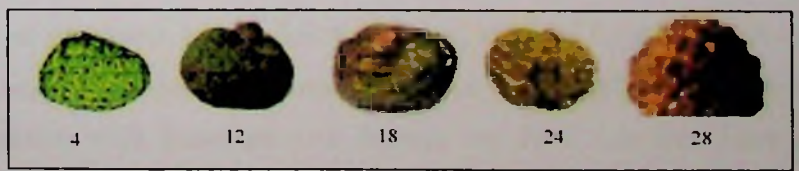


Figure 4.17 Development and ripening stages (weeks after fruiting) of *M. arboreus* in Lwamunda forest reserves.

At stage 1 (4 weeks after fruiting), the composite fruit was green and immature but during periods of food scarcity, mangabeys bit through the fruit to pick out only the endosperm. The enclosing sheaths and the pulp were discarded. At *stage 2*, (12 weeks after fruiting), the fruit was not ripe enough and the desired thin pulp around the seed had bland taste. As such, only the endosperm was utilized as a food source. At *stage 3* (18 weeks after fruiting), the fruit started ripening from the petiole to the posterior and the sweetness of the thin pulp increased. Consequently, both the pulp and endosperm were consumed. When the fruit was yellow and fully ripe (*Stage 4* and *5* i.e. 24-28 weeks after fruiting), the seed enveloped by a thin layer of pulp was plucked out of the fruit and shoved into the mouth. The thin, slimy and sugary pulp was gleaned off seed which was passed out in the excreta.

4.4 Discussion

Fruit abundance and quality appear to be the two probable factors that could have influenced fruit processing among mangabeys in Mabira and Lwamunda (M&L) forest reserves. Fruit abundance tended to vary with seasons and habitats which had been previously subjected different management histories. Consequently, the number of priority fruit trees commonly utilized as food were not available in all the three habitats. For instance, *M. arboreus*, *R.edulis, B. unijugata* and *F. sur* were abundant in Lwamunda but the first two were non-existent while the last two were scanty in M1&M2. Typically these four fruit tree species occur along river banks, forest edge or gaps in degraded forests (Basuta, *unpublished data*). The fruit trees that occurred in all the three habitats namely; *C. indicum, M. eminii F, exasperata,* and *F. mucuso* exhibited varying degrees of fruit processing. It was highest in the severely degraded Lwamunda than in M1 and M2 for each of the fruit trees occurring in all habitats. Generally, the degree of fruit processing seemed to vary with fruit abundance but also with seasonality in M&L forests reserves although tropical forests typically show less dramatic seasonality than temperate or savannah habitats (Okecha and Newton-Fisher, 2006). In the absence of anthropogenic disturbances as observed in M1, forest fauna in tropical forests experience a wider and potentially more consistent food resource base than their counterparts in temperate forests. However, with incessant tree felling, the food resource base is bound to be

inconsistent as demonstrated in Lwamunda forest reserve. In this particular forest, the inconsistence probably contributed to fruit scarcity and subsequent initiation of fruit processing. The vegetation undergrowth in Lwamunda was thick with high species diversity similar to M2. The feeding behaviour of mangabeys during periods of food scarcity in this study was similar to that observed by other researchers cited above and elsewhere (Ham, 1994) though with slight variation between the different forest habitats.

Seasonality in frugivory refers to patterns of variation in fruit abundance (Buzzard, 2006). In the present study, variation in fruit abundance was indicative of the level of forest degradation. At a glance, the overall level of fruit abundance decreased from the part of Mabira that was fairly undisturbed to Lwamunda which was severely degraded. The temporal variation of fruit availability seemed to be influenced by climatic change and specifically the amount of rainfall received during the period of study (Uganda Metrological Department, 2008). This finding was in agreement with Moscovice *et al.*, (2007) who reported that tree fruit availability was positively correlated with rainfall, with a period of relative tree fruit scarcity corresponding with the long dry season in Rubondo Island, Tanzania. Seasonality in Lake Victoria Basin (LVB) is best described in terms of dry or wet spells characterized by low ($\leq$ 50mm) or high rainfall ($\geq$51mm) per month. Admittedly, the limited timeframe of the study and number of fruit trees monitored does not allow definitive influence of seasonality and amount of rainfall on phenological trends. Other studies (Chapman *et al.*, 1999) had also established positive correlation between number of fruiting trees and amount of rainfall but later on revised the claim. However, the major influence on fruit abundance in the three habitats was their management histories. Whereas there was strict enforcement of the 1993 UNESCO management strategy (Alpert, 1996) in Mabira forest reserve, it was relaxed in Lwamunda which might have contributed to its low number of trees in fruit. Differences in availability and abundance will lead mangabeys to consume different types of fruits at different levels of maturation (Pienkowski *et al.*, 1998; Ham, 1994). For that to happen, mangabeys have to devise processing mechanisms to access the selected fruit or fruit part at different stages of maturation and availability based on various criteria as advanced by

several authors (Felton *et al.*, 2009; Leighton, 1993; Kinzey and Norconk, 1990; Herrera, 1982).

Theoretically, when food becomes scarce either because of low production, famine or increased population, humans formulate mitigation strategies for sustainable utilization of the available meagre food items (Godfray *et al.*, 2010; Braun and Olofinbiyi, 2007; Braun et al., 1999; Webb and Braun, 1994). Understandably, non-human primates tend to be extravagant with food during glut seasons and thrifty during seasons of scarcity. They have developed strategies for mitigating food scarcity for example mangabeys in the Dja Reserve, Cameroon shifted from a diet dominated by fruit to one dominated by seeds, flowers, and young leaves during periods of scarcity (Poulsen *et al.*, 2001). In Tana riverine forests, Kimuyu *et al.* (2012) also observed the same dietary shift during periods of food scarcity. Sometimes, mangabeys reverted to feeding on fall-back foods (Marshall and Wrangham, 2007; Lambert *et al.*, 2004) as described exhaustively in Chapter 6 of this thesis. It appears therefore that fruit processing was an adaption employed by mangabeys to cope with food scarcity.

The level of seed or fruit maturity or ripeness also determines the quality and quantity of macro-nutrient contained therein which may vary with season, type of tree species, location in the canopy, spatial as well as temporal disposition. Mangabey fruit selection criteria was based on fruit quality as predetermined by fruit ripeness, fruit weight and different fruit parts consumed. Apart from the latter quality index, the rest of the quality indices did not vary with habitat. Other studies have included type of fruit ingested (Wrangham and Waterman 1993) and maturity of fruit (Stickler and Chapman, *unpublished data*; Baranga, 1984). As the fruit matured, its hue changed from different shades of green to red, orange and other bright colours depending on fruit species or type. Fruit weight increased exponentially up to the ripening stage and processing varied with fruit size and development stage. Consumption of fruit at different stages of maturity and ripeness may be a factor which may influence fruit processing. Size and sometimes colour changes were a function of fruit/seed maturity. The level of fruit ripeness varied from the yellowish green colour of a mature fruit to a tint of red which was indicative of a

very ripe fruit that varied with type of fruit. The different fruit manipulation methods and manipulation skills varied with stages of ripeness or development. When ripening, the colour of the fruit turns from green to orange then to shades of maroon-red depending on tree species. From evolution standpoint, fruit ripening signals to potential seed dispersers by change in fruit colour (Mack, 2000) and usually exhibit bright colours that can be seen from a distance (Herrera, 1982). The ripening process always started from the blossom end and completed colour change at the stem end as it was also observed by Gargiullo and Stiles (1993). The number of different stages of ripening varied with fruit species. Whereas figs showed 7 stages, *Celtis* hardly showed significant colour change as it remained apple green from fruiting to consumption. Mangabeys showed preference along the ripening trend i.e. from bright maroon-red to pale yellow.

It was observed that mangabeys utilized three major fruit parts as a food. They included; endosperm, seed and pulp. To access any of them, mangabeys employed different methods that were comparable to what Kimuyu *et al.* (2012) noted in their Tana River study. Seed-eating was common in the three study sites but more frequently observed in Lwamunda than Mabira (M1) and according to Ham (1994), it may be a result of differences in forest composition and presence of a higher number of species from the family Leguminosae. According to Ham (1994), mangabeys ate unripe seeds in Lope reserve, Gabon, as a form of exploitation competition since they were sharing their home range with other sympatric primate species.

Accessing endosperm requires more energy and elaborate fruit processing than accessing ripe pulp. Generally, primates practice various forms of food processing that modifies the physical structure of food to increase intake rates and passage time as well as maximizing nutrient absorption (Hohmann, 2009). However, they have to overcome several adaptation obstacles by the plant prior to accessing vital nutrient foods. The deterrents may include hardened pericarps, thorns and size that may be too large for the intending frugivores (Leighton and Leighton, 1983). Endosperm consumption appeared to be associated more with food scarcity than periods of plenty. This association was illustrated in the severely degraded Lwamunda forest reserve where on average 91% of the priority

trees were fruitlessness which was indicative of fruit scarcity. Consequently, 60% fruits were processed compared to only 20% in regenerating Mabira (M2) and 0.1% in fairly undisturbed Mabira (M1). This assertion has been vindicated in Table 4.2 where endosperm consumption was more in Lwamunda than in Mabira 1 or 2. It was also further observed that during periods of food scarcity in Lwamunda and Mabira-M2, mangabeys often climbed down to the forest floor or forage over large areas. Foraging on the forest floor was a risky activity for arboreal mangabeys as it exposed them to potential disease (Freeland, 1980) and possible death by humans especially in Lwamunda. Besides, most of the food sources on the forest floor were also competitively sought after by humans; for example *Afromomum* fruit and mushrooms. The former sprouted from the forest floor during the dry spell (July-December 2006) while the latter were available in August which coincided with a period of food scarcity in Lwamunda. Undeniably, climbing down and traversing long distances increases travel costs as it was also observed by Olupot *et al.,* (1997). During this study, it was also observed that mangabeys raided domesticated crops in the nearby gardens in Lwamunda forest reserve. This crop-raiding phenomenon was authenticated by Ogango's (2006) study who was concurrently conducting a study on crop-raiding by mangabeys in the same forest. In Mabira (M2), mangabeys climbed down on the forest floor to eat domesticated fruits left behind by encroachers (Alpert, 1996) but it was also probable that they also crop-raided the nearby gardens as reported by Fungo *et al.*, (2013). Climbing down on the forest floor and crop raiding are high risk and hazardous activities for mangabeys to perform. Nevertheless primates must strike a balance between meeting dietary requirements and predator avoidance (Chapman *et al.*, 2012).

Kimuyu *et al.* (2012) observed four main fruit and seed handling behaviour among the mangabeys in the following descending order: ingesting fruits and later defecating seeds; processing fruits in cheek pouches and spitting seeds; picking of dry seeds of non-fleshy fruits and seed eating and processing the fruit outside the mouth (ingesting only the pulp) and later dropping the seeds or half eaten fruit. However, in the present study, we observed three distinct forms of processing; either fruits were shoved into the mouth

whole, or the fruit pulp was gnawed or the seed was hacked through to access other parts like the endosperm depending on level of seed development.

It appears there were other inter-related factors which may have influenced fruit processing among mangabeys. The nutrient content of fruit/fruit may have played a critical as noted by other researchers (Houle *et al.*, 2007; Worman and Chapman, 2005; Waser, 1977). Previous nutritional studies (Matsumoto-Oda and Hayashi, 1999; Milton, 1979) in non-human primates have indicated that protein content is positively correlated with food selection and conversely fibre and condensed tannins are negatively correlated. As fruits ripen, toxic substances and chemical defences like secondary compounds decrease (Gargiullo and Stiles, 1993) which increases fruit selectivity by primates (Olupot, 1999; Waser, 1977). In the event of severe degradation, Van Schaik *et al.* (1993) reported that mangabeys foraged among herbaceous plants known to be of low quality (Waser, 1975) due to presence of high tannins levels. As such, mangabeys which regularly foraged on the forest floor in Lwamunda and M2 were more exposed to the risk of consuming low quality and tannin laden foods than their counterparts in M1 which was devoid of herbaceous plants. The consequence of consuming such foods is poor body condition (McCabe *et al.* (2013) because of inadequate food supply and high energy used to detoxify tannins (Nabihamba,1996)

Apart from herbaceous plants on forest floor, many unripe fruits also contain high levels of secondary compounds. Plants manufacture secondary metabolites presumably for protection against attacks by frugivores that do not disperse the seeds (Dai and Mumper, 2010). The secondary compounds may be toxic or non-toxic depending on the evolutionary relationship between plant defence mechanisms and potential seed dispersers (Levey and Cipollini, 1998). For optimal nutritional benefits, fruits must be handled and processed efficiently by frugivores.

From the perspective of the fruiting tree, the frugivores or other dispersers play a critical propagation role (Terborgh, 1986). As such, fruits have been evolving mechanisms to ensure that animals eat them at the right time and not before. The mutualistic relationship between fruit producing trees and their dispersers is partially based on the nutritional

value offered by the fruit (Izhaki, 1992) and the disposition of the disperser's digestive tract (Milton, 1979). From the fruit tree perspective, accumulation of relevant nutrients is a strategy employed to ensure propagation of the species. The fruit morphology and disposition is an adaptation for easy dispersion which frugivores exploit. As such, most fruits are brightly coloured to attract dispersers. Similarly, animals have evolved taste preferences for sweet-tasting foods because the sugars contained therein provide readily available source of energy (Reynolds, 2005; Milton, 2004). In the present study, the choice to process the fruit or not was probably dependent on the perceived low levels of secondary compounds in preferred fruit parts. For instance, processing of *C. indicum M. eminii*, *P. microcapa* and *B. unijugata* to access endosperm or ripe pulp or aril was based on the notion that tannin thresh-holds were less than 2.6g/100g catechin equivalent as comprehensively discussed in Chapter 7 of this thesis.

4.5 Conclusion

As preferred food resources (ripe fruit pulp) declined, it appears mangabeys sought alternative food items like fruit endosperms hence the initiation of the fruit processing behaviour. Food scarcity therefore appears to be a consequence of habitat degradation and a precursor for fruit manipulation by mangabeys inhabiting in the forest reserves of Mabira and Lwamunda. Fruit manipulation per se is an adaptative and selective strategy to acquire food items that supply dietary requirements from a resource-poor habitat. This was explicitly illustrated by a comparison between Lwamunda that was severely degraded and Mabira (M1) that was fairly undisturbed. The level of fruit development and nutritional content of respective fruits also played a part in selection of fruit type for processing and subsequent consumption.

4.6 Acknowledgement

The authors wish to extend their gratitude to NUFU for funding for this study. National Council of Science and Technology for granting permission to work in Uganda forest reserves. Other colleagues within the Department of Biological Sciences are thanked for constructive criticism of the manuscript.

4.7 References

Alpert, P. (1996). Integrated conservation and developmental projects. Examples from Africa. *BioScience*, **46** (11), 845-855.

Baldwin, L. A., Teleki, G. & Kavanagh, M. (1976) Field research on colobus, guenon, mangabey and patas monkeys: a historical, geographical and bibliographical listing. *Primates*, 17, 233-251.

Baranga, D. (1984). Changes in chemical composition of food parts in the diet of colobus monkeys. *Ecology*, **64**(4), 668-673.

Braun, J.V. & Olofinbiyi, T. (2007). *Famine and Food Insecurity in Ethiopia: Case study #7-4 of the program – Food Policy for developing countries: The role of Government in global food system.* Cornell University, Ithaca NY, pp 1-9.

Braun, J.V, Teklu, T. & Webb, P. (1999). Famine in Africa: causes, responses and prevention. *IFPRI Publications. Food Policy Statement*, No 28, pp 1-3

Buzzard, P. J. (2006). Ecological partitioning of Cercopithecus campbelli, C. petaurista, and C. diana in the Tai Forest. *International Journal of Primatology*, **27**(2), 529-558.

Chalmers, N. R. (1968) The visual and vocal communication of free living mangabeys in Uganda. *Folia Primatologica*, 9, 258-280.

Chapman, C.A., Rothman, J.M. and Lambert, J.E. (2012). Food as a selective force in primates. In Mitani, J.C., Call, J., Kappeler, P.M., Palombit, R.A. and Silk, J.B. (Eds), *The Evolution of primate societies* (pp. 149-168). University of Chicago Press.

Chapman, C. A., Wrangham, R. W., Chapman, L. J., Kennard, D. K., & Zanne, A. E. (1999). Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*, **15**(02), 189-211.

Chapman, C. A., Chapman, L. J., Wangham, R., Hunt, K., Gebo, D., & Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica*, 527-531.

Dai, J., & Mumper, R. J. (2010). Plant phenolics: extraction, analysis and their antioxidant and anticancer properties. *Molecules*, **15**(10), 7313-7352.

Di Fiore, A., Link, A., & Dew, J. L. (2008). 4 Diets of wild spider monkeys. Spider monkeys: *The biology, behavior and ecology of the* genus *Ateles*, 55, 81.

Di Fiore, A. & Rodman, P.S. (2001). Time Allocation Patterns of Lowland Woolly Monkeys (*Lagothrix lagotricha poeppigii*) in a Neotropical Terra Firma Forest. *International Journal of Primatology*, **22**(3), 449-480

Felton, A.M., Felton, A., Raubenheimer, D., Simpson, S.J., Foley, W.J., Wood, J.T., Wallis, I.R. & Lindenmayer, D.B. (2009). Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioral Ecology,* **20**(4), 685-690.

Freeland, W.J. (1980). Mangabey (*Cercocebus albigena*) movement patterns in relation to food availability and faecal contamination. *Ecology* **61**(6), 1297-1303.

Fungo B, Eilu G, Tweheyo M & Baranga D (2013). Forest disturbance and cropping mixtures influence crop raiding by red-tailed monkey and grey-cheeked mangabey around Mabira Forest Reserve, Uganda. *Journal of Ecology and the Natural Environment* 5(2), 14-23.

Gargiullo, M. B & Stiles, E. W. (1993). Development of secondary metabolites in the fruit pulp of Ilex opaca and Ilex verticillata. *Bulletin of the Torrey Botanical Club*, 423-430.

Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., & Toulmin, C. (2010). Food security: the challenge of feeding 9 billion people. *Science*, 327(5967), 812-818.

Ham, R.M. (1994). *Behaviour and ecology of grey-cheeked mangabeys (Cercocebus albigena) in the Lope Reserve, Gabon*. eTheses from School of Natural Sciences legacy departments, University of Stirling.

Herrera, C. M. (1982) Seasonal variations in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology,* **63,** 772-785.

Hohmann, G. (2009). The diets of Non-human Primates: Frugivory, food manipulation and food sharing. In Hublin, J-J. and Richards, M.P. (Eds), *The Evolution of Hominin Diets: Integrating Approaches to the study of Palaeolithic subsistence* (pp. 1-14). Springer Science and Business media B. V.

Homewood, K.M. (1978). Feeding strategy of the Tana mangabey (*Cercocebus galeritus galeritus*) (Mammalia: Primates). *Journal of Zoology*, **186**(3), 375–391.

Houle, A., Chapman C.A. & Vickery, W.L. (2007). Intratree Variation in Fruit Production and Implications for Primate Foraging. *International Journal of Primatology*. **28**(6), 1197-1217.

Howard, P. C., Butler, J., & Howard, P. (1991). Nature conservation in Uganda's tropical forest reserves. IUCN, Gland, Switzerland and Cambridge, UK with the financial support of WWF-International.

Izhaki, I. (1992). A comparative analysis of the nutritional quality of mixed and exclusive fruit diets for Yellow-vented Bulbuls. *Condor*, 912-923.

Janson, C. H., & Chapman, C. A. (1999). 14• Resources and primate community structure. In Primate Communities. Eds J. G. Fleagle, Charles Janson, Kaye Reed. Pg 237. Cambridge University Press

Jordano, P. (2000). Fruits and frugivory. In Fenner, M. (Ed). *Seeds: the ecology of regeneration in plant communities*, 2nd Edition (pp. 125-166). CABI Publication, Wallingford, UK.

Kimuyu, D.M., Wahungu, G.M. & Otieno, D.O. (2012). Seed dispersal by Tana River mangabeys in fragmented gallery forests. *Open Journal of Ecology* **2**(1), 12-20

Kinzey, W.G. & Norconk, M.A. (1990). Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology*, **81**(1), 5–15.

Kizza, M., Rodhe, A., Xu, C. Y., Ntale, H. K., & Halldin, S. (2009). Temporal rainfall variability in the Mabira and Lwamunda in East Africa during the twentieth century. *Theoretical and applied climatology*, **98**(1-2), 119-135.

Kunz, B.K. and Linsenmair, K.E. (2007). Changes in Baboon Feeding Behaviour: Maturity-dependent Fruit and Seed Size Selection within a Food Plant Species. *International Journal of Primatology,* **28**(4), 819-835

Lambert, J.E., Chapman, C.A., Wrangham, R.W. & Conklin-Brittain, N.L. (2004). Hardness of cercopithecine foods: Implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology*, **125**(4), 363-368.

Lambert, J.E. (2002). Exploring the link between animal frugivory and plant strategies: the case of primate fruit processing and post-dispersal seed fate. In Levey, D.J.,

Silva, W.R. and Galeth, M. (Eds), *Seed dispersal and frugivory: ecology, evolution and conservation* (pp. 365-379). CAB International, Wallingford, UK.

Lambert, J.E. (1999). Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): Implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropol*ogy, **109**(3), 365–386. Levey, L. and Cipollin, M.L. (1998). A glycoalkaloid in ripe fruit deters consumption by cedar waxwings. *The Auk*, **115**(2), 359-362.

Lawes, M. J. (1990). The distribution of the samango monkey (Cercopithecus mitis erythrarchus Peters, 1852 and Cercopithecus mitis labiatus I. Geoffroy, 1843) and forest history in southern Africa. *Journal of Biogeography*, 669-680.

Leighton, M. & Leighton D.R. (1983). Vertebrate responses to fruiting seasonality within Bormean rainforest. *British Ecological Society,* **2**(1983), 181-196.

Levey, D. J., & Cipollini, M. L. (1998). A glycoalkaloid in ripe fruit deters consumption by Cedar Waxwings. *The Auk,* 359-367.

Mack, A. L. (2000). Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism?. *Journal of Biosciences*, **25**(1), 93-97.

McCabe, G.M., Fernández, D. & Ehardt, C.L. (2013), Ecology of reproduction in Sanje mangabeys (*Cercocebus sanjei*): Dietary strategies and energetic condition during a high fruit period. *American Journal of Primatology*, **75**(12), 1196-1208.

Marshall, A.J. & Wrangham, R.W. (2007). Evolutionary Consequences of Fallback Foods. *International Journal of Primatology*, **28**(6), 1219-1235

Matsumoto-Oda, A. & Hayashi, Y. (1999). Nutritional aspects of fruit choice by chimpanzees. *Folia Primatology,* **70**(3), 154-162.

Milton, K. (2004). Ferment in the family tree: Does a frugivorous dietary heritage influence contemporary patterns of human ethanol use?. *Integrative and Comparative Biology*, **44**(4), 304-314.

Milton, K. (1979) Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *American Naturalist*, **114**(3), 363-378.

Moscovice, L. R., Issa, M. H., Petrzelkova, K. J., Keuler, N. S., Snowdon, C. T., & Huffman, M. A. (2007). Fruit availability, chimpanzee diet, and grouping patterns on Rubondo Island, Tanzania. *American Journal of Primatology*, **69**(5), 487-502.

Nabihamba, E. (1996). Factors determining dietary choices among arboreal frugivores in Kibale forest in Western Uganda. Msc. Thesis, Makerere University, Kampala.

Nowell, A.A & Fletcher, A.W. (2008). The development of feeding behaviour in wild western lowland gorillas (Gorilla *gorilla gorilla*). *Behaviour*, **145**(2), 171-193.

Olupot, W. (1999). *Mangabey dispersal and conservation in Kibale National Park, Uganda*. PhD Thesis. Purdue University.

Olupot, W., Chapman, C.A., Waser, P.M. & Isabirye-Basuta, G. (1997). Mangabey (*Cercocebus albigena*) Ranging Patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *American Journal of Primatology,* **43**(1), 65-78

Ogango, A. (2006). Crop Raiding by Mangabeys in Lwamunda forest reserve, Uganda. A Research Project Submitted to the Zoology Department in Partial Fulfilment of the Requirements for a Degree in Bachelor of Science, Makerere University.

Okecha, A.A. & Newton-Fisher, N.E. (2006). The diet of olive baboons (*Papio* anubis) in the Budongo Forest Reserve, Uganda. In Newton-Fisher, N.E., Notman, H., Peterson, J.D. and Reynolds, V. (Eds), *Primates of Western Uganda* (pp. 61-73). Springer, New York.

Pienkowski, M.W., Watkinson, A.R., Kerby, G., Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R. (1998). Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, **35**(4), 596–606.

Poulsen, J.R., Clark, C.J. & Smith, T.B. (2001). Seasonal variation in the feeding ecology of the Grey-cheeked Mangabey (*Lophocebus albigena*) in Cameroon. *American Journal of Primatology*, **54**(2), 91–105.

Reynolds, V. (2005). The chimpanzees of the Budongo forest: Ecology, behaviour and conservation. Oxford University Press. HOMEPAGE:http://www.dfid.gov.uk/r4d/

Rosenberger, A.L. & Strier, K.B. (1989). Adaptive radiation of the ateline primates. *Journal of Human Evolution*, **18**(7), 717–750

Schaefer, H. M., Schmidt, V., & Winkler, H. (2003). Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos*, **102**(2), 318-328.

Spuhler, J. N., & Jorde, L. B. (1975). Primate phylogeny, ecology, and social behavior. *Journal of Anthropological Research*, 376-405.

Stickler, C.M & Chapman, C.A. (press). Redtail Monkey behavioural responses to differences in habitat structure induced by logging. *International Journal of Primatology*

Strier, K.B. (1992). Atelinae adaptations: Behavioral strategies and ecological constraints *American Journal of Physical Anthropology*, **88**(4), 515–524.

Terborgh, J. (1986). Community aspects of frugivory in tropical forests. In Estrada, A. and Fleming, T.H. (Eds), *Frugivores and seed dispersal* (pp. 371-384). Springer, Netherlands.

Uganda Metrological Department (2008). Weather and climate database.

Van Schaik, C.P., Terborgh, J.W. & Wright, S.J. (1993). The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, **24**(1993), 353-377.

Waser, P.M. (1977). Feeding, Ranging and Group size in the Mangabey *Cercocebus albigena*. In Clutton-Brocks, T.H. (Ed), *Primate Ecology* (pp. 183-222). Academic Press, London.

Waser, P.M. (1975). Monthly variations in feeding and activity patterns of the mangabey, Cercocebus albigena (Lydekker). East African Wildlife Journal, 13(3-4), 249-264

Webb, P. & Braun, J.V (1994). *Famine and food security in Ethiopia: lessons for Africa.* John Wiley, London. pp. 164.

Worman, C.O. & Chapman, C.A. (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *Journal of Tropical Ecology* **21**(6), 689-697.

Wrangham, R.W. & Waterman, P.G. (1983). Condensed tannins in fruits eaten by chimpanzees. *Biotropica*, **15**(3), 217-222.

CHAPTER FIVE

5 The challenge of interpreting primate diets: Mangabey foraging on *Blighia unijugata* fruit in relation to changing nutrient content

Margaret Masette[1], Gilbert Isabirye-Basuta[1], Deborah Baranga[1], Colin A. Chapman[1,2], and Jessica M. Rothman[1,3]

[1]*Department of Biological Sciences, Makerere University, P.O. Box 7062, Kampala, Uganda*

[2]*Department of Anthropology and McGill School of Environment, 855 Sherbrooke Street West, McGill University, Montréal, Québec, Canada H3A 2T7 and Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, New York, USA 10460*

[3]*Department of Anthropology, Hunter College of the City University of New York, and New York Consortium in Evolutionary Primatology, 695 Park Avenue, New York, NY 10065 USA*

Published in peer reviewed journal and cited as:
Masette, M., Isabirye-Basuta, G., Baranga, D., Chapman, C. A., & Rothman, J. M. (2015). The challenge of interpreting primate diets: mangabey foraging on Blighia unijugata fruit in relation to changing nutrient content. *African Journal of Ecology*. Vol. 53 (3) 259-267. doi: 10.1111/aje.12174. Received in August 2014 and published Sept 2015

Abstract

Primates often make foraging selections that are not apparent. For example, they may eagerly consume a particular plant part and species in some instances, but reject it at other times. *Blighia unijugata* (Baker) fruit is one of the most frequently eaten foods of mangabeys (*Lophocebus ugandae*) in Lwamunda Forest Reserve, Uganda. However, its use varies strikingly depending on the fruit's developmental stage. We conducted feeding

observations to investigate the nutritional criteria that mangabeys may have used for the consumption of specific fruit parts by conducting analysis of fruit parts eaten and rejected at different developmental stages. When seeds had low condensed tannins, mangabeys ate them, but seeds were rejected when the levels increased. In the first five stages of fruit development tannin levels in arils declined and the frequency of consumption of the aril increased. While fat content in seeds increased with maturity, it did not appear to influence seed consumption, but fat content was related to frequency of consumption of the aril. Considering that primates are often making food selections among many species/part combinations, our results illustrate the value of using nutritional analyses to understand foraging decisions. Furthermore, they demonstrate how very specific trade-offs between consumption of critical nutrients and anti-feedants can drive which foods and parts are eaten.

Key words: diet choice, food selection, forest restoration, macronutrients, tannins, nutritional ecology,

5.1 Introduction

Tropical frugivores and folivores often make unusual food choices. For example, gorillas (*Gorilla beringei*) eat rotten wood (Harcourt and Stewart, 2007; Rothman *et al.*, 2006), elephants (*Loxodonta africana*) eat soil from termite mounds (Rode *et al.*, 2006b; Holdo and McDowell, 2004; Ruggiero and Fay, 1994), red colobus (*Procolobus rufomitratus*) eat the very fibrous last centimetre of the petioles on *Markhamia lutea* (K. Schum.) leaves (Ryan *et al.*, 2013; Rode *et al.*, 2003; Baranga, 1983), and the frugivores in Kibale National Park forest, Uganda eat the fruits of *Celtis durandii* (Engl.) only during a very small time period, even though they are available over longer periods (Worman and Chapman, 2005). However, upon careful evaluation, nutritional explanations for unusual foraging behaviour often become apparent – gorillas, elephant, and red colobus are selecting foods high in sodium and the frugivores that eat *C.durandii* cue in on changes in fruit fat content that are not apparent by assessing fruit colour, size, or morphology.

Considering that many tropical frugivores and folivores make selections from hundreds of plant species and thus thousands of species/part combinations, understanding the dietary choices of tropical animals is challenging. For example, in 26 vegetation plots totalling 2.4 ha of forest in a 10 km^2 area of Kibale National Park, Uganda there are more than 60 tree species (Chapman *et al.*, 2010, Isabirye-Basuta and Lwanga, 2008; Chapman *et al.*, 1997). If one only considers the most basic plant parts (leaf buds, young leaves, mature leaves, leaf petioles, ripe fruit, unripe fruit, bark, flowers) an animal with a home range of this size would have to select among approximately 480 different foods; each with changing phenological states. Furthermore, items that appear to be of one consistent type to a human observer (e.g., ripe fruit) often vary dramatically in chemical constituents (Worman and Chapman, 2005) and there can be significant temporal and spatial differences in the quality of the same food item over small scales (Rothman *et al.*, 2012, Rothman *et al.*, 2008; Houle *et al.*, 2007; Chapman *et al.*, 2003).

Despite the difficulty of understanding dietary selections, such a comprehension is very important for the construction of informed conservation plans. In an ideal situation, conservation plans are built on general principles (e.g., this class of animal can be protected following this general strategy). This is important because there can be differences in the composition of the forest over small spatial and temporal scales (Isabirye-Basuta and Lwanga, 2008; Chapman *et al.*, 1997), yet most detailed dietary studies are collected at one particular location over a short time (i.e., 1 year or less). If we understand what critical nutrients and anti-feedants drive food consumption, it becomes feasible to construct conservation plans for specific animals that relate plant chemistry to food consumption especially when they are associated at the genus or family level (i.e., protect trees in the Fabaceae family as they often have high protein levels, since protein to fiber levels have been shown to correlate with the biomass of arboreal folivores (Davies, 1994, Oates *et al.*, 1990, Waterman and Kool, 1994, Chapman *et al.*, 2004)). Such tree species (Fabaceae for folivores – Omeja *et al.*, 2011, food trees of frugivores – Felton *et al.*, 2010, Ficus – Felton *et al.*, 2013) can be promoted in restoration programs or avoided in logging operations.

Here we determine factors influencing the selection of parts of the fruits of one frequently consumed food, *B. unijugata* (Sapindaceae), in the diet of grey-cheeked mangabeys (*Lophocebus ugandae*) in Lwamunda Forest Reserve, Uganda in relation to macronutrients and condensed tannin. We focused on tannins as an antifeedants, because they bind protein, reduce the digestibility and nutritional quality of foods (Rothman *et al.*, 2009b, Robbins *et al.*, 1987, Rothman *et al.*, 2012), and nitrogen (a major component of protein) is limiting in many environments (White, 1993).

Blighia unijugata grows in open habitats including woodlands, forest edges, and along river banks. The Lwamunda Forest Reserve is mainly riverine forest, thus *B. unijugata* is commonly found along the river, but it is also found at the forest edges. It is a small to medium-sized tree and grows to a height of 15-30 m depending on locality; the tree bole is often quite short, usually straight, and can be up to ~200 cm in diameter. It has a bi-annual fruiting period and when in fruit it contributes ~10% of the mangabey diet in the Lwamunda Forest. *B. unijugata* is important in the diet of mangabeys (Baranga, 2004, Olupot *et al.*, 1998, Wieczkowski and Kinnaird, 2008), black and white colobus – *Colobus guereza (*Rode *et al., 2003)*, red colobus – *Procolobus rufomitratus* (Ryan *et al.*, 2013, Rode *et al.*, 2003) (the colobines eat the aril along with the seed), chimpanzees – *Pan troglodytes* (Krief *et al.*, 2005), blue monkeys – *Cercopithecus mitis* (Butynski, 1990), and redtail monkeys – *C. ascanius* (Rode *et al.*, 2006a, Stickler, 2004). Furthermore, humans have been described to eat the related *B. sapida* (K.D. Koenig) (Abolaji *et al.*, 2007, Brown *et al.*, 1991, Feng and Patrick, 1958, Hassall and Reyle, 1955). Unfortunately, no previous study reporting the eating of *B. sapida* fruit by primates indicated the fruit part being consumed.

5.2 Methods

We studied the mangabeys in Lwamunda Forest Reserve, Uganda (67 km^2 - 0° 15′ N and 0° 23′ N longitude 32° 30′ E and 32° 43′ E; 1200 elevation; 80 km SW of the larger Mabira Forest Reserve) from June 2004 to March 2007 for 5 consecutive days a month. The animals were well-habituated prior to our study because of previous and continuous research in the area (Chalmers, 1968, Waser, 1975, Baldwin *et al.*, 1976, Spuhler and

Jorde, 1975). The area receives 1200-1500 mm annually and the rains are typically distributed between two distinct wet seasons; April-May and October-November (Howard, 1991). Lwamunda Forest Reserve is a riverine forest surrounded by flat-topped hills with steep slopes. In 1993 when efforts were made to prohibit human encroachment of the Mabira and Lwamunda forest reserves (Alpert, 1996), Lwamunda was not included in prohibition strategy and therefore it is severely degraded as a result of illegal pit sawing. Consequently food options for the threatened Mangabey populations are limited. Generally forest reserves in Uganda are not well protected because of the open-access policy and poorly structured land tenure system (Naughton *et al.*, 2011).

To determine the feeding habits of the mangabeys, we focused on a group of 14 individuals (4 adult males, 2 sub-adult males, 4 adult females, 2 sub-adult females, and 2 infants). Systematic 5 minute-scan sampling (Altmann, 1974) was conducted of all group members from 6 am to 12 pm, and then from 4 pm to 7 pm on weekdays and 7 am to 1 pm on Saturdays, which was supplemented with ad libitum observations of the exact parts of the fruits eaten. A total of 1200 hours of observations were made of the mangabeys. Notes on food remains under trees where mangabeys had fed were carefully taken.

We collected a 50 g sample of fruit at each development stage and the sample was analysed at the Animal Science Laboratory, Makerere University, Uganda. Two samples of each plant part/stage were collected and they were analysed in triplicate. Mass and size measurements were taken before splitting the fruit to access the seed and aril and analysis was made only on the seeds and aril, since mangabeys rarely ate other fruit parts. Given the small mass of the aril, samples were taken from multiple trees and pooled for analysis; samples were all collected on the same day and sufficient trees and fruit were used until the 50 g amount was obtained (the number of trees collected from varied depending on availability (Table 5.1).

Table 5.1 The number of *Blighia unijugata* arils that were collected to make up 50 g used in the nutritional analysis for each of the developmental stages

Stage of fruit development	Mean wt (g) & sd	No. arils in 50g	No. of fruits contributing to 50g
1	0.01±0.00	5000	1,667
2	0.03± 0.00	1667	556
3	0.10±0.01	500	167
4	0.15 ±0.01	334	111
5	0.22 ±0.01	227	76
6	0.26±0.01	192	64

The seed and aril were oven dried at 60°C to a constant weight then ground using a Cyclotech 1093 Model 4 mill, or a mortar and pestle. The powdered sample was packed in a vinyl bag, labelled, and stored in plastic containers at room temperature until analyses. The Kjeldahl method (AOAC, 1990, Rothman et al., 2012) was used to quantify crude protein; standard methods were used to determine crude fibre (AOAC, 1990), while Harris's (1970) soxhlet method for ether extract was used to determine lipid content, and soluble carbohydrates (sugar) were determined by using the anthrone method (Loewus, 1952). Tannins were estimated using the Price and Butler method (Price and Butler, 1977), with quebracho as a standard. Although we acknowledge the problems using quebracho as a standard (Rothman *et al.*, 2009b), because we are comparing the same species and part, it is appropriate to compare the absorbance values of *B. unijugata* to determine the magnitude of change. Since the aril on the seed is very small, we only measured its fat and tannin content.

Partial correlation analysis was used to explore the relationship between tannin concentration and the rest of the proximate composition variables in *B. unijugata* seeds, while controlling for development stage. The reported relationship in the text is the effect of the variable being discussed, while statistically controlling for the effects of the other variables being considered. To test whether antifeedants explain fruit part selection by mangabeys, we used a logistical regression with the response variable fruit part eaten or avoided and the tannin level as a predictor.

5.3 Results

Blighia unijugata fruit an important food for the mangabeys (*Lophocebus ugandae*) sampled in Lwamunda Forest Reserve, Uganda, exhibited six developmental stages featured in Figures 5.1-5.6). With respect to stage 1 fruits (2 weeks after fruiting), mangabeys ate the barely formed green seeds which weighed 0.15 g and ignored the green aril. The green coloured aril was not available for consumption by mangabeys (Fig. 5.1). Prior to this stage fruits were not eaten; they were green and when plucked they exuded sticky sap that may deter consumers.

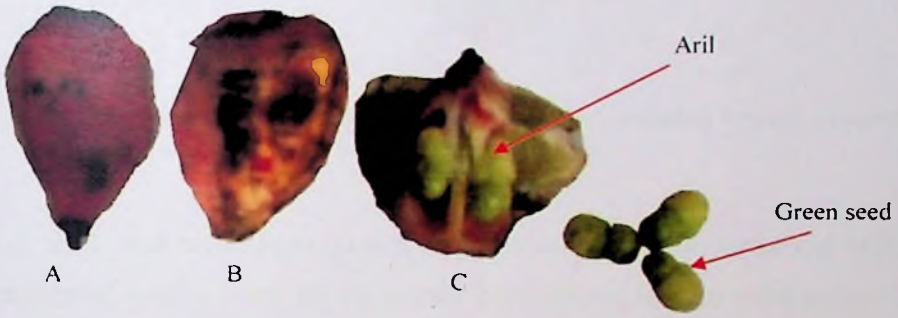


Figure 5.1 The first development stage of *B. unijugata* fruit showing the outer bright reddish orange colour "A" and bitten fruit "B" to access the green seed "C". The green coloured aril not available for consumption by mangabeys

At stage 2 the fruit had been on the tree for approximately 3 months (12 weeks after fruiting). During periods of general food scarcity, mangabeys consumed fairly young *B. unijugata* fruit at stages 1 and 2 fruits. The seed with the brown hue, weighed 0. 21 g as shown in Fig 5.2.

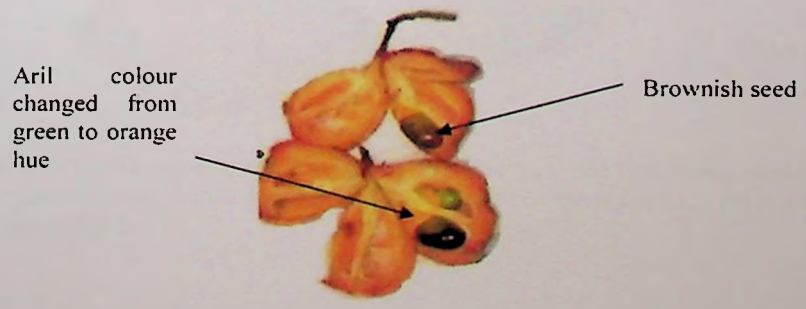


Figure 5.2 The second development stage of *B. unijugata* fruit showing the brown tinted seed with an orange coloured aril and still unripe that makes it inedible by mangabeys

Stage 3 fruits were about 4 months old and the aril was bright orange, but it was not eaten by mangabeys. The brown coloured seed weighed 0.25 g and the orange aril was still inedible (Fig 5.3).

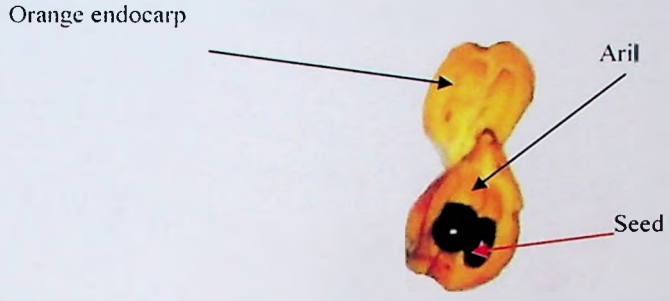


Figure 5.3 The third development stage of *B. unijugata* fruit showing brown coloured seed and orange aril which was still inedible by mangabeys

At stage 4, fruits had been on the tree for approximately 4-5 months and both the seed and aril appeared mature from the observer's perspective, but only the seeds were eaten by mangabeys and the aril was discarded. The dark brown coloured seed weighed on average 0.27 g, the endocarp had a tint of red and the bright orange aril was still inedible (Fig 5.4).

Figure 5.4 The fourth development stage of *B. unijugata* fruit, showing dark brown coloured seed, endocarp with a tint of red and bright orange aril which still remains inedible by mangabeys.

Stage 5 fruits were between 4-6 months of age. The fruit is mature and the pericarp was too fibrous to be easily bitten through by mangabeys (Fig 5.5) to retrieve the seed. As such, the fruit was not utilize as food at this stage of development. Apart from the tough fibrous pericarp, it was probable that the levels of tannin in the dark coloured seed and weighing 0.31g were too high to be palatable.

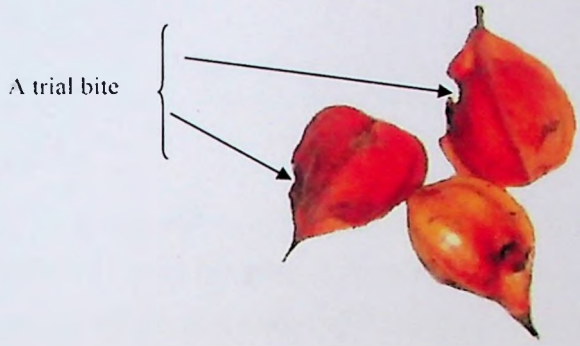


Figure 5.5 The fifth development stage of a mature *B. unijugata* fruit showing signs of attempted bite by mangabeys

At stage 6 fruits were crimson red and had been developing on the tree for approximately 6 months. The pericarp naturally split open allowing easy seed removal. None of the fruit pericarp shells found underneath the trees at this stage contained an aril, implying that they had been eaten and probably the seed dispersed by the frugivore that ate the aril. At stage 6, fruits were eaten by many birds, particularly turacos (great blue turacos - *Corythaeola cristata* and Ross's turacos *Musophaga rossae*), and other primates, particularly the redtail monkey (*Cercopithecus ascanius*). The fruits split open (Fig 5.6) and the aril was available for consumption by mangabeys but the seed which weighed 0.35 g was not eaten.

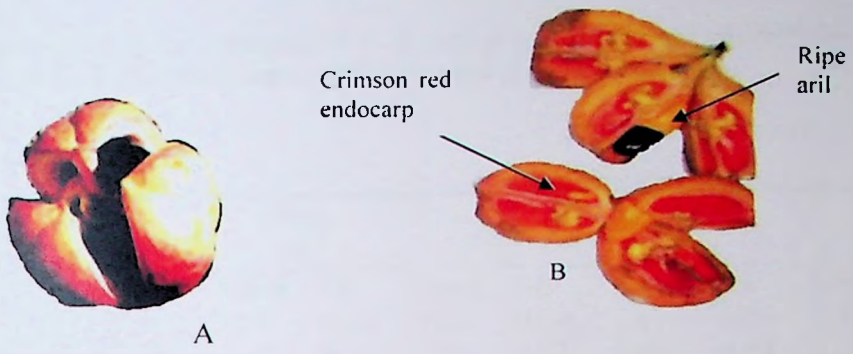


Figure 5.6 The sixth development stage of *B. unijugata* fruit showing a split from posterior end "A" a crimson-red endocarp and ripe orange aril "B" available for consumption by mangabeys

The Mangabey foraging effort was devoted to the different stages which varied accordingly (Table 5.2). The foraging effort was calculated from the number of feeding records based on systematic scan sampling of each stage of development for the 4 months this species was available. Then divided by the total feeding scores involving all foods available for that month and then expressed as percentage. The figures in Table 5.2 are the averages for respective stages during the 4 months.

Table 5.2 The foraging effort devoted to eating the different developmental stages of *B. unijugata* made by the mangabeys of Lwamunda Forest Reserve

Developmental Stage	Foraging Effort		
	Aril	Seed	Other
1	0	10.84	0.2
2	0	15.12	0
3	0	9.86	0
4	0	3.28	0
5	0	0	0
6	8.71	0	0

When all the major *B. unijugata* seed and aril components were analysed for chemical composition and tannin levels at all development stages (Table 5.3, Fig. 5.7), a linear increase was described for all components. However, the gradient was more pronounced in sugar, protein, and fibre, than in fat for the first four stages. The level of tannins

increased gradually from stage 1 to 4 and then increased steeply during stages 5 to 6 (Fig 5.7).

Table 5.3 Variation in chemical composition of *B. unijugata* seed (a) and aril (b) from stage 1 to 6 as a percentage of dry matter. N= 6 for each plant part and stage.

a) Seed

Development stage	Sugar (%)		Fibre (%)		Fat (%)		Protein (%)		Tannin g/100	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	3.03	0.05	3.21	0.15	0.64	0.04	7.41	0.22	1.24	0.16
2	6.36	0.03	5.21	0.11	1.29	0.03	9.63	0.07	2.76	0.16
3	9.74	0.20	9.43	0.22	2.65	0.06	12.89	0.17	3.73	0.04
4	12.22	0.16	11.27	0.14	3.41	0.10	15.33	0.17	4.13	0.10
5	15.09	0.08	12.30	0.17	4.99	0.10	16.42	0.25	7.02	0.05
6	15.87	0.15	12.99	0.05	7.08	0.08	17.94	0.21	8.87	0.08

b) Aril

	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	6.18	1.56	9.14	0.42	1.97	0.02	9.30	0.12	7.01	0.12
2	6.49	0.02	3.67	0.03	3.11	0.09	9.42	0.04	6.02	0.05
3	7.06	0.29	3.71	0.12	5.58	0.10	5.51	0/07	4.13	0.10
4	9.74	0.51	4.60	0.11	8.31	0.13	2.98	0.01	3.73	0.04
5	13.57	0.70	4.53	0.14	16.53	0.13	3.61	0.22	2.76	0.16
6	13.93	0.19	5.51	0.07	25.02	0.24	4.59	0.10	1.24	0.16

Regardless of the development stage, protein constituted more of the seed, followed by sugar, then fiber, and lastly lipid (Fig 5.7). The tannin level in the seed increased gradually from stages 1 to 4 and then increased rapidly between stages 4 and 5 and remained high in stage 6 (Fig 5.7). The relatively high levels of tannins may be one of the factors that influenced the choice of developmental stage eaten by mangabeys because they ate the seeds from stage 1 to 4, but avoided seeds in stage 5 and 6.

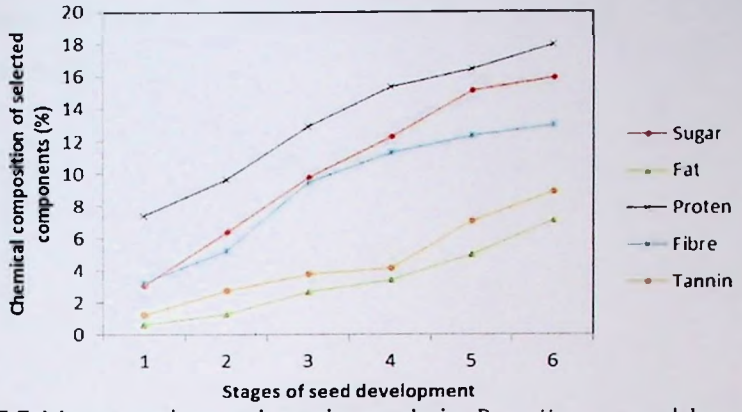


Figure 5.7 Macro-nutrient and tannin trends in *B. unijugata* seed based on six developmental stages

The fat content of the *B. unijugata* aril increased with development stage. The increase was gradual from stage 1 to 4, and then there was a dramatic increase in the last two stages (Fig. 5.8). A similar pattern was documented in the seeds, which implies stage 4 was a critical stage influencing animal handling patterns. Contrary to the trend observed in seeds, the tannin levels in arils decreased as the fruit matured (Fig. 5.8). The low levels documented for stage 6 may have facilitated frugivores dispersing the seeds.

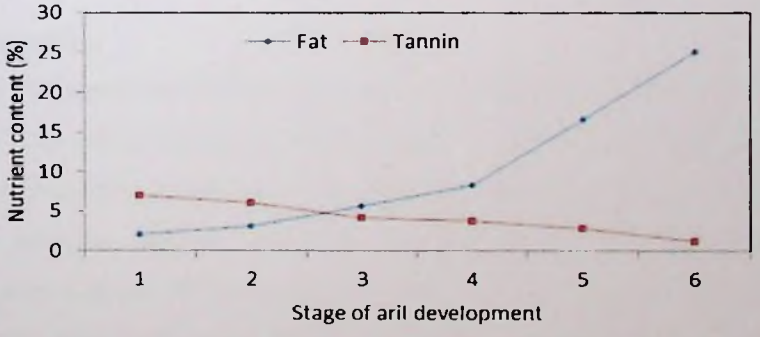


Figure 5.8 Levels of fat and tannin content in *B. unijugata* aril along developmental stages

The level of tannins appears to influence the likelihood of mangabeys eating either aril or seed depending on developmental stage. At the intersection C (Fig. 5.9), we expected mangabeys to consume both the aril and the seed but they consumed only seed despite its high tannin levels. The tannin concentration in the edible parts of the fruits was about 1.783 times less than the concentration in the inedible parts (Chi-squared 27.0, P <0.001).

In contrast, aril tannin concentration in the inedible stages was 1.48 times higher than it was in the edible stages.

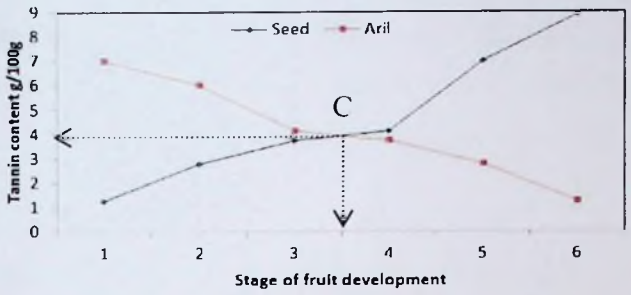


Figure 5.9 The level of tannin levels in seed and aril during *Blighia* fruit development

There were strong positive partial correlations between tannin and fat content ($r = 0.72$, $P<0.01$). Tannins were negatively correlated with fiber ($r = -0.76$, $P<0.001$) and with crude protein ($r = -0.71$, $P< 0.01$). No correlation existed between tannin concentration and sugar content ($r = -0.35$, $P >0.05$). An inspection of zero order correlation suggested that controlling for the seed development stages had very strong effects on the strength of the relationship between tannin levels and crude protein, fiber, sugar, and fat.

5.4 Discussion

Mangabey consumption of *B. unijugata* fruit parts appears to be influenced by nutrient and antifeedant content. Considering that seed fat, sugar, and protein increased with fruit maturity, mangabeys would have been expected to eat seeds up to maturity because of their high nutrient content. However, they stopped eating seeds at stage 4, which we speculate was a result of the increase in tannins. We did not, however, measure starch content in the fruits and it was likely higher in the younger fruits because fat, sugar, and protein all increased. Because starch is an easily digestible carbohydrate, it also may have had an influence on Mangabey fruit part consumption.

If the mangabeys were consuming the part of the fruits based on a trade-off between tannin and fat, one would predict animals start consuming arils just before stage 3 as indicated by the intercept that was similar to tannin level in seed (Fig. 5.8). The other plausible trade-off was speculated at the intercept C (Fig 5.9) when mangabeys consumed

seeds with high tannin content but avoided the aril. However, mangabeys waited to consume arils until stage 6, suggesting that other nutrients/antifeedants within the aril influenced consumption. The consumption of the seed at stage 4 with tannins beyond the threshold of 2.6g/100g (Chapter 7) may be attributed to arbitrary and erroneous visual maturity determination method. Probably, if an objective method was used, the designated stage 4 might have been less than stage 3 with tannins around the threshold. The likelihood of the aril being eaten in either case tended to increase with increasing stages of ripening, as tannin levels declined. Generally, the tannin levels were lower in aril than in seeds.

It was also possible for mangabeys to consume arils just before stage 3, but they did not. We speculate that this is due to the avoidance of toxic hypoglycin A, since the aril of *B. sapida* is known to contain hypoglycin A before maturity (Ayodele *et al.*, 2008). It is possible that *B. unijugata* aril had similar levels of hypoglycin A since they belong to the same genus. Brown *et al.* (1991) reported that the level of hypoglycin A declined from 1000 ppm to undetectable levels (<0.1 ppm) as the fruit matured. At all stages the seed contained appreciable hypoglycin A, ~ 1000 ppm, as such unopened or partially opened fruit were not consumed (*Ibid*). We therefore speculate in the present study that the levels of hypoglycin A in stage 4 were lower than in stage 3 and that is why mangabeys ate stage 4 of seed, but did not eat stage 3 arils. Alternatively, mangabeys may not have eaten arils in stage 3 of the present study because of low fat content as corroborated by Herrera, (1982) who reported that in the stages before maturity, the fat content is normally low in most fruit parts.

Theoretically, many macronutrients increase in seeds as they mature to facilitate seed germination and subsequent growth (Chapman *et al.*, 2008; Zanne *et al.*, 2005; Richards, 1996). In contrast, as the seed matures, the secondary compounds increase to potentially inhibit animals from consuming and destroying the seed. Here, we speculate that mangabeys may have avoided tannins by consuming the seeds prior to its development. In contrast to the seed, fleshy pericarps and arils attract seed dispersers that move seeds away from the parent tree, providing vital dispersal services (Russo and Chapman, 2011;

Chapman, 1989,). Thus, it confirms the hypothesis that we documented that secondary compounds in the arils declined with maturity. Ripe aril is brightly coloured, soft, with high levels of lipid, but low tannins; desirable characteristics for seed-dispersing birds and mammals (Fischer and Chapman, 1993; Stiles, 1982, Howe and Smallwood, 1982). Although the ripe arils of *B. unijugata* fruit appeared to be the most preferred fruit part, during periods of food scarcity mangabeys ate seeds up to stage 4 (Homewood, 1978).

Our results re-enforce the notion that it is inappropriate to consider diet simply in terms of plant parts (e.g., fruit, leaves), but rather it is important to consider the nutritional value of specific food items (Janson and Chapman, 1999, Chapman *et al.*, 2012, Rothman *et al.*, 2009a, McNaughton, 1988). For example, a food (i.e., item) that is typically thought to have high protein levels (e.g., young leaves), may have less protein than a plant part typically considered to be low in protein (e.g., fruit). To advance the field and gain a better understanding of diet selection and foraging strategies, it will be useful to analyse food items from the species of interest and, if possible, the actual plant from which the animal fed. With the development of near-infrared reflectance spectroscopy methods for field work, this is now possible and relatively easily accessible (Rothman *et al.*, 2009a). Further research should consider other metabolites, as these may play roles in the parts eaten at different developmental stages.

5.5 Acknowledgments

Funding for this research was provided by NUFU. National Council of Science and Technology for granting permission to work in Uganda forest reserves. We thank Patrick Omeja for helpful comments on this project.

5.6 References

Abolaji, O. A., Adebayo, A. H. & Odesanmi, O. S. (2007) Nutritional qualities of three medicinal plant parts (*Xylopia aethiopica, Blighia sapida* and *Parinari polyandra*) commonly used by pregnant women in the western part of Nigeria. *Pakistan Journal of Nutrition,* **6,** 665-668.

Alpert, P. (1996). Integrated conservation and developmental projects. Examples from Africa. *BioScience*, **46** (11), 845-855.

Altmann, J. (1974) Observational study of behavior: Sampling methods. *Behaviour,* **48,** 227-268.

AOAC (1990) *Official methods of analysis,* Association of Official Analytical Chemists, Arlington, VA.

Ayodele, R. O., Ajayi, I. A. & Adewuyi, A. (2008) Nutritional elements, antibacterial activity and cytotoxicity of the leaf, root and stem bark of *Blighia unijugata* Baker (Sapindaceae). *Medicinal and Aromatic Plant Science and Biotechnology,* **2,** 137-140.

Baldwin, L. A., Teleki, G. & Kavanagh, M. (1976) Field research on colobus, guenon, mangabey and patas monkeys: a historical, geographical and bibliographical listing. *Primates,* **17,** 233-251.

Baranga, D. (1983) Changes in chemical composition of food parts in the diet of colobus monkeys. *Ecology,* **64,** 668-673.

Baranga, D. (2004) Forest fragmentation and primate survival status in non-reserve forests of the Kampala area, Uganda. *African Journal of Ecology.,* **42,** 70-77.

Brown, M., Bates, R. P., McGowan, C. & Cornell, J. A. (1991) Influence of fruit maturity on the hypoglycin a level in ackee (*Blighia sapida*). *Journal Food Safety,* **12,** 167-177.

Butynski, T. M. (1990) Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density sub-populations. *Ecology Monographs,* **60,** 1-26.

Chalmers, N. R. (1968) The visual and vocal communication of free inhabiting mangabeys in Uganda. *Folia Primatologica,* **9,** 258-280.

Chapman, C. A. (1989) Primate seed dispersal: the fate of dispersed seeds. *Biotropica,* **21,** 148-154.

Chapman, C. A., Chapman, L. J., Jacob, A. L., Rothman, J. M., Omeja, P. A., Reyna-Hurtado, R., Hartter, J. & Lawes, M. J. (2010) Tropical tree community shifts: Implications for wildlife conservation. *Biological Conservation,* **143,** 366-374.

Chapman, C. A., Chapman, L. J., Naughton-Treves, L., Lawes, M. J. & McDowell, L. R. (2004) Predicting folivorous primate abundance: Validation of a nutritional model. *American Journal of Primatology,* **62,** 55-69.

Chapman, C. A., Chapman, L. J., Rode, K. D., Hauck, E. M. & McDowell, L. R. (2003) Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal Primatology,* **24,** 317-333.

Chapman, C. A., Chapman, L. J., Wrangham, R. W., Isabirye-Basuta, G. & Ben-David, K. (1997) Spatial and temporal variability in the structure of a tropical forest. *African Journal of Ecology,* **35,** 287-302.

Chapman, C. A., Kitajima, K., Zanne, A. E., Kaufman, L. S. & Lawes, M. J. (2008) A 10-yr evaluation of the functional basis for regeneration habitat preference of trees in an African evergreen forest. *Forest Ecology Management,* **225,** 3790-3796.

Chapman, C. A., Rothman, J. M. & Lambert, J. E. (2012) Food selection in primates. In: *The Evolution of Primate Societies* (Eds. J. Mitani, J. Call, P. Kappeler, R. Palombit & J. Silk). Chicago University Press, Chicago.

Davies, A. G. (1994) Colobine populations. In: *Colobine monkeys. Their ecology, behaviour and evolution* (Eds. A. G. Davies & J. F. Oates). Cambridge University Press, Cambridge.

Felton, A. M., Felton, A., Rumiz, D. I., Pena-Claros, M., Villaroel, N., Chapman, C. A. & Lindenmayer, D. B. (2013) Commercial harvesting of *Ficus* timber – An emerging threat to frugivorous wildlife and sustainable forestry. *Biological Conservation,* **159,** 96-100.

Feng, P. C. & Patrick, S. J. (1958) Studies of the action of hypoglycin-a, an hypoglycaemic substance *British Journal of Pharmacology and Chemotherapy,* **13,** 125-130.

Fischer, K. E. & Chapman, C. A. (1993) Frugivores and fruit syndromes - differences in patterns at the genus and species level. *Oikos,* **66,** 472-482.

Harcourt, A. H. & Stewart, K. J. (2007) *Gorilla society: conflict, compromise, and cooperation between the sexes,* University of Chicago Press, Chicago.

Harris, L. E. (1970) *Nutrition research techniques for domestic and wild animals,* Animal Science Department Utah State University, Logan Utah, USA. .

Hassall, C. H. & Reyle, K. (1955) Hypoglycin A and B, two biologically active polypeptides from *Blighia sapida. Biochemistry Journal,* **60,** 334-339.

Herrera, C. M. (1982) Seasonal variations in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology,* **63,** 772-785.

Holdo, R. M. & McDowell, L. R. (2004) Termite mounds as nutrient rich food patches for elephants. *Biotropica,* **36,** 231-239.

Homewood, K. M. (1978) Feeding strategy of the Tana mangabey (*Cercocebus galeritus galeritus*) (Mammalia: Primates). *Journal of Zoology,* **186,** 375-391.

Houle, A., Chapman, C. A. & Vickery, W. L. (2007) Intratree variation in fruit production and implication for primate foraging. *International Journal of Primatology,* **28,** 1197-1271.

Howard, P. C. (1991) *Nature conservation in Uganda's tropical forest reserves,* IUCN, Gland, Switzerland.

Howe, H. F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics,* **13,** 201-228.

Isabirye-Basuta, G. M. & Lwanga, J. S. (2008) Primate populations and their interactions with changing habitats. *International Journal of Primatology,* **29,** 35-48.

Janson, C. H. & Chapman, C. A. (1999) Resources and the determination of primate community structure. In: *Primate Communities* (Eds. J. G. Fleagle, C. H. Janson & K. E. Reed). Cambridge University Press, Cambridge.

Krief, S., Hladik, C. M. & Haxaire, C. (2005) Ethnomedicinal and bioactive properties of plants ingested by wild chimpanzees in Uganda. *Journal of Ethnopharmacology,* **101,** 1-15.

Loewus, F. A. (1952) Improvement in anthrone method for determination of carbohydrates. *Analytical Chemistry* **24,** 219.

McNaughton, S. J. (1988) Mineral nutrition and spatial concentrations of African ungulates. *Nature,* **334,** 343-345.

Naughton, L., Alix-Garcia, J. & Chapman, C. A. (2011) A decade of forest loss and economic growth around Kibale National Park, Uganda: Lessons for poverty reduction and biodiversity conservation. *Proceedings of the National Academy of Sciences of the United States of America,* **108,** 13919-13924.

Oates, J. F., Whitesides, G. H., Davies, A. G., Waterman, P. G., S.M., G., DaSilva, G. L. & Mole, S. (1990) Determinants of variation in tropical forest primate biomass: New evidence from West Africa. *Ecology,* **71,** 328-343.

Olupot, W., Waser, P. M. & Chapman, C. A. (1998) Fruit finding by mangabeys (*Lophocebus albigena*): Are monitoring of fig trees and use of sympatric frugivore calls possible strategies? *International Journal Primatology,* **19,** 339-353.

Omeja, P. A., Chapman, C. A., Obua, J., Lwanga, J. S., Jacob, A. L., Wanyama, F. & Mugenyi, R. (2011) Intensive tree planting facilitates tropical forest biodiversity and biomass accumulation. *Forest Ecology Management,* **261,** 703-709.

Price, M. L. & Butler, L. G. (1977) Rapid visual estimation and spectrophotometric determination of tannin content of sorghum grain. *Journal of Agriculture, Food & Chemistry,* **25,** 1268-1273.

Richards, P. W. (1996) *The Tropical Rain Forest,* Cambridge University Press, Cambridge.

Robbins, C. T., Hanley, T. A., Hagerman, A. E., Hjeljord, O., Baker, D. L., Schwartz, C. C. & Mautz, W. W. (1987) Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology,* **68,** 98-107.

Rode, K. D., Chapman, C. A., Chapman, L. J. & McDowell, L. R. (2003) Mineral resource availability and consumption by colobus in Kibale National Park, Uganda. *International Journal of Primatology,* **24,** 541-573.

Rode, K. D., Chapman, C. A., McDowell, L. R. & Stickler, C. (2006a) Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*). *Biotropica,* **38,** 625-634.

Rode, K. D., Chiyo, P. I., Chapman, C. A. & McDowell, L. R. (2006b) Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behaviour. *Journal of Tropical Ecology,* **22,** 441-449.

Rothman, J. M., Chapman, C. A., Hansen, J. L., Cherney, D. J. & Pell. , A. N. (2009a) Rapid assessment of the nutritional value of mountain gorilla foods: applying near-infrared reflectance spectroscopy to primatology. *Int. J. Primatol.,* **30,** 729-742.

Rothman, J. M., Chapman, C. A. & Van Soest, P. J. (2012) Methods in primate nutritional ecology: A user's guide. *International Journal of Primatology,* **33,** 542-566.

Rothman, J. M., Dierenfeld, E. S., Hintz, H. F. & Pell, A. N. (2008) Nutritional quality of gorilla diets: consequences of age, sex and season. *Oecologia,* **155,** 111-122.

Rothman, J. M., Dusinberre, K. & , A. N. (2009b) Condensed tannins in the diets of primates: a matter of methods? *American Journal of Primatology,* **71,** 70-76.

Rothman, J. M., Van Soest, P. J. & Pell, A. N. (2006) Decaying wood is a sodium source for mountain gorillas. *Biology Letters,* **2,** 321-324.

Ruggiero, R. G. & Fay, J. M. (1994) Utilization of termitarium soils by elephants and its ecological implications. *African Journal of Ecology,* **32,** 222-232.

Russo, S. S. & Chapman, C. A. (2011) Primate seed dispersal: Linking behavioural ecology and forest community structure. In: *Primates in Perspective* (Eds. C. J. Campbell, A.

F. Fuentes, J. C. Mackinnon, M. Panger & S. Bearder). Oxford University Press, Oxford.

Ryan, A. M., Chapman, C. A. & Rothman, J. M. (2012) How do differences in species and part consumption affect diet nutrient concentrations? A test with red colobus monkeys in Kibale National Park, Uganda. *African Journal of Ecology,* **51,** 1-10.

Spuhler, J. N. & Jorde, L. B. (1975) Primate phylogeny, ecology and social behaviour. *Journal of Anthropological Research,* **31,** 376-405.

Stickler, C. M. (2004) *The effects of logging on primate-habitat interactions: A case study of redtail monkeys (Cercopithecus ascanius) in Kibale National Park, Uganda,* M.Sc. Thesis, University of Florida, Gainesville, Florida.

Stiles, E. W. (1982) Fruit flags: hypotheses. *American Naturalist,* **120,** 500-509.

Waser, P. M. (1975) Monthly variations in feeding and activity patterns of the mangabey, *Cercocebus albigena* (Lydekker). *East African Wildlife Journal,* **13,** 249-264.

Waterman, P. G. & Kool, K. M. (1994) Colobine food selection and plant chemistry. In: *Colobine monkeys: their ecology, behaviour, and evolution* (Eds. A. G. Davies & J. F. Oates). Cambridge University Press, Cambridge.

White, T. C. R. (1993) *The inadequate environment: Nitrogen and the abundance of animals,* Springer-Verlag, Berlin.

Wieczkowski, J. & Kinnaird, M. (2008) Shifting forest composition and primate diets: A 13-year comparison of the Tana river mangabey and its habitat. *American Journal Primatology,* **70,** 339-348.

Worman, C. O. & Chapman, C. A. (2005) Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *Journal Tropical Ecology,* **21,** 689-697.

Zanne, A. E., Chapman, C. A. & Kitajima, K. (2005) Evolutionary and ecological correlates of early seedling morphology in East African trees and shrubs. *American Journal of Botany,* **92,** 972-978.

CHAPTER SIX

6 The importance of fall-back fruits in the nutritional ecology of Grey-cheeked mangabeys (*Lophocebus ugandae* Groves) in Mabira and Lwamunda forest reserves, Uganda.

M. Masette, G. Isabirye-Basuta and D. Baranga

Department of Biological Sciences, Makerere University, P.O. Box 7062, Kampala, Uganda

Abstract

During periods of low food availability, frugivores are known to rely on fall-back fruits (FBFs) for their dietary requirements. However, the identity and role of FBFs in the diet of Grey-cheeked mangabeys (*Lophocebus ugandae*, Groves) inhabiting Mabira and Lwamunda forest reserves is unknown. A 24 month study was undertaken to identify FBFs and preferred fruits (PFs), their availability and nutrient content. Availability index distiquished between FBFs and PFs. Fruit trees that were available for $\geq$ 10 months were FBFs while those available for < 10 months were PFs or seasonal. Results indicated that *Ficus spp. sur*, *mucuso* & *exasperata*, *C. indicum* and *M. eminii* qualified as FBFs while *C. durandii, C. africana, C. mildbraedii*, *B. unijugata*, *P. microcapa*, *R. edulis* and *M. arboreus* qualified as PFs. The ratio of FBFs to PFs was 2:1 and 1:1 in the severely degraded Lwamunda and fairly undisturbed Mabira (M1) respectively. The ratio was indicative of forest health ecosystem. The protein, fat and sugar content in PFs was twice as much as there was in FBFs. The incremental nutrient factor between individual PFs and FBFs varied from 0.08 to 3.68 depending on nutrient component, fruit type and habitat. Based on availability index, FBFs could not have possibly sustained the dietary requirements of mangabeys during the study period. We therefore concluded that there must have been another food source which we suspect could have been raided crops and domesticated fruits in Lwamunda and in the regenerating Mabira (M2) respectively.

Key words: Seasonality, food availability, macronutrients and fall-back fruits.

6.1 Introduction

Fallback fruits (FBFs) are resources used seasonally by a frugivore in the absence of preferred fruit (Marshall, *et al.*, 2009; Marshall and Wrangham, 2007; Lambert *et al.*, 2004). There are usually deemed to be less preferred and negatively correlated with the availability of preferred fruits (Conklin-Brittain *et al.*, 1998). Owing to their proximity to urban centres with insatiable demands for forestry products (Baranga, 2004) Mabira and Lwamunda forest reserves are prone to high levels of degradation. Quiet often, habitat degradation results into food declines and during periods of fruit scarcity, mangabeys rely on available fruits for sustainability. According to Furuichi *et al.* (2001), fruits that play a prominent role in sustaining frugivores during periods of general food scarcity are referred to as FBFs. Indeed Chapman *et al.*, (2012) asserts that FBFs are significant components in primate diets because of their contribution to the sustainability role.

In a forest environment, FBFs may be selected as a matter of preference or importance. Whereas preference is a matter of dietary choice, importance is a measure of dietary composition (Marshall and Wrangham, 2007). According to them, FBFs tend to be foods of low preference but with high seasonal importance and tend to be eaten all year round. The distinction between preference and importance have led to the classification of FBFs into two classes; staples and fillers. According to Marshall, *et al.*, (2009) the former constituted up to 100% of the frugivore diet and they were available all year round while the latter constituted less than 100% and they were completely avoided for long periods of time. Most primates have evolved specific masticatory and digestive adaptations to consume fallback foods when preferred foods are scarce (Porter *et al.*, 2009). Fallback foods can be categorized into nuts, seeds, fruits and root vegetables (Lucas *et al.*, 2009). Fall-back fruits (FBFs) are important in the diet of frugivores especially during periods of low food availability exacerbated by anthropogenic activities.

Essentially, there are five major characteristics of FBFs fruits; abundance and availability over time, hardness of the protective structures like seed coat, nutritional attributes and their proportion to the overall primate diet (Marshall, *et al.*, 2009). FBFs tend to have high abundance but spatiotemporally dispersed and thrive in patchy sized habitats (Saito 1996). They also tend to bear fruit all year round like many fig species (Marshall *et al.*,

2009; Naughton-Treves *et al.*, 1998; Wrangham *et al.*, 1996; Milton *et al.*, 1982). They bear large quantities of fruits (Chapman *et al.*, 1992) and can be found in many rainforest ecosystems as source of food for many frugivores including mangabeys. Figs were listed as one of the most important 50 species utilized as food by mangabeys in Central Uganda four and a half decades ago (Waser, 1975).

Most FBFs show distinct patterns of availability; particularly in tropical rainforests (Krishnadas *et al.*, 2011; Milton *et al.*, 2005). The seasonal fluctuations of preferred fruits obtaining therein create periods of resource scarcity for frugivores and readily available FBFs assume priority significance in their diets. Habitat alteration has a direct effect on food availability which compels mangabeys to consume FBFs in the absence of preferred fruits. Low fruit availability especially in Mabira and Lwamunda forest reserves may be due anthropogenic activities characterized by human population increases, encroachment for agricultural purposes, bushfires, mining/drilling, construction, skewed policies and legislation pertaining to the forestry sector and civil strife (Hamilton, 1984). These factors synergistically impose quantitative as well as qualitative changes in food nutrition and availability with direct effect on forest fauna populations. Primates are known to be more sensitive to habitat disturbances (Olupot, 2000) than other forest fauna with the exception of butterflies (Akite, 2008) and birds (Plumptre *et al.*, 2001).

Most FBFs are characterized by hardness of fruit structures especially the lignified exocarp or endocarp which plays the protective role against fungi, bacteria and other environmental stress elements (Seidel *et al.*, 2010). To access the desired edible part, frugivores have to devise processing techniques to overcome the hardness. For example, Hohmann (2009) observed that chimpanzees used stones to crack-open the hard nuts. According to Kinzey and Norconk (1990), hardness is an important physical fruit and seed property which determines food choice, processing method and influences feeding behaviour among primates. Besides dietary choice, hardness of some FBFs could have also contributed to the evolutionary development of *L. ugandae* thick enamel (Lambert *et al.*, 2004) and in great apes (Constantino *et al.*, 2009).

Nutrition is a vital aspect of primate life and a major determinant in the selection of a habitat. Under normal circumstances, primates generally select a diet that is rich in protein, carbohydrates and low in fibre (Janson and Chapman, 1999). However, during periods of food scarcity brought about by seasonality and degradation, mangabeys are compelled to consume foods that are high in fibre, low in protein and carbohydrates. Most frugivores prefer ripe fruit (O'Driscoll and Chapman, 2005) but in their absence, mangabeys may shift to consumption of unripe fruit and endosperms. Unripe fruit is known to have high levels of condensed tannins (Poulsen *et al.*, 2001) which compromises their nutritional status. In this regard, these alternative fruit parts may be loosely categorized as FBFs.

When foraging for seasonal foods, primates employ different foraging patterns depending on severity of habitat disturbance (Olupot, 1999; Freeland, 1979; Waser, 1975). According to Worman and Chapman (2005) when food resources become severely compromised in terms of quantity and quality, mangabeys tend to have dietary shifts (Waser, 1975) and nutritional trade-off (Schaefer *et al.*, 2003). There are divergent dietary switches that have been observed in other primates regarding fall-back foods (Vogel *et al.*, 2009) during periods of low fruit availability. Low food scarcity also forces primates to forage over a large area so that they can meet their energetic and nutritional requirements (Chapman and Chapman, 2000). In the process, they encounter intra and interspecific stiff competition within a home range which forces low ranking individuals to switch to inferior low quality food items (Saito, 1996). As a mitigation to such stiff competition, mangabeys regularly incorporate low quality chemically defended unripe fruits, immature seeds and legumes in their diet (Doran-Sheehy *et al.*, 2006). Such inferior low quality food items were regarded as FBFs according to Marshall and Wrangham (2007). Scarcity of minerals in fruit and seed compels mangabeys to consume leaves and clay-like soils (Janson and Chapman, 1999) as a dietary shift or nutrient trade-off mechanism (Schaefer *et al.*, 2003). Dietary shifts have been associated with heavily degraded habitats (Olupot, 1999). Presumably, with the incessant habitat degradation of Mabira and Lwamunda forest reserves, mangabeys may be consuming low quality foods exemplified by FBFs because these two forests have experienced degradation since 1950s

(Hamilton, 1984; Howard *et al.*, 1991). Studies on dietary shifts (Worman and Chapman, 2005; Poulsen *et al.*, 2001; Janson and Chapman, 1999) and trade-offs (Schaefer *et al.*, 2003) in other primates will be refernce for the present study on mangabeys.

Several fruits have been identified as fall-back items in the nutritional ecology of mangabeys or indeed other primates but *Ficus* species appear to be the commonest FBF (Krishnadas *et al.*, 2011; Felton *et al.*, 2010; Vogel *et al.*, 2009; Kagoro-Rugunda and Baranga *et al.*, 2009; Naughton-Treves *et al.*, 1998). However, figs are nutritionally deficient (Wrangham *et al.*, 1993) although some species like *Ficus insipida* contains high concentrations of almost all amino acids, minerals and proteins (Wendeln *et al.*, 2000). Although figs are generally regarded as FBFs in some forest habitats, they are keystone fruits in other habitats (Basuta, *unpublished data*). Other food items have also been regarded as FBFs for instance; tree stem piths, seed and unripe fruit (Wrangham *et al.*, 1998), terrestrial herbaceous vegetation (THV) (Inogwabini and Matungila, 2009; Wrangham *et al.*, 1996) and fruit of *Musaga leo-errerae* (Furuichi *et al.*, 2001).

Knowledge of FBFs is necessary for evaluation of Mangabey's ability to response to food scarcity caused by anthropogenic habitat alteration (Chapman *et al.*, 2012). However, information on FBFs availability in Mabira and Lwamunda is glaringly missing but by inference, several studies (Naughton-Treves *et al.*, 1998; Tweheyo *et al.*, 2005) on mangabeys or other primates have been conducted in other forests across Africa which correlate FBFs with fruit availability. In this study, the distinction between FBFs and preferred fruits (PFs) was not clear-cut as described by other researchers (Marshall, *et al.*, 2009; Lucas *et al.*, 2009; Marshall and Wrangham, 2007). So availability and nutrient content of fruits have been used as criteria to differentiate between the two categories. For purposes of this paper, FBFs denotes those fruits or fruit parts which were available all year-round and the PFs have been designated as seasonal (SL) because they are available for short periods of time. We propose that mangabeys inhabiting severely degraded Lwamunda forest reserve were compelled to diversify food sources as a way of mitigating food scarcity and in the process meeting their dietary requirements than their counterparts in Mabira (M1) or (M2). This paper therefore examines the role(s) of FBFs

in the nutritional ecology of mangabeys inhabiting both Mabira and Lwamunda forest reserves with the main focus on fruit availability, fruit abundance and nutritional quality. We hypothesized that FBFs contribute immensely in the diet of mangabeys in Mabira and Lwamunda forest reserves.

6.2 Materials and Methods

6.2.1 Study area

The study was conducted in Mabira and Lwamunda forest reserves specifically in Lwamunda and Mabira, Uganda. The Basin has a bimodal rainfall pattern varying between 1200-1500 mm annually and it is distributed between two rainy distinct seasons April-May and October-November (Kizza, *et al.*, 2009). Mabira is located 54 km from Kampala along Jinja road and between latitudes 0° 24`N and 0° 35`E and longitude 32° 52`N and 33° 07`E. It covers an area of 306 km^2 with a total boundary length of 347.4 km on undulating hills and valleys at an elevation of 1070–1340 m above sea level (Howard *et al.*, 1991). Lwamunda on the other hand, is a riverine forest reserve surrounded by isolated flat-topped hills with steep slopes and stands at an average elevation of 1200 m above sea level. It is located 27 km along Kampala-Mityana road between latitude 0° 15′ N and 0° 23′ N longitude 32° 30′ E and 32° 43′ E with a relatively small area of only 67 km^2.

6.2.2 Study design

Three groups of habituated mangabeys, two (2) in Mabira forest reserve and one in Lwamunda forest reserve were observed for a period of 24 months from April 2005 to March 2007. The Lwamunda group consisted of 14 individuals (2 adult males, 3 sub-adult males, 4 adult females, 2 sub-adult females and 3 infants). The Mabira (M1) group comprised of 12 individuals; (2 adult males, 2 sub-adult males, 3 adult females, 2 sub-adult females and 3 infants) occupied the area that was relatively undisturbed. The Mabira (M2) group comprised of 13 individuals (1 adult males, 2 sub-adult males, 3 adult females, 2 sub-adult females and 2 infants) occupied an area which was formerly cultivated then abandoned due to implementation of a restrictive management policy.

Essentially, the study sites could be adequately described as: heavily degraded (Lwamunda), regenerating Mabira (M2) and fairly undisturbed Mabira (M1) forests. During the first quarter of the study period, selected groups of mangabeys in each forest type were observed intently for 5 consecutive days in a month. The groups were trailed from 7am to 3pm to establish fruit trees they utilized as food on a regular basis and the fruit part consumed. In addition, level of fruit maturity and ripeness, abundance in relation to other food sources and other factors influencing food availability were recorded.

Based on 5- minute systematic scan sampling method, the activity patterns (feeding, resting and socialising) of mangabeys was determined over a period of six months. The activity of "feeding" was considered only when the Mangabey was actively choosing a food item or holding it in its hand. An individual chewing was not considered "feeding" (Harcourt and Stewart, 1984). Observation data on diet was collected over a period of 2 consecutive days per group in a month. For purposes of this study, only fruits since they constitute over 50% of Mangabeys diet (Waser, 1975; Olupot *et al.*, 1997) were considered as major contributions to FBFs as opposed to seed, pith and leaves consumption was limited to a few tree species. The top 10 priority fruit tree species utilized by mangabeys in each study area were identified after 1 year of study (Table 6.1) and marked with a well-labelled 20 x 15 cm metal plate and their location noted using a Garmin Channel XL GPS. For each fruit tree species, a total of 10 replicas were similarly identified marked and monitored for phenological data collection based on a visual abundance score (VAS: 0-4) according to Chapman *et al.* (1992). Using food availability scores, the ten individual trees of the 10 priority fruit tree species were further designated as fall-back fruits (FBF) and seasonal fruits (SF) depending on temporal variations. Whereas FBFs were available and utilized by mangabeys throughout the year, the SFs were only available for half the period or less. The difference between FBFs and SFs was further ascertained by their nutritive content.

Table 6.1 Selected fruit tree species for monitoring fruit availability and abundance in Mabira fairly undisturbed (M1) and regenerating (M2) and severely degraded Lwamunda forest reserves

M1 & M2 fruit trees		Lwamunda fruit trees	
Fall-back (FBF)	**Seasonal (SF)**	**Fall-back (FBF)**	**Seasonal (SF)**
Ficus mucuso (FM)	*Celtis durandii* (CD)	*Ficus mucuso* (FM)	*Blighia unijugata* (BU)
Ficus exasperata (FE)	*Celtis africana* (CA)	*Ficus sur* (FS)	*Treculia africana* (TR)
Measopsis eminii (ME)	*Celtis mildbraedii* (CU)	*Ficus exasperata* (FE)	*Myrianthus arboreus* (MA)
Canarium indicum (CS)	*Antiaris toxicaria* (AT)	*Measopsis eminii* (ME)	*Rheedia edulis* (YF)
	Albizia grandibracteata (AG)	*Canarium indicum* (CS)	*Pseudospondias microcapa* (PM)
			Albizia grandibracteata (AG)

After six months of study, it was observed that certain fruit species exhibited distinct stages of fruit development and mangabeys utilized different parts of fruit as food depending on stage of development. The frequently consumed part of fruit or stage of ripeness was collected on a monthly basis using a hooked long pole for reachable trees. However, picking out samples from high trees was a challenge especially in Mabira M1 and therefore some samples were picked from the forest floor which compromised the authenticity of ripening stages but subsequent nutrient analysis indicated insignificant difference between samples that were directly harvested from the tree and those picked from forest floor. Nutrient analysis was mainly focussed on sugars, fats, crude fibre and energy which vary significantly across fruit species (Conklin-Brittain *et al.*, 1998). The overall mean value of the selected nutrient parameter for each FBF was compared with mean value of fruits that were seasonal.

6.2.3 Sample size

To determine the sample size, a quadratic equation: $n = (Z_{\alpha/2})pq/E^2$ (Cochran, 1977) was used. The minimal number of months during which the respective priority fruit tree was in-fruit denoted the sample size in each study site.

Where

n = sample size

Z = tabulated value from the normal Z table ($z = 1.96$);

α = level of significance ($\alpha = 0.05$);

p= probability that a priority fruit tree was available throughout the 24 months of the study;

q= probability that a priority fruit tree was not available and

E represents the sampling error that may be due to mis-identification of fruiting tree species.

Fruit samples at different stages of ripening from selected fruit trees were collected monthly, over a period of 22 months. Depending on the fruit part and size, 500g to 1-2 kg of sample was picked from each of the 10 marked individual trees of the 10 priority fruit trees that were fruiting then sealed in plastic bag and transported to the Department of Animal Science- Makerere University on the same day. The fruit sample was stabilized by drying in an air oven at 45°C, ground into powder and then stored in an airtight vial until respective analyses. Samples were analysed for their nutritional composition using standard analytical methods cited in *Section* 6.2.4.

6.2.4 Chemical analyses

In the absence of the hi-tech Near-Infrared Reflectance Spectroscopy (NIRS) method that offers rapid and cost-effective means of analysis (Rothman *et al.*, 2009), the traditional nutritional analytical methods were used. AOAC (1995) was used to quantify gross energy); fat or lipid was determined by soxhlet system of extraction method (AOAC, 1990). To determine crude fibre, Van Soest *et al.*, (1991) was used while Price *et al.* (1978) method was used to determine soluble carbohydrates (sugar) in fruit samples consumed at various stages of maturity by mangabeys. The actual nutritional quality of the diet was calculated from the amount of specific nutrients in the diet.

The fruit abundance and nutritional content was limited to fat, sugars, protein and energy of all trees that were fruiting during the five consecutive of every month. Theoretical postulation of dietary shifts in mangabeys feeding ecology as a consequence of fruit scarcity induced by forest degradation was contrasted with actual realities observed during the study. Comparative analysis of the three habitats at different levels of

degradation with regard to fruit abundance and nutrient content of the selected four tree species is discussed in relation to levels of secondary compounds as a deterrent. However, the study did not consider feeding bouts by mangabeys for FBFs or seasonal fruits, growth rates and frequence of tree falls or logging.

6.2.5 Data analysis

One way ANOVA was used to compare nutrient content (sugar, protein and fat) between FBFs and seasonal or preferred fruits. The same analytical method was used to compare FBFs and seasonal fruits existing in the three study sites of Lwamunda, Mabira that was fairly undisturbed and regenerating forest reserves. Using Stata version 12, the two-way ANOVA using Sigma plot was used to establish the relationship between fruit abundance or fruit cover and forest type or with stage of fruit development. All data generated from chemical analyses were coded, cleaned, edited and entered into SPSS version 15 for analysis that involved descriptive and inferential packages. The ANOVA entailed comparison between species, stages of fruit development and forest types to establish relationships between independent and primary variables.

6.3 Results

6.3.1 FBFs versus seasonal fruits

Although the distinction between fall-back fruits (FBFs) and preferred fruits was not clear-cut in the present study, we used Conklin-Brittain *et al.* (2001) criterion to differentiate between the two categories. They assumed that seasonal fruits could be regarded as preferred fruits and seasonality as a befitting criterion for drawing the distinction between the two. Based on this assumption, we have classified *Celtis africana*, *Celtis durandii Celtis mildbraedii Myrianthus arboreus, Rheedia edulis*, *Pseudospondias microcapa* and *Blighia unijugata* as preferred fruits while the three figs (*F. exasperata*, *F. mucuso* and *F. sur*) *Canarium indicum* and *Maesopsis eminii* were designated as FBFs. It was observed that FBFs were fruiting for at least 10 months of the year while seasonal fruits only fruited for five months on average which implied that FBFs were more available and played a crucial role in the diet of mangabeys than SFs.

Based on the quadratic equation, there were four out of 10 priority fruit trees that could be considered as FBFs in Mabira M1 & M2 (Fig. 6.1). They included *F. exasperata*, *F. mucuso, C. indicum* and *M. eminii.* The seasonal fruits included *Celtis* species, *P. microcapa*, *A. grandibracteata* and *T. africana.*

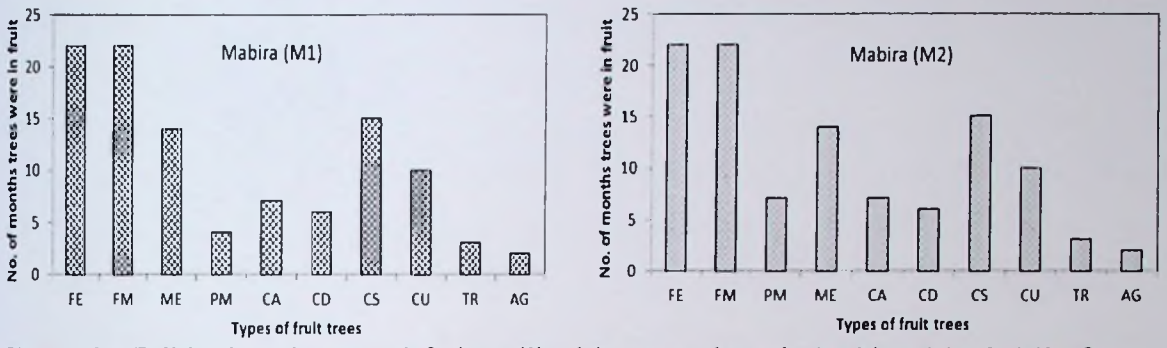


Figure 6.1 Fall-back and seasonal fruits utilized by mangabeys in Mabira (M1 & M2) forest reserves between July 2005 and June 2007 (*Names for types of fruits are decoded in* Table 6.1)

In the severely degraded Lwamunda forest reserve; there were five out of 10 priority fruit trees that could be considered under FBFs category (Fig 6.2). They included *F. exasperata*, *F. mucuso, F. sur, C. indicum* and *M. eminii.* The seasonal fruits included *P. microcapa*, *Treculia africana, M. arboreus; B. unijugata; A. grandibracteata and R. edulis.*

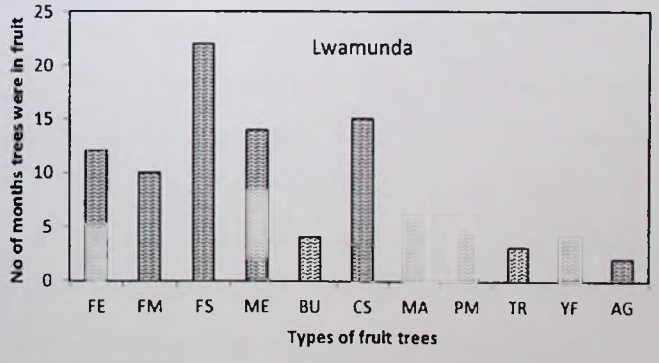


Figure 6.2 Fall-back and seasonal fruits utilized by mangabeys in Lwamunda forest reserves between July 2005 and June 2007 (*Fruit trees decoded in* Table 6.1)

In the three forests, Mangabey diet was dominated by FBFs food resources. Of the five FBFs in Lwamunda forest reserves, *F. sur* was the most important and reliable FBF. However, in fairly undisturbed Mabira forest reserve, it was a seasonal fruit and the few *F. sur* trees available in this part of Mabira were confined at the forest edge. Instead the most reliable FBFs for mangabeys in Mabira forest reserve were *F. exasperata* and *F. mucuso* that were available in equal proportions. This scenario was replicated in regenerating the portion of Mabira despite the presence of domesticated fruits like bananas (*Musa acuminata*), jack fruit (*Artocarpus heterophyllus*) and passion fruits (*Passiflora edulis*). Although *C. indicum* and *M. eminii* were regarded as FBFs in Mabira and Lwamunda forest reserves, their proportion in the Mangabey diet was not as prominent as the role played by figs. Whereas *C. indicum* and *M. eminii* fruited for only 15 and 14 months respectively in both forests, Figs (*F. mucuso* and *F. exasperata*) fruited for 22 months in Mabira and *F. sur* fruited for 23 months in Lwamunda out of the study period of 24 months.

It was observed that mangabeys consumed various parts of FBFs at different levels of ripeness. The three fig species, *C. indicum* and *M. eminii* exhibited 7, 5 and 6 distinct ripening stages respectively (i.e. 3 -32 weeks after fruiting). While the first three stages of ripening in figs were not utilized as food probably due to high levels of secondary compounds, the endosperm of young *C. indicum* and *M. eminii* were regularly consumed by mangabeys during the early stages of fruit development (1-3) especially in severely degraded Lwamunda forest reserve. When the seasonal fruits were available, mangabeys utilized them like FBFs except for *A. grandibracteata* and *R. edulis* whose seed and pulp were utilized exclusively. From field observation without nutritional data, the choice of fruit stage for consumption appeared to be influenced by fruit abundance, level of competition exerted by other frugivores and availability of other food items within the home range. For example, in Lwamunda when *P. microcapa*, *M. eminii* and *B. unijugata* were in season, mangabeys only consumed stage 7 of *F. Sur* and when off-season, stages 4-6 were consumed. The same feeding behaviour was observed in the regenerating portion of Mabira forest reserve (M2). When domesticated fruits like passion fruits,

pineapples and jackfruit were available, mangabeys only consumed the final stage of ripeness for all fruit types.

The number of FBF trees that were bearing fruit over the study period, varied spatiotemporally (Fig. 6.3). Generally, there were more trees fruiting in Mabira M1 and M2 than in the severely degraded Lwamunda as exemplified by *F. exasperata* during 2006.

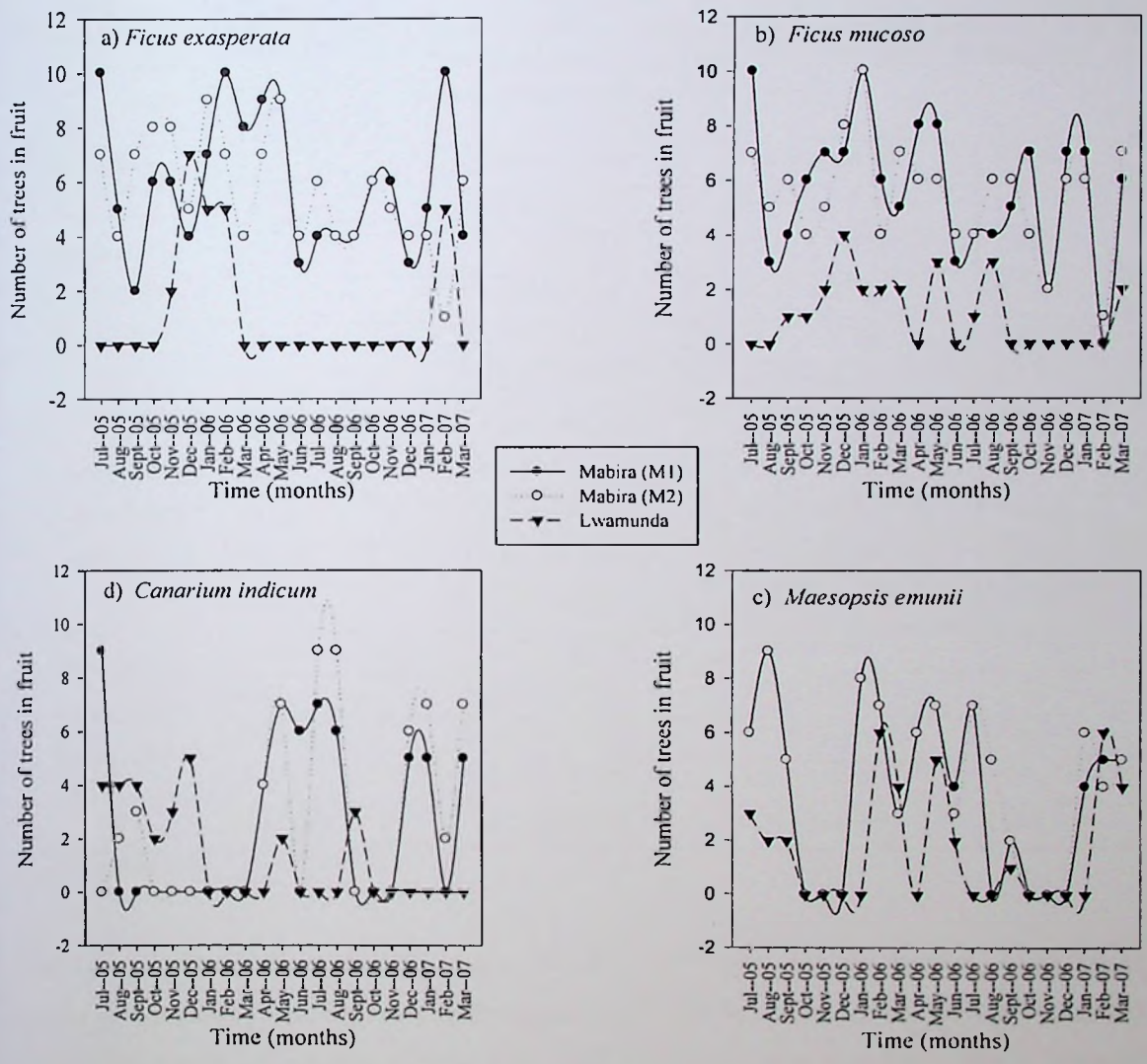


Figure 6.3 Spatiotemporal variations in food availability represented by fruiting trees species occurring in the three study sites.

6.3.2 Chemical composition

Nutritional content of FBFs plays a crucial role in Mangabey diet especially during periods of food scarcity when seasonal fruits are scarce or unavailable. Apart from the fibre component all other macro-nutrient components generally indicated that FBFs were significantly different from seasonal in the three forest reserves (Table 6.2) with the exception of sugar in Lwamunda. This may be attributed to the overall sample size and diversity of seasonal fruits.

Table 6.2 Mean values and standard errors of macro-nutrients in fall-back and seasonal fruits of Mabira and Lwamunda forest reserves (One way ANOVA used to establish the significant differences between macro-nutrients at 5% level)

Forest reserve	Macro-nutrient	Fall-back fruit	Seasonal fruit	P-value
Mabira (M1) n = 690 (FBF) n= 75 (SF)	Sugar*	1.658 ± 0.023	1.884 ± 0.041	< 0.016
	Fat*	0.734 ± 0.021	1.080 ± 0.073	< 0.001
	Protein*	1.618 ± 0.014	2.211 ± 0.046	< 0.001
	Fibre*	2.127 ± 0.026	2.047 ± 0.062	> 0.317
	Energy	3.831 ± 0.031	4.659 ± 0.125	< 0.001
Mabira (M2) n = 618 (FBF) n= 36 (SF)	Sugar*	1.601 ± 0.022	1.771 ±0.087	> 0.182
	Fat*	0.622 ± 0.024	0.728 ± 0.091	< 0.001
	Potein*	1.709 ± 0.017	2.168 ± 0.6	< 0.004
	Fibre*	2.085 ±0.026	1.981 ±0.089	> 0.346
	Energy	3.706 ± 0.026	4.418 ± 0.251	< 0.001
Lwamunda (LD n = 1014 (FBF) n= 198 (SF)	Sugar*	1.675 ± 0.019	1.661 ± 0.057	> 0.781
	Fat*	0.666 ± 0.018	0.194 ± 0.075	< 0.001
	Protein*	1.642 ± 0.013	1.758 ±0.045	< 0.009
	Fibre*	2.074 ± 0.020	1.939 ±0.038	< 0.006
	Energy	3.755 ± 0.025	3.964 ± 0.102	< 0.0036

* Log transformed

During periods of food scarcity especially in Lwamunda forest reserve, mangabeys regularly consumed endosperms of both seasonal and fall-back fruits which contained substantial levels of protein (Table 6.3). The difference between the various nutrient components of different fruits was insignificant (ANOVA, $p > 0.05$)

Table 6.3 Mean values and standard deviations of macro-nutrients in endosperms of seasonal and fall-back fruits in Lwamunda forest reserve.

Fruit type	n	Protein (%)	Fat (%)	Sugar (%)	Fibre (%)	Energy Kcal/g
C. indicum	24	9.26 ±3.62	5.52±2.29	1.59±0.65	3.96±1.22	9.26±3.62
M. arboreus	9	10.59 ±5.86	6.21±4.79	0.91±0.48	3.12±0.74	10.59±5.86
M. eminii	21	8.47 ±1.40	3.84±1.21	0.88±0.31	3.10±0.61	5.47±1.40
P. microcapa	18	10.00 ±1.46	5.73±1.74	2.02±0.89	3.57±0.80	10.00±1.46

In the absence of seasonal fruits, mangabeys like other frugivores shift to other sources of food to meet their dietary requirements. In such incidences, FBFs come in handy among other resources like leaves, flower buds and mushrooms. Based on the selected macro-nutrients (Figs. 6.4, 6.5, 6.6, 6.7 & 6.8); the majority of seasonal fruits showed relatively high values in sugars and proteins as opposed to FBFs that were consistently low. However, sugars in *F. sur* and *F. mucuso* were comparable to seasonal fruits. The mean sugar content varied between 4-8% in all priority fruits but the standard deviations varied more widely in FBFs than in seasonal fruits (Fig. 6.4). However, the standard deviation in Lwamunda seasonal fruits especially *R. edulis* and *B. unijugata* was similar to FBFs.

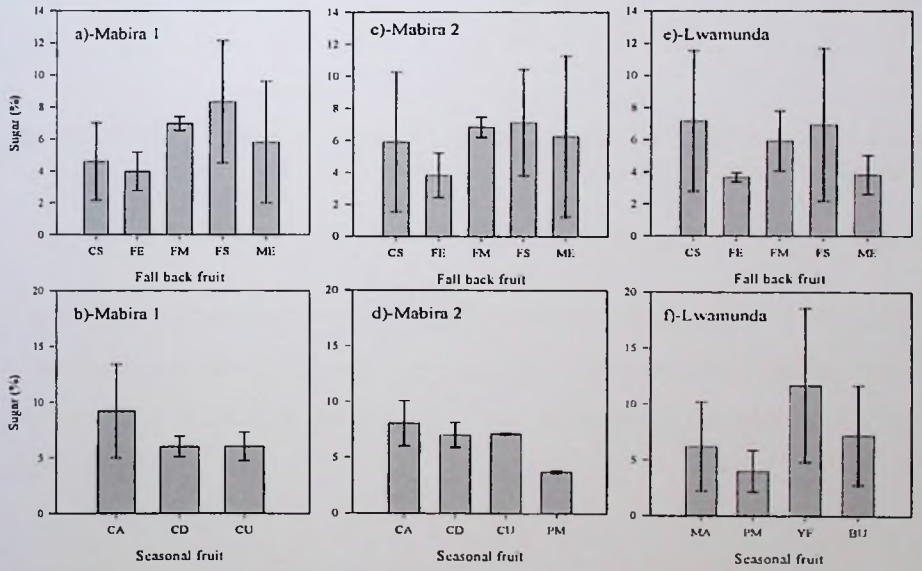


Figure 6.4 Mean sugar content (%) variation in the fall back (a, c & e) and seasonal (b, d & f) fruits in Mabira (M1 & M2) and Lwamunda (LD) forest reserves. (Fruits *decoded in* Table 6.1)

The protein component for all the priority fruits was mostly derived from endosperms and seed since most fruit pulps contained low protein content. The mean protein content was less than 8% in FBFs and about 10% in seasonal fruits except in Lwamunda which was slightly less than 9%. Essentially, average protein content in FBF was more in seasonal or preferred fruit. The standard deviation in Mabira (M1) and Lwamunda seasonal fruits by mangabeys varied widely.

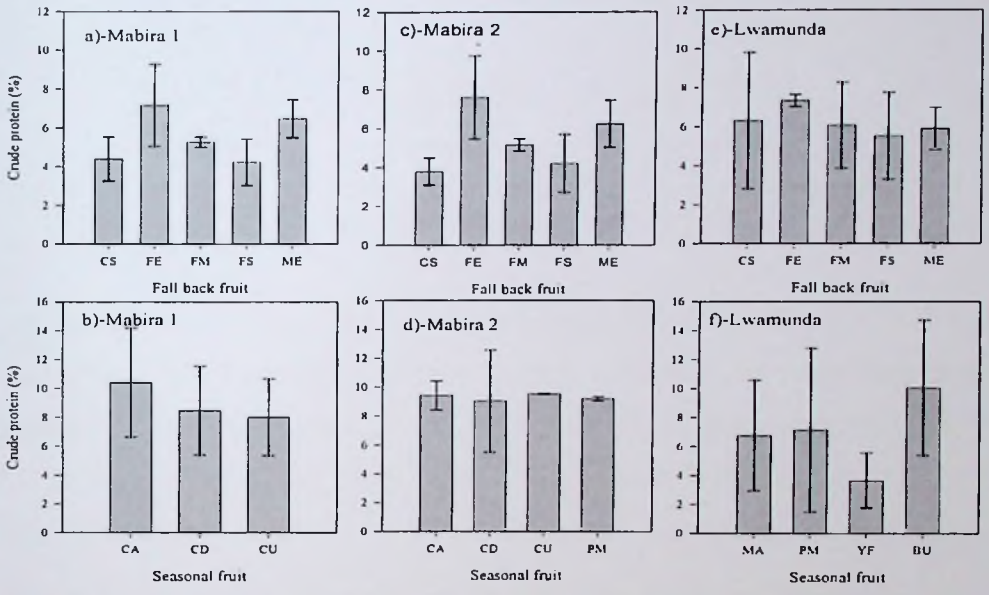


Figure 6.5 Mean protein content (%) variation in the fall back (a, c & e) and seasonal (b, d & f) fruits in Mabira (M1 & M2) and Lwamunda (LD) forest reserves. (Fruits *decoded in* Table 6.1)

The fat component for all the priority fruits consumed by mangabeys in both Mabira forest reserves was relatively low (<5%) regardless of whether the fruit was FBF or seasonal (Fig. 6.6). The *sd* variation was more pronounced in Lwamunda FBFs than in either M1 or M2.

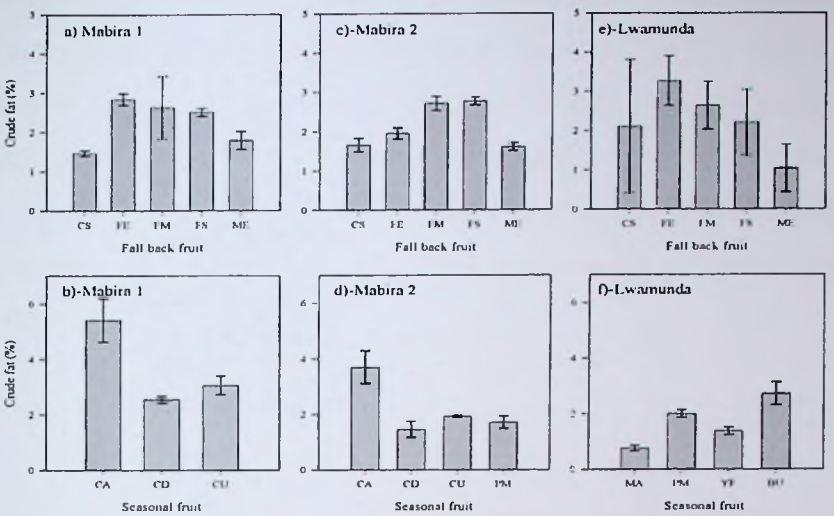


Figure 6.6 Mean fat content (%) variation in the fall back (a, c & e) and seasonal (b, d & f) fruits in Mabira (M1 & M2) and Lwamunda (LD) forest reserves. (Fruits *decoded in* Table 6.1)

The mean fibre content varied with type of fruits regardless of whether the fruit was FBF or seasonal (Fig. 6.7) but oscillated between 5-20%. However, the mean fibre content in both categories of fruits in Mabira M1 & M2 did not significantly vary from each other (ANOVA, $p > 0.05$) and yet FBF and SL significantly varied from each other ($p < 0.05$) in Lwamunda forest reserve

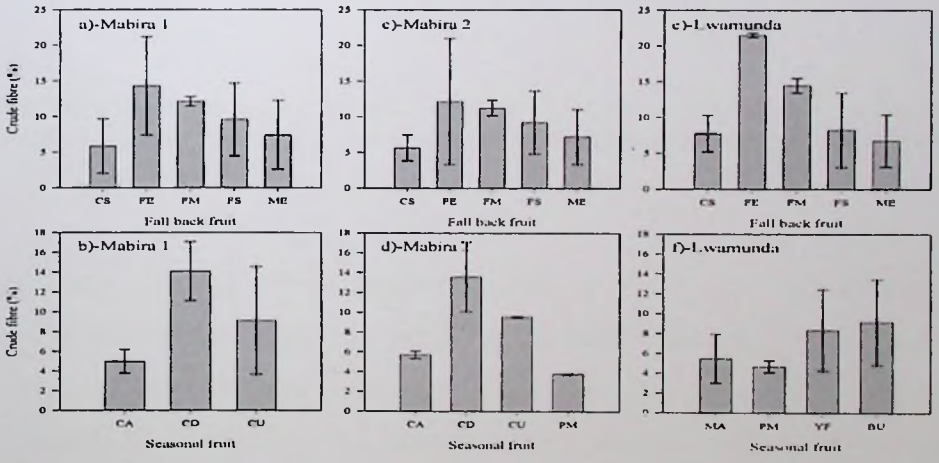


Figure 6.7 Mean fibre content (%) variation in the fall back (a, c & e) and seasonal (b, d & f) fruits in Mabira (M1 & M2) and Lwamunda (LD) forest reserves. (Fruits *decoded in* Table 6.1)

The energy derived from consumption of seasonal fruits was slightly more than energy from consumption of FBFs in Mabira forest reserve (Fig 6.8) which did not exceed 4 Kcal/100g of sample. Apart from *B. unijugata* none of the seasonal fruits exceeded 4 Kcal/100g mark. The type of forest habitat hardly influenced the outcomes. Unlike the differences observed in Mabira forest reserve, the energy derived from consumption of either seasonal or FBFs in Lwamunda forest reserves was not significantly different ($p > 0.05$ using one-way ANOVA).

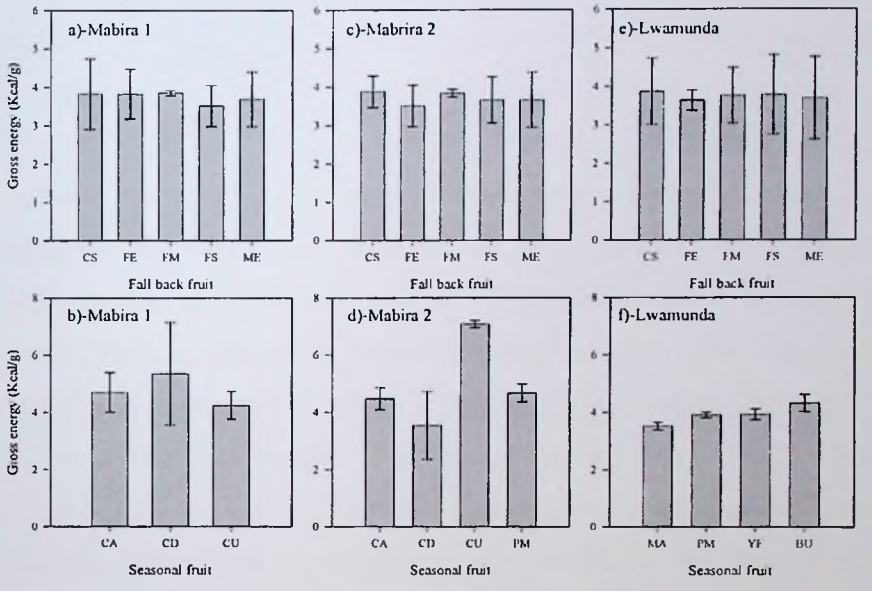


Figure 6.8 Mean gross energy content (%) variation in the fall back (a, c & e) and seasonal (b, d & f) fruits in Mabira (M1 & M2) and Lwamunda (LD) forest reserves. (*Type of fruits decoded in* Table 6.1)

Generally, sugar, fat and protein content of most seasonal fruits was relatively higher than in FBFs with the exception of protein in *F. exasperata* which was comparatively higher than in *M. arboreus* and *R. edulis* (Fig. 6.4). The fat component for all the priority fruits consumed by mangabeys in Lwamunda forest reserves was relatively lower than those in Mabira. The standard deviations of most fruits were quite wide because of the wide spectrum of samples that varied from ripe to unripe fruit including endosperms.

6.4 Discussion

Fruit availability and nutrient content of priority fruits regularly utilized as food by mangabeys in LVB forest reserves appear to be the most credible differentiation criteria between FBFs and seasonal or preferred fruits (PFs). The FBFs fruited for 22 months out of 24 months (or 76%) of the study period at different stages of development compared to 6 months on average of the study period (or 14%) attributed to PFs.

Based on fruit availability as a criterion, figs are undeniably the principal FBFs in the three forest reserves. This was particularly true for *F. sur* in Lwamunda forest reserve that fruited throughout the year. This is in agreement with other studies (Krishnadas *et al.*, 2011; Felton *et al.*, 2010; Vogel *et al.*, 2009; Naughton-Treves *et al.*, 1998) that classified figs as FBFs. In most tropical forests, figs were abundant and fruited throughout the year (Kagoro-Rugunda and Baranga, 2009; Marshall and Wrangham, 2007). Although figs have been regarded as FBFs in the present study, Felton *et al.*, (2008) reckoned that at times some species of figs were regarded as staple food resources for primates. This assertion has been corroborated with other studies conducted in Uganda's Kibale National Park, whereby figs were regarded as FBFs in Kanyawara and yet they were staple food resources in Ngogo (Watts *et al.*, 2012). During periods of scarcity, van Schaik *et al.* (1993) noted that certain plant products acted as keystone resources in one habitat and as mainstays in another habitat. As such, in the present study, *F. sur* in Lwamunda and *F. exasperata* in the fairly undisturbed Mabira forest reserve could be regarded as keystone fruits although this assertion contradicts Gautier-Hion and Michaloud (1989) findings in Gabonese tropical rainforest who did not regard figs as FBFs at all. Worman and Chapman (2005) study also described *C. durandii* as an important fruit tree species in the diet of many frugivorous primates since it fruited all-year round. As such, they duly categorized it as FBF instead of seasonal which conflicted with the results of the present study. From abundance view point, *C. indicum* and *M. eminii* should also be considered as FBFs since they were available and consumed when seasonal fruits were scarce. The addition of these two species on the list of FBFs in this study is a pioneering attempt. Based on availability criterion, the designated FBFs probably played a pivotal role in the diet of mangabeys inhabiting in Mabira and

Lwamunda forest reserves especially during periods of food scarcity. On the contrary, the seasonal fruits were available for less than 10 months which implied that mangabeys could not rely on them for their dietary requirements. Fruit scarcity creates a negative energy balance and a reliance on FBFs (Ehlers-Smith *et al.*, 2013).

Generally, FBFs were nutritionally inferior to seasonal fruits in terms of sugar, fat and protein with the exception of *F. exasperata* protein which was comparatively higher than *M. arboreus* and *R. edulis*. This was attributed to the composition of *F. exasperata* samples that were whole fruit as opposed to *M. arboreus* and *R. edulis* samples that were exclusively pulp. Fruit pulp is known to have low protein content (Jagtap *et al.*, 2010; Rode *et al.*, 2006; Osman, 2004). The nutritional inferiority of FBFs cut-across all the three study sites although the differences were not significant ($p > 0.5$) especially with regard to the energy component. The poor nutritional nature of FBFs is exemplified by figs (Ajayi *et al.*, 2012; Wrangham *et al.*, 1993). Several studies on fig nutrient quality have been conducted to explain the causes which include the large proportional indigestible seed and small portion of digestible fraction (Urquiza-Haas *et al.*, 2008). Morphological disposition that consist of numerous seeds thoroughly interspersed with pulp does not allow optimal utilization of digestible material (Milton, 1984). Consequently, nutrients tightly adhered onto the seed cannot be efficiently utilized due to limited passage time through the guts. However, mangabeys could have valued the consumption of *F. mucuso* because according to Ahoua *et al.* (2012), it has anti-oxidant properties in the fruit and leaves that may be accessed in diet to cure diseases related to oxidative stress. Unripe fruit contain toxic or distasteful secondary compounds, structurally difficult to process and contain low concentration of sugars (Nelson *et al.*, 2000).

With the exception of fibre, all other macro-nutrients were significantly lower in FBFs than in PFs. The perceived deviation exhibited by fibre component may be attributed to the analytical method. Mertens (2003) contends that van Soest *et. al.*(1991) method does not measure all the insoluble dietary fibre (IDF) instead we should have used the amylase-treated neutral detergent fibre (aNDF) method. There was therefore a possibility of

underestimation; hence the observed deviation. Fibre imparts physical properties to food and usually lowers caloric density thus it is inversely related to digestibility and offers limited nutritional benefits to non-ruminants (van Soest, 1994). Consequently, primates like mangabeys tend to minimize intake of foods with high fibre content. During periods of food scarcity, primates tend to convert proteins into glucose through the process of gluconeogenesis (MAFF, 1995) but it a health risk. Consequently, primates tend to select food items with high protein content. Indeed Oftedal *et al.* (1991) noted that food selection in some species of primates appears to be correlated with the protein concentration of foods. Previous nutritional studies (Matsumoto-Oda and Hayashi, 1999; Milton, 1979) in non-human primates have indicated that protein content is positively correlated with food selection and conversely with fibre. In this regard proteins are a better and more critical parameter for identification of FBFs than fat. In the severely degraded Lwamunda forest reserve, the additional use of seeds and fruit endosperms enhanced the protein content and importance of FBFs. With the exception of *Blighia* aril and seldomly *Celtis species*, fall-back and seasonal fruits had unusually low fat content regardless of their ecological status. As such, fat would be a poor criterion for differentiating between FBFs and PFs. Although gross energy content does not vary greatly among many plant species (Dearing and Cork, 1999), food crops are generally regarded as highly digestible with high energy and low secondary compounds (Rode *et al.*, 2006). Probably that was the reason behind the frequent crop raiding observed in Lwamunda forest reserve during the period of study.

The consumption of FBFs when preferred fruits were scarce or unavailable was in agreement with several authors (Hockings *et al.*, 2009; Marshall *et al.*, 2009; Marshall and Wrangham, 2007; Lambert *et al.*, 2004; Conklin-Brittain *et al.*, 1998). Although FBFs were nutritionally deficient as exemplified by the low mean sugar and protein content in the present study, they are known to contribute partly sustainability a primate population. This was in agreement with findings of Furuichi *et al.* (2001) and Chapman *et al.* (2012). The role of FBFs during periods of general food scarcity was more prominent in severely degraded Lwamunda than in fairly undisturbed Mabira M1. Since consumption of unripe fruit (Wrangham *et al.*, 1998) and seeds (Poulsen *et al.*, 2001) was regarded as fall-back food source, consumption of development stages 3 and 4 for figs, endosperm of *C. indicum*

and *M. eminii* by mangabeys should also be considered as fall-back food resource especially in Lwamunda forest reserve. Although unripe fruit pulp contain toxic or distasteful secondary compounds, structurally difficult to process and contain low concentration of sugars (Nelson *et al.*, 2000), they contain the desired amounts of protein during periods of food scarcity. According to Doran-Sheehy *et al.* (2006), mangabeys regularly incorporated low quality, chemically defended unripe fruit pulps, seeds and legumes in their diet as an adaptation for survival. Most unripe fruit are also hard and may contain sclerified cells or calcium oxalate crystals known to be irritants to both humans and other mammals (Gargiullo and Stiles, 1993). However, during periods of food scarcity, mangabeys have limited food options so consumption of unripe fruit is rampart as observed in Lwamunda.

It was abundantly clear that FBFs in the three study sites contained low levels of sugars, protein and fats. From quality standpoint, FBFs offered inadequate amounts of the basic components of mangabey nutritional requirements. To meet their daily nutritional requirements when PFs were scarce, mangabeys devised various mechanisms to sustain themselves depending on the degradation status of the habitat. In Lwamunda, we found 5 FBFs and only *F. sur* was available throughout the study period which implied that mangabeys had other sources of food. Since humans had cultivated several agricultural crops like bananas, cassava, maize, sweet potatoes, pineapples and sugarcanes in close proximity or within the forest reserves, mangabeys probably engaged in crop-raiding to sustain themselves during periods of food scarcity. This speculation was confirmed by Ogango's (2006) study in the same forest reserve and Fungo *et al.* (2013) in Mabira. Whereas, crop-raiding was not observed in Mabira (M1), in regenerating forest of Mabira (M2), mangabeys had access to domesticated fruits like passions, jackfruit, pineapples and bananas. These fruits had been abandoned after the imposition of the 1993 UNESCO management strategy that prohibited encroachment of Mabira forest reserve for agricultural purposes (Alpert, 1996). It would therefore seem to be nutritionally challenging for mangabeys to sustain themselves in these habitats without access to domesticated crops. It is highly plausible that in severely degraded Lwamunda and regenerating Mabira forest reserves, the alternative source of dietary requirements for

mangabeys were the domesticated fruits and crops. Although they are not nutrient deficient like typical FBFs, they provide an alternative food resource and therefore qualify to be FBFs based on Furuichi's *et al.*, (2001) definition.

6.5 Conclusion and Recommendations

6.5.1 Conclusion

Indeed FBFs played a critical role in the diet of mangabeys because they were available for most of the study period and composed three quarters of priority fruit trees. However, owing to their low nutritive quality and inadequality quantity, they probably could not sustain the dietary requirements of mangabeys. It was therefore speculated that mangabeys must have foraged alternative food resources to sustain themselves during periods of fruit scarcity. For example, in Lwamunda mangabeys raided crops within the vicinity of the forest while in regenerating Mabira (M2) they consumed domesticated fruits left-behind after implementation of a restrictive policy on encroachment. Since these alternative sources of food sustained mangabeys and played a critical role in their diet in both study sites during periods of fruit scarcity, they may be considered as fallback food items. Since reliance on FBFs by primates is associated with low food availability, their presence in a habitat may define its health status.

6.5.2 Recommendations

Since the domesticated fruits and crops were the mainstay for mangabeys in both forest reserves, efforts should be made to genetically engineer some wild trees with traits high digestibility index, high energy ratios and low secondary compounds. Genetic engineering has been done for some domesticated crops, it therefore possible to do the same for forest trees if the economic returns on primate conservation are high enough. Secondly, future work on nutritional ecology of mangabeys should include commonly utilized non-fruit foods. Thirdly, National Forest Authority (NFA) should develop management strategies to ensure conservation of figs, *C. indicum* and *M. eminii* in the Mabira and Lwamunda forest reserves because of their important role in the Mangabey

diet. By so doing, the IUCN status of mangabeys will improve from threatened to least concern.

6.6 Acknowledgments

The authors wish to extend their gratitude to NUFU for funding for this study. National Council of Science and Technology for granting permission to work in Uganda forest reserves. Other colleagues within the Department of Biological Sciences are thanked for constructive critism of the manuscript.

6.7 References

AOAC (Association of Official Analytical Chemists) (1995). Official methods of analysis'. 16th edition. Chapter 4. *Animal Feed.* AOAC International, Arlington, VI, USA. pp 30.

Ahoua, A.R.C., Kone, M.W., Konan, A.G., TRA Bi, F.H. & Bonfoh, B. (2012). Antioxidant activity of eight plants consumed by great apes in Côte d'Ivoire. *African Journal of Biotechnology,* **11**(54), 11732-11740.

Ajayi, O.B., Oluyege, J.O., Olalemi, O.M. & Ilesanmi, T.M. (2012). Nutritional composition, phytochemical screening and antimicrobial properties of the leaf of *Ficus exasperata* (vahl). *Asian Journal of Biological and Life Science,* **1**(3), 242-246.

Akite, P. (2008). The effects of anthropogenic disturbances on the diversity and composition of the butterfly fauna of sites in the Sango Bay and Iriri areas, Uganda: Implications for conservation. *African Journal of Ecology*, **46**(1), 3–13.

Alpert, P. (1996). Integrated conservation and developmental projects. Examples from Africa. *BioScience*, **46** (11), 845-855.

Baranga, D., Chapman, C. A., & Kasenene, J. M. (2009). The structure and status of forest fragments outside protected areas in central Uganda. *African Journal of Ecology,* **47**(4), 664-669.

Baranga, D. (2004). Forest fragmentation and primate survival status in non-reserved forests of the Kampala area, Uganda. *African Journal of Ecology,* **42**(1), 70-77.

Chapman, C.A., Rothman, J.M. & Lambert, J.E. (2012). Food as a selective force in primates. In Mitani, J.C., Call, J., Kappeler, P.M., Palombit, R.A. and Silk, J.B. (Eds), *The Evolution of Primate Societies,* (pp. 149-168). University of Chicago Press.

Chapman, C.A. & Chapman, L.J. (2000). Determinants of group size in primates: the importance of travel costs. In Boinski, S. and Garber, P.A. (Eds), *On the move: How and why animals travel in groups* (pp. 24-42). University of Chicago press.

Chapman, C.A., Chapman, L.J., Wangham, R., Hunt, K., Gebo, D. & Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica*, **24**(4), 527-531.

Cochran, W. G. (1977). Sampling techniques (3rd ed.). New York: John Wiley & Sons.

Conklin-Brittain, N.L., Knott, C.D. & Wrangham, R.W. (2001). The feeding ecology of apes. In *The apes*: *Challenges for the 21st century* (pp. 167–174). Brookfield Zoo, Chicago, IL. http://www.brookfieldzoo.org/pagegen/inc/ACConklin.pdf

Conklin-Brittain, N.L., Wrangham, R.W. & Hunt, K.D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *International Journal of Primatology*, **19**(6), 971-998.

Constantino, P.J. & Wright, B.W. (2009). The importance of fallback foods in primate ecology and evolution. *American Journal of Physical Anthropology*, **140**(4), 599-602.

Constantino, P.J., Lucas, P.W., Lee, J.J.W. & Lawn, B.R. (2009). The influence of fallback foods on great ape tooth enamel. *American Journal of Physical Anthropology*, **140**(4), 653-660.

Dearing, M.D. & Cork, S. (1999). Role of detoxification of plant secondary compounds on diet breadth in a mammalian herbivore, Trichosurus vulpecula. *Journal of Chemical Ecology*, **25**(6), 1205-1219.

Doran-Sheehy, D.M., Shah, N.F. & Heimbauer, L.A. (2006). Sympatric western gorilla and mangabey diet: re-examination of ape and monkey foraging strategies. In Gottfried, H., Robbins, M.M. and Boesch, C. (Eds), *Feeding Ecology in Apes and Other Primates* (pp. 47-68). Cambridge University Press.

Ehlers Smith, D. A., Husson, S. J., Ehlers Smith, Y. C., & Harrison, M. E. (2013). Feeding ecology of red langurs in Sabangau tropical peat-swamp forest, Indonesian Borneo: extreme granivory in a non-masting forest. *American journal of primatology*, **75**(8), 848-859.

Felton, A.M., Felton, A., Foley, W.J. & Lindenmayer, D.B. (2010). The role of timber tree species in the nutritional ecology of spider monkeys in a certified logging concession, Bolivia. *Forest Ecology and Management*, **259**(8), 1642-1649.

Felton, A.M., Felton, A., Wood, J.T. & Lindenmayer, D.B. (2008). Diet and feeding ecology of *Ateles chamek* in a Bolivian semihumid forest: the importance of *Ficus* as a staple food resource. *International Journal of Primatology*, **29**(2), 379-403.

Fungo, B., Eilu, G., Tweheyo, M. & Baranga, D. (2013). Forest disturbance and cropping mixtures influence crop raiding by red-tailed monkey and grey-cheeked mangabey around Mabira Forest Reserve, Uganda. *Journal of Ecology and the Natural Environment*, **5**(2), 14-23.

Freeland, W. J. (1979). Primate social groups as biological islands. *Ecology*, **60**(4), 719-728.

Furuichi, T., Hashimoto, C. & Tashiro, Y. (2001). Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: examination of fallback foods. *International Journal of Primatology*, **22**(6), 929-945.

Gargiullo, M. B., & Stiles, E. W. (1993). Development of secondary metabolites in the fruit pulp of Ilex opaca and Ilex verticillata. *Bulletin of the Torrey Botanical Club*, 423-430.

Gautier-Hion, A. & Michaloud, G. (1989). Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology*, **70** (6), 1826-1833.

Hamilton, C.A. (1984). *Deforestation in Uganda*. Oxford University Press, Nairobi.

Hockings, K.J., Anderson, J.R. & Matsuzawa, T. (2009). Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced environment. *American Journal of Primatology*, **71**(8), 636–646.

Hohmann, G. (2009). The diets of non-human primates: frugivory, food processing, and food sharing. In Hublin, J-J. and Richards, M.P. (Eds) *The Evolution of Hominin Diets* (pp. 1-14). Springer, Netherlands.

Howard, P. C., Butler, J., & Howard, P. (1991). Nature conservation in Uganda's tropical forest reserves. IUCN, Gland, Switzerland and Cambridge, UK with the financial support of WWF-International.

Inogwabini, B.I. & Matungila, B. (2009). Bonobo food items, food availability and bonobo distribution in the Lake Tumba Swampy forests, Democratic Republic of Congo. *The Open Conservation Biology Journal*, **3**(1), 14-23.

Jagtap, U.B., Panaskar, S.N. & Bapat, V.A. (2010). Evaluation of antioxidant capacity and phenol content in jackfruit (*Artocarpus heterophyllus* Lam.) fruit pulp. *Plant foods for human nutrition*, **65**(2), 99-104.

Janson, C. H., & Chapman, C. A. (1999). 14• Resources and primate community structure. In Primate Communities. Eds J. G. Fleagle, Charles Janson, Kaye Reed. Pg 237. Cambridge University Press

Kagoro-Rugunda, G. & Baranga, J. (2009). The fruit phenology of Musanga leo-errerae and its importance for chimpanzee diet in Kalinzu Forest Uganda. *African Journal of Ecology*, **47**(1), 14-19.

Kinzey, W.G. & Norconk, M.A. (1990). Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology*, **81**(1), 5–15.

Kizza, M., Rodhe, A., Xu, C. Y., Ntale, H. K., & Halldin, S. (2009). Temporal rainfall variability in the Mabira and Lwamunda in East Africa during the twentieth century. *Theoretical and applied climatology*, **98**(1-2), 119-135.

Krishnadas, M., Chandrasekhara, K. & Kumar, A. (2011). The response of the frugivorous lion-tailed macaque (*Macaca silenus*) to a period of fruit scarcity. *American Journal of Primatology*, **73**(12), 1250-1260.

Lambert, J.E., Chapman, C.A., Wrangham, R.W. & Conklin-Brittain, N.L. (2004), Hardness of cercopithecine foods: Implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology*, **125**(4), 363–368.

Lucas, P.W., Constantino, P.J., Chalk, J., Ziscovici, C., Wright, B.W., Fragaszy, D.M., Hill, D.A., Lee, J.J.-W., Chai, H., Darvell, B.W., Lee, P.K.D. & Yuen, T.D.B. (2009). Indentation as a technique to assess the mechanical properties of fallback foods. *American Journal of Physical Anthropology*, **140**(4), 643-652.

MAFF (1995). Manual of nutrition. Published for the Ministry of Agriculture, Fisheries and Food by Her Majesty's Stationery Office. ISBN 0 11 242991 2

Marshall, A.J., Boyko, C.M., Feilen, K.L., Boyko, R.H. & Leighton, M. (2009). Defining fallback foods and assessing their importance in primate ecology and evolution. *American Journal of Physical Anthropology*, **140**(4), 603-614.

Marshall, A.J. & Wrangham, R.W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*, **28**(6), 1219-1235.

Matsumoto-Oda, A. & Hayashi, Y. (1999). Nutritional aspects of fruit choice by chimpanzees. *Folia Primatology*, **70**(3), 154-162.

Mertens, D. R. (2003). Challenges in measuring insoluble dietary fiber. *Journal of Animal Science*, 81(12), 3233-3249.

Milton, K., Giacalone, J., Wright, S.J. & Stockmayer, G. (2005). Do frugivore population fluctuations reflect fruit production? Evidence from Panama. In Dew, L.J. and Bouli, J.P. (Eds), *Tropical Fruits and Frugivores* (pp. 5-35). Springer Netherlands.

Milton, K. (1984). The role of food-processing factors in primate food choice. In Rodman, P. and Cant, J. (Eds), *Adaptations for foraging in nonhuman primates* (pp. 249-279). Columbia University Press, New York.

Milton, K., (1981). Food choice and digestive strategies of two sympatric primate species. *The American Naturalist*, **117**(4), 496-505

Milton, K., Windsor, D.M., Morrison, D.W. & Estribi, M.A. (1982). Fruiting phenologies of two Neotropical Ficus species. *Ecology*, **63**(3), 752-763.

Milton, K. (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *American Naturalist*, 362-378.

Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R. (1998). Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, **35**(4), 596-606.

Nelson, S.L., Miller, M.A., Heske, E.J. & Fahey Jr. G.C. (2000). Nutritional quality of leaves and unripe fruit consumed as famine foods by the flying foxes of Samoa. *Pacific Science*, **54**(4), 301-311.

O'Driscoll, W.C. & Chapman, C.A. (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *Journal of tropical ecology*, **21**(06), 689-697.

Oftedal, O.T., Whiten A., Southgate, D.A.T. & Van Soest, P. (1991). The Nutritional Consequences of Foraging in Primates: The Relationship of Nutrient Intakes to Nutrient Requirements [and Discussion. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **334**(1270), 161-170.

Olupot, W. (2000). Mass differences among male mangabey monkeys inhabiting logged and unlogged forest compartments. *Conservation Biology*, **14**(3), 833-843.

Olupot, W. (1999). *Mangabey dispersal and conservation in Kibale National Park, Uganda.* PhD Thesis. Purdue University.

Ogango, A. (2006). *Crop Raiding by Mangabeys in Lwamunda forest reserve, Uganda*. A Research Project Submitted to the Zoology Department in Partial Fulfilment of the Requirements for a Degree in Bachelor of Science, Makerere University.

Osman, M.A. (2004). Chemical and nutrient analysis of baobab (Adansonia digitata) fruit and seed protein solubility. *Plant foods for human nutrition*, **59**(1), 29-33.

Plumptre, A., Dranzoa, C. & Owiunji, I. (2001). Bird communities in logged and unlogged African forests. Lessons from Uganda and Beyond. In Fimbel, R.A., Grajal, A. and Robinson, J.G. (Eds), *The Cutting Edge: Conserving Wildlife in Logged Tropical Forests.* Columbia University Press.

Porter, L.M., Garber, P.A. & Nacimento, E. (2009). Exudates as a fallback food for Callimico goeldii. *American Journal of Primatology*, **71**(2), 120-129.

Poulsen, J.R., Clark, C.J. & Smith, T.B. (2001). Seasonal variation in the feeding ecology of the Grey-cheeked Mangabey (*Lophocebus albigena*) in Cameroon. *American Journal of Primatology*, **54**(2), 91-105.

Price, M. L., Van Scoyoc, S., & Butler, L. G. (1978). A critical evaluation of the vanillin reaction as an assay for tannin in sorghum grain. *Journal of Agricultural and Food Chemistry*, **26**(5), 1214-1218.

Rode, K.D., Chapman, C.A., McDowell, L.R. & Stickler, C. (2006). Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*). *Biotropica*, **38**(5), 625–634.

Saito, C. (1996). Dominance and feeding success in female Japanese macaques: effects of food patch size and inter-patch distance. *Animal Behaviour*, **51**(5), 967-980.

Seidel, R., Thielen, M., Schmitt, C., Bührig-Polaczek, A., Fleck, C. & Speck, T. (2010). Fruit walls and nut shells as an inspiration for the design of bio-inspired impact resistant hierarchically structured materials. In Brebbia, C.A. and Carpi, A. (Eds) *Design and Nature V* (pp. 421-430). WIT Press, Southampton.

Schaefer, H.M., Schmidt, V., & Winkler, H. (2003). Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos,* **102**(2), 318–328.

Tweheyo, M., & Lye, K. A. (2005). Patterns of frugivory of the Budongo Forest chimpanzees, *Uganda. African Journal of Ecology*, **43**(4), 282-290.

Urquiza-Haas, T., Serio-Silva, J.C. & Hernández-Salazar, L.T. (2008), Traditional nutritional analyses of figs overestimates intake of most nutrient fractions: a study of *Ficus perforata* consumed by howler monkeys (*Alouatta palliata mexicana*). *American Journal of Primatology,* **70**(5), 432-438.

Van Schaik, C.P., Terborgh, J.W. & Wright, S.J. (1993). The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, **24**(1993), 353-377.

Van Soest, P.J. (1994). *Nutritional ecology of the ruminant*, 2nd Edition. Cornell University Press, Ithaca, New York.

Van Soest, P.V., Robertson, J.B. & Lewis, B.A. (1991). Methods for dietary fiber, neutral detergent fiber, and non-starch polysaccharides in relation to animal nutrition. *Journal of dairy science*, **74**(10), 3583-3597.

Vogel, E.R., Haag, L., Mitra-Setia, T., van Schaik, C.P. & Dominy, N.J. (2009). Foraging and ranging behaviour during a fallback episode: *Hylobates albibarbis* and *Pongo*

pygmaeus wurmbii compared. *American Journal of Physical Anthropology*, **140**(4), 716-726.

Waser, P.M. (1975). Monthly variations in feeding and activity patterns of the Mangabey, *Cercocebus albigena* (Lydekker). *East African Wildlife Journal,* **13**(3-4), 249-263.

Watts, D. P., Potts, K. B., Lwanga, J. S., & Mitani, J. C. (2012). Diet of chimpanzees (Pan troglodytes schweinfurthii) at Ngogo, Kibale National Park, Uganda, 2. Temporal variation and fallback foods. *American Journal of Primatology*, **74**(2), 130-144.

Wendeln, M.C., Runkle, J.R. & Kalko, E.K.V. (2000). Nutritional Values of 14 Fig Species and Bat Feeding Preferences in Panama. *Biotropica*, **32**(3), 489–501.

Worman, C.O. and Chapman, C.A. (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *Journal of Tropical Ecology* **21**(6), 689-697.

Wrangham, R.W., Conklin-Brittain, N.L., & Hunt, K.D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. 1. Antifeedants. *International Journal of Primatology*, **19**(6), 949-970.

Wrangham, R.W., Chapman, C.A., Clark-Arcadi, A.P. & Isabirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In McGrew, W.C., Marchant, L.F. and Nishida, T. (Eds). *Great ape societies* (pp. 45-57). Cambridge University Press, Cambridge, United Kingdom.

Wrangham, R.W., Conklin, N.L., Etot, G., Obua, J., Hunt, K.D., Hauser, M.D. & Clark, A.P. (1993). The value of figs to chimpanzees. *International Journal of Primatology*, **14**(2), 243-256.

CHAPTER SEVEN

7 Levels of tannins in fruit diet of Grey-cheeked mangabeys (*Lophocebus ugandae*, Groves) in Mabira and Lwamunda forest reserves.

*M. Masette, G. Isabirye-Basuta, D. Baranga, M. Chemurot

Department of Biological Sciences, Makerere University, P.O. Box 7062, Kampala, Uganda

* Corresponding author

Published in peer reviewed Journal and cited as:

Masette, M., Isabirye-Basuta, G., Baranga, D., & Chemurot, M. (2015). Levels of tannins in fruit diet of grey-cheeked mangabeys (*Lophocebus ugandae*, Groves) in Mabira and Lwamunda forest reserves. *Journal of Ecology and the Natural Environment* Vol. 7(5), pp. 146-157

Abstract

Tannins are known to have anti-digestive properties among primates and undoubtedly influence food selection among Grey-cheeked mangabeys (*Lophocebus ugandae*) inhabiting Mabira and Lwamunda forest reserves. During the 24 month study, we observed the feeding behaviour of three groups of mangabeys inhabiting forests at different levels of degradation. Results indicated that mangabeys selected fruit parts based on tannin levels. Fruit parts with tannin levels exceeding 2.6g/100 catechin equivalent were invariably rejected. These were unripe fruit pulp and mature seed. Accepted parts included endosperms of immature fruit and ripe pulp belonging to 12 priority tree species. This selection criterion applied to all types of fruit regardless of forest habitat. The level of fruit parts rejection due to high levels of tannins was more frequent in the severely degraded Lwamunda forest reserve than in Mabira. Consumption of endosperms of unripe fruit appears to be an adaptation to fruit scarcity.

Key words: Tannins, food scarcity, fruit processing and Mabira and Lwamunda forests.

7.1 Introduction

Grey-cheeked mangabeys inhabiting Mabira and Lwamunda forest reserves are faced with spatio-temporal food scarcity due to anthropogenic activities which have resulted in a reduction of potential food tree density. To meet their daily dietary requirements, mangabeys in these forests are compelled to consume food items known to have high levels of secondary compounds and specifically tannins. These are water-soluble and complex polyphenolic secondary metabolites with anti-nutritional properties (Kraus *et al.*, 2003). Plants manufacture them for protection against herbivory (Kraus *et al.*, 2003; Coley, 1986) and potential frugivores (Reynolds, 2005). Tannins are sometimes called antifeedants because they have anti-digestive properties. Some tannins (condensed or hydrolysable) react with proline-rich proteins secreted in saliva to form a complex that is usually insoluble and unabsorbable (Lua and Bennick, 1998) or more difficult for animals to digest (Norconk and Veres, 2011; Robbins *et al.*, 1987); hence protein digestibility is highly compromised. Too much tannin in the gut, leaves an animal unable to digest its food properly and in the case of some species it can be fatal (Wrangham *et al.*, 1998) or destructive (Erikasson and Ehrlén, 1998).

Cercopithecines have developed effective internal mechanisms for detoxification of secondary compounds (Reynolds, 2005) although it may be too expensive and sometimes as costly as reproduction process (Sorensen *et al.*, 2005). External mitigation measures include; biotransformation, avoidance and regulation (Sorensen and Dearing, 2003; Sorensen *et al.*, 2004). Biotransformation entails elimination of plant secondary metabolites (PSMs) from the body by excretion in form of urine or chemical change or a combination of the two processes (Schwedhelm *et al.*, 2003; Wiggins *et al.*, 2003). In nature, PSMs appear to play a major role either in restricting the palatability of the plants in which they occur or in causing animals to avoid the plants altogether. Frugivorous primates avoid consumption of some toxic fruits (Herrera, 1982). The consumption of unripe fruits is a regulated trade-off mechanism (Schaefer *et al.*, 2003) although it exposes mangabeys to PSMs with a wide range of physiological effects ranging from direct toxicity to digestion impairment (Dearing *et al.*, 2005). The regulation of PSM intake ensures that low potency toxins do not cause damage to the primate.

One of the strategies used by primates to regulate PSM intake is the development of salivary proline-rich proteins (PRPs) as a defence against tannins. This is done by forming complexes with them and thereby preventing their interaction with other biological compounds and absorption from the intestinal canal. The consequences of binding tannins with PRPs are twofold. Tannins are inactivated as toxins, enabling the animal to eat tannin-rich browse and the absorption of PSMs by gut cells is regulated by the permeability of glycoprotein and cytochrome P4503A (Sorensen and Dearing 2003, Sorensen *et al.*, 2004). Another mechanism used by mangabeys to regulate PSMs intake is by trade-offs between macro- nutrients and PSMs (Schaefer *et al.*, 2003). Pre-ingestive mechanisms where taste and trigeminal stimulation are applied can also be used to regulate intake of PSMs. Foods can be repellent to animals by irritating trigeminal nerves in the mouth and causing a burning sensation. If it is too intense, food consumption is reduced. Animals use trigeminal feedback to regulate their intake of these irritant PSMs. For example, Jakubas *et al.* (1993) showed that coniferyl benzoate (CB) was a trigeminal irritant in birds and that ruffed grouse could regulate their intake of CB in aspen. Compounds that are intensely bitter like phenolic glycoside may also be effective deterrents at high concentrations. They can also lead to thresholds in the ingestion of the PSM which constrain feeding rates of mammalian herbivores (Dearing *et al.*, 2005). These PSMs can be eliminated from the body by biotransformation of lipophilic PSMs (Boyle *et al.*, 1999) prior to excretion through urine. Terrestrial animals have evolved a powerful suite of biotransformation enzymes to convert lipophilic PSMs into more polar metabolites readily excreted in urine or bile. These enzymes are considered to have evolved in part as a response to dietary plant toxins (Gonzalez and Gelboin, 1994; Gonzalez and Nebert, 1990).

Unripe fruits are usually well protected chemically with secondary metabolites similar to those found in leaves. Most unripe fruit have mechanical protection as they are hard to crack and may contain sclerified cells or calcium oxalate crystals which are known to irritate humans and other mammals (Gargiullo and Stiles, 1993). The concentrations of some secondary compounds may change during fruit ripening (Barnea *et al.*, 1993) but while they last, they may limit the quantity of fruits consumed and length of a single

foraging bout thereby prompting frugivores to forage elsewhere. As the chemically and mechanically well defended fruits ripen, the chemical defence reduces. However, the qualitative nature of phenolics does not change in a ripe fruit to compensate for the over-all quantitative loss (Gargiullo and Stiles, 1993). According to Mack (2000), tannins are also found in ripe fruits of broad and diverse array of plants. Generally, most food resources with high PSMs are not only toxic but they are also poor in quality and low in nutrients (Coley, 1986). Consequently, some frugivores may switch foraging patches because of the defensive role of secondary compounds. This natural selection has favoured animals that avoid tannin-rich foods (Reynolds, 2005). During times of scarcity mangabeys seem to either develop tolerance to higher levels of tannins (Chapman *et al.*, 2012; Doran-Sheehy *et al.*, 2006; Wrangham *et al.*, 1998) or engage in crop-raiding (Ogango, 2006). Raided food crops are selected on account of high digestibility, high energy content and low concentration in secondary compounds (Rode *et al.*, 2006).

We hypothesized that plant secondary compounds exemplified by tannins, determine fruit parts consumed by mangabeys in Mabira and Lwamunda forest reserves. We tested this hypothesis by analysing the tannin levels of fruit parts eaten by 3 social groups of magabeys inhabiting 3 forests with varying levels of degradation.

7.2 Materials and Methods

7.3 Study area

We studied grey-checked mangabeys in Mabira Forest Reserve with an area of 306 km^2, between 0° 24`and 0° 35`North latitudes and 32° 52` and 33° 07`East longitudes. On the other hand, Lwamunda Forest Reserve was located between 0° 15′ and 0° 23′ North latitudes and 32° 30′ and 32° 43′ East longitudes with an estimated are of 67 km^2. The study was conducted from June 2005 to March 2007. Researchers have conducted studies in Lwamunda forest since 1965 (Gombya-Ssembajjwe, 1999; Baldwin *et al.*, 1976; Chalmers, 1968; Spuhler and Jorde, 1975; Waser, 1975), so the animals were fairly habituated. Both forests being within the Mabira and Lwamunda, they have bimodal rainfall patterns with 1200-1500 mm per year and typically distributed between two distinct rainy seasons: April-May and October-November (Kizza, *et al.*, 2009). Mabira is located on undulating hills and valleys at an elevation range of 1070–1340 m above sea level while Lwamunda is a riverine forest reserve situated at 1200 m of altitude and

surrounded by isolated flat-topped hills with steep slopes (Howard *et al.*, 1991). Mabira consists of fairly undisturbed (M1) and regenerating (M2) portions but in the same location.

The influence of tannins on fruit parts consumed by mangabeys was investigated by examining a total of 2076 samples comprising of 786 whole fruit, 888 pulp, 261 endosperm and 141 seed at different stages of development. The samples were collected from the top 10 priority fruit tree species consumed by mangabeys. Three (3) groups of habituated mangabeys one in Lwamunda and two in Mabira were systematically observed for 5 consecutive days at the beginning of each month which constituted 1200h during the 24 month study period. However, the number of hours varied on daily basis depending on our ability to follow them. A systematic 5 minute-scan sampling was conducted (Flashing, 2001; Waser, 1975) to collect data on fruit species and development stage of fruit being eaten by mangabeys. When regular systematic sampling was obstructed by mid-storey tree canopies especially in Mabira forest reserves, systematic sampling was supplemented with ad libitum observations. The parts of fruit/seed and the remains consumed by mangabeys were noted. Fruit remains under trees where mangabeys had been feeding were also carefully examined for identification of the exact parts the mangabeys were feeding on and mechanisms of fruit processing prior to consumption. Ten individual trees comprising of top 10 priority fruit tree species and utilized by mangabeys as food in each study area were identified (Table 8.1) marked and their location noted by GPS.

Table 7.1 The top 10 priority fruit tree species utilized by mangabeys in Mabira and Lwamunda forest reserves

SN	Mabira	Lwamunda
1	*Ficus mucuso*	*Blighia unijugata*
2	*Measopsis eminii*	*Ficus mucuso*
3	*Celtis durandii*	*Maesopsis eminii*
4	*Celtis africana*	*Myrianthus arboreus*
5	*Celtis mildbraedii*	*Antiaris toxicaria*
6	*Canarium indicum*	*Ficus sur*
7	*Antiaris toxicaria*	*Canarium indicum*
8	*Albizia grandibracteata*	*Ficus exasperata*
9	*Ficus exasperate*	*Pseudospondias microcapa*
10	*Pseudospondias microcapa*	*Treculia africana*

The availability of fruit on the marked fruit trees was recorded on a monthly basis using a visual abundance score (VAS: 0-4), where 0 denoted total absence of fruit, 1 denoted 1-25% of fruit cover, 2 denoted 26-50% 3 denoted 51-75% and 4 represented above 76% fruit availability (Chapman *et al.*, 1992). The level of food availability was calculated from the

percentage of marked trees with edible ripe fruits within the range of each group. The age of fruit maturity and level of ripeness (Saini *et al.*, 2009) were determined by first establishing the time when the tree fruited and subtracted from the time of the visit during phenological data collection. However, the stages of fruit ripeness were recorded on a weekly basis. Furthermore, the weight and size of the fruit were measured to verify the age of the fruit. The actual fruit ripening was visually assessed by colour changes. Immature green fruits were designated stages I-III of development with age variation of ≤ 12 weeks, yellowish colours were normally stages III-V with age variation of ≤ 36 weeks and red or maroon represented stages V-VII with age >36 weeks of development.

7.3.1 Analysis of tannins

According to Conklin-Brittain *et al.* (1998), tannins are one of the major classes of secondary compounds or antefeedants that occur in higher concentrations in the diets of cercopithecines. Other researchers (Rode *et al.*, 2006; Krief *et al.*, 2005; Chapman and Chapman, 2002; Cipollini and Levey, 1997; Herrera, 1982) have used a whole spectrum of secondary compounds to study nutritional quality of non-human diets but owing to lack of critical laboratory equipment it was not possible to determine a whole spectrum of secondary compounds in this study. Instead, only condensed tannins using vanillin assay (Broadhurst and Jones, 1978) was used to determine their levels. Essentially, 7 test tubes with varying concentrations of catechin standard were prepared as follows: (0; 0.05; 0.10; 0.15; 0.20; 0.25 and 0.30 mg/ml (in 100% methanol). 1ml of each replicate of sample extract was added to test tubes, in duplicate, whilst in a water bath at 30°C. 5ml of freshly prepared vanillin reagent (1:1 ratio of 1% vanillin/methanol and 8% Conc. HCl / methanol) was added at 1 minute intervals. The mixture was left in the water bath at 30°C for 20 minutes. The absorbance was read at 500nm against a blank. The blank is equivalent to 1ml vanillin reagent 5ml of 4% Conc. HCl/ methanol was added at 1 minute intervals and then kept at 30°C for 20 min. Small differences in the original weight were corrected by multiplying absorbance by 200/ (sample weight in milligrams). Tannin levels were used as basis for establishing one of the contributory factors influencing fruit choice or rejection of certain parts of some 10 priority fruits. The assumption was that mangabeys in both forest reserves avoided or traded-off fruit parts of the priority fruits with tannin levels above acceptable threshold.

7.3.2 Data analysis

Due to different micro-environments obtaining in different forests or study sites and different stages of fruit development and fruit parts consumed or rejected, it was deemed necessary to compare level of tannins in the same fruit type occurring in all the three sites. Combined effects of forest type, tree species, fruit part and ripening stage on the level of tannin in fruits were explored using mixed model factorial ANOVA. Forest type had three groups, tree species were 12, trees with edible fruit parts were five, while ripening stages were nine. In case of significant interactions, data were split and independent main effects of each parameter explored using one-way analysis of variance while adjusting for the unique effect of other independent variables.

7.4 Results

There were statistically significant main effects of forest type ($F(2,9.94) = 7.099$, $P<0.001$)), tree species ($F(11, 53.514) = 38.207$, $P<0.001$), edible fruit part ($F(4,277.074)=197.818$, $P<0.001$) and ripening stage ($F(8,61.325)=43.783$, $P<0.001$). The respective Eta squared for forest type, tree species, fruit part and ripening stage were 0.007, 0.182, 0.295 and 0.139; indicating that the order of importance of the independent variables in explaining fruit tannin levels is fruit part, followed by tree species and ripening stage. Forest type which explained fruit tannin levels to only 0.7% was dropped from further analysis. The results also showed significant two and three level interactions of tree species, edible fruit part and ripening stage ($P <0.001$). After adjusting for the effect of edible fruit part and ripening stage, the concentration of tannin in fruit species was significantly different (mean ±sd, $P<0.001$) and in the following order *C. mildbraedii* (1.17±0.81)< *M. arboreus* (1.42±1.71)< *B. unijugata* (1.95±1.25)< *R. edulis* (2.30±1.43)< *F. mucuso* (2.94±1.49)< *C. africana* (3.06±1.53)< *F. sur* (3.25±1.50)< *C. durandii* (3.46±2.17)< *F. exasperata* (4.05 ±2.02)< *M. eminii* (4.05±1.26)< *P. microcapa* (4.11 ±2.11)< *C. indicum* (4.89±2.45). Generally, fall back fruits had significantly higher tannin concentration (3.78±2.93) than seasonal or preferred fruits (2.86±2.73), $P<0.001$. Adjusting for both fruit species and ripening stage, the concentration of tannin in the different edible parts of the fruits was significantly different (mean ± sd, $P<0.001$) and in the order: Pulp (4.63±3.59)> Whole (3.47±1.75)> Seed (2.49±1.31)> Endosperm (1.31±0.52)> Aril (0.57±0.06). As expected, tannin level significantly decreased

(mean ± sd, P<0.001) with increasing ripening, after adjusting for the unique effects of fruit species and edible fruit part regardless of fruit type (Table 7.2).

Table 7.2 Decline of tannins in fruit pulp from immaturity to maturity and final ripening stage (*The letterings* (a, b, c, d & e) *indicates relationship between maturity and level of tannins at 5%* whereby similar letterings indicate insignificance and dissimilar letterings indicate significant difference between maturity and tannin levels).

Maturity stage (weeks)	Tannin g/100g	Minimum	Maximum
2-4	4.97 ± 4.17^{a}	0.003	15.24
8-12	4.34 ± 3.06^{ab}	0.22	17.70
10-18	3.64 ± 1.82^{b}	0.22	10.34
15-24	2.45 ± 1.37^{c}	0.10	9.56
20-28	$1.81.15^{cd}$	0.05	5.33
21-28	1.26 ± 0.77^{de}	0.52	3.67
24-32	0.94 ± 0.32^{e}	0.38	1.61
>32	2.05 ± 0.41^{c}	1.64	2.58
P-value	<0.001	-	-

It was observed that mangabeys utilized specific fruit parts at certain stages of development. The fruit development stage at which mangabeys consumed the priority fruit part varied with the type of fruit (Table 7.3). In most cases, fruit maturity corresponded with level of fruit ripeness.

Table 7.3 Fruit parts frequently consumed by mangabeys and development stages for priority trees utilized as food by mangabeys

	Time duration after tree fruiting (weeks)				
Fruit tree type	**Whole**	**Endosperm**	**Pulp**	**Seed**	**Aril**
C. africana				4-28	
C. durandii				4-16	
C. mildbraedii				4-24	
F. exasperata	20-32				
F. mucuso	20-32				
F. sur	20-32				
M. arboreus		4-18	24-28		
M. eminii		3-10	15-20		
C. indicum		3-10	15-20		
P. microcapa		3-10	15-24		
B. unijugata				2-18	24
R. edulis			18-22		

The level of tannin appears to determine the stage at which different parts of the fruit were eaten by mangabeys. It varied from 0.7g/100g in pulp of *M. arboreus* to *C. mildbraedii* pulp that registered 2.6g/100g. The weighted mean for maximum allowable limit for consumption of the priority fruit part was around 2.6g/100 as indicated in Table 7.4.

Table 7.4 Tannin levels and development stage at which mangabeys start eating priority fruit part

Fruit tree type	Priority fruit part eaten	Age at fruit ripening (weeks)	Average tannin levels at stage of consumption (g/100g
C. africana	pulp	28	2.272±0.06
C. durandii	pulp	28	2.355±0.12
C. mildbraedii	pulp	28	2.598±0.03
F. exasperata	whole	32	2.473±0.11
F. mucuso	whole	32	2.466±0.04
F. sur	whole	32	2.566±0.02
M. arboreus	pulp	28	0.692±0.26
M. eminii	pulp	24	2.235±0.14
C. indicum	pulp	24	2.289±0.17
P. microcapa	pulp	24	1.801±1.02
B. unijugata	aril	24	1.237±0.92
R. edulis	pulp	24	2.297±0.19

However, during periods of fruit scarcity, mangabeys consumed different fruit parts which tended to vary with the type of fruit (Table 7.3). Whereas mangabeys consumed young seeds and fairly ripe pulp of *Celtis* species, they consumed whole fruit of *Ficus* species from weeks 20-32 after fruiting, young endosperms and ripe pulp of *C. indicum, M. arboreus*, *M. eminii* and *P. microcapa* and the ripe pulp of *R. edulis*. Mangabeys concentrated on the consumption of *B. unijugata* seed up to 18 weeks after fruiting then switched to aril after fruit ripening. Generally, the level of tannins in whole fruit declined with maturity (Figs 7.1; 7.2; 7.3). The rate of decline in tannin content as indicated by R^2 value varied with fruit type and habitat. In Mabira - M1 (Fig 7.1), M2- Mabira (Fig 7.2) and Lwamunda forest reserves (Fig 7.3), the rate of decline varied from $R^2 = 0.7835$ for *M. eminii* to $R^2 = 1$ for *C. indicum*. Consumption of whole fruit was limited to fig species and yellow fruits (*R. edulis*). The level of tannins in figs varied from 4.7g/100g in the three months old whole fruit to 0.5g/100g at week 28 which was the preferred stage for

consumption. *R. edulis* was ingested whole, the fruit skin spat out and the seed passed out in faeces. Consumption of whole ripe *M. eminii* and *C. indicum* fruit was observed more often in Lwamunda than in Mabira and the mode of consumption was similar to when feed on *R. edulis*.

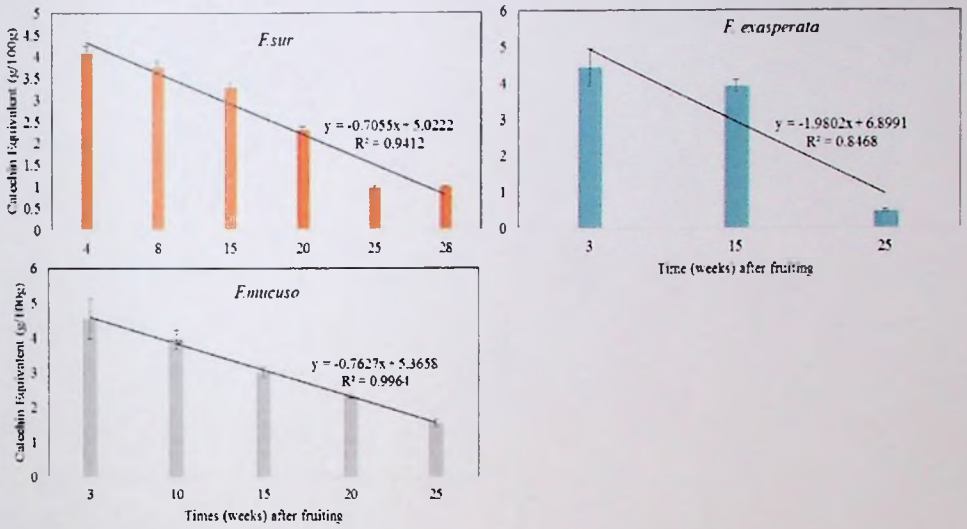


Figure 7.1 Tannin variations in whole fruit at different stages of development for priority fruit trees commonly utilized as food in the fairly undisturbed portion of Mabira forest reserve (M1).

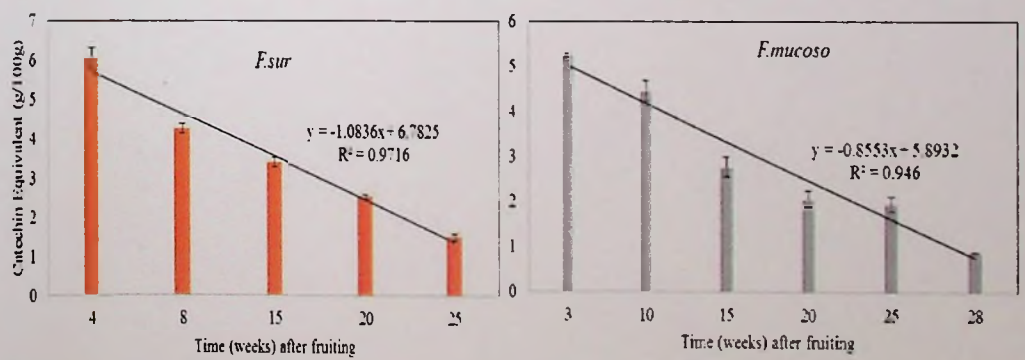


Figure 7.2 Tannin variation in whole fruit at different development stages of priority fruit trees commonly utilized as food in the regenerating portion of Mabira forest reserve (M2).

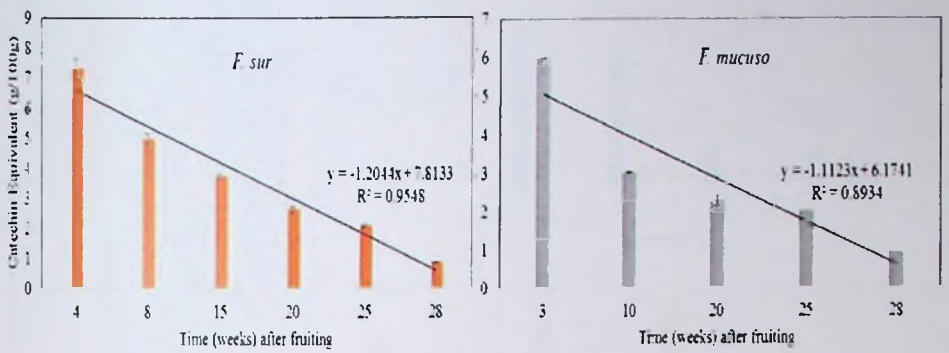


Figure 7.3 Tannin variation in whole fruit at different development stages of priority fruit trees commonly utilized as food in the severely degraded Lwamunda forest reserve.

According to our field observations, pulp was the most consumed fruit part regardless of the fruit type as depicted by the number of fruits whose pulp was regularly picked out as food. Generally, tannin content decreased with pulp maturity and rate of decline (R^2) varied with type of fruit regardless of habitat (Fig.7.4; 7.5; 7.6). Mangabeys started consuming pulps from most fruits from 10 weeks when the tannin content was around 2.6g/100g up to weeks 28 or 32 when tannin levels were less than 1g/100g.

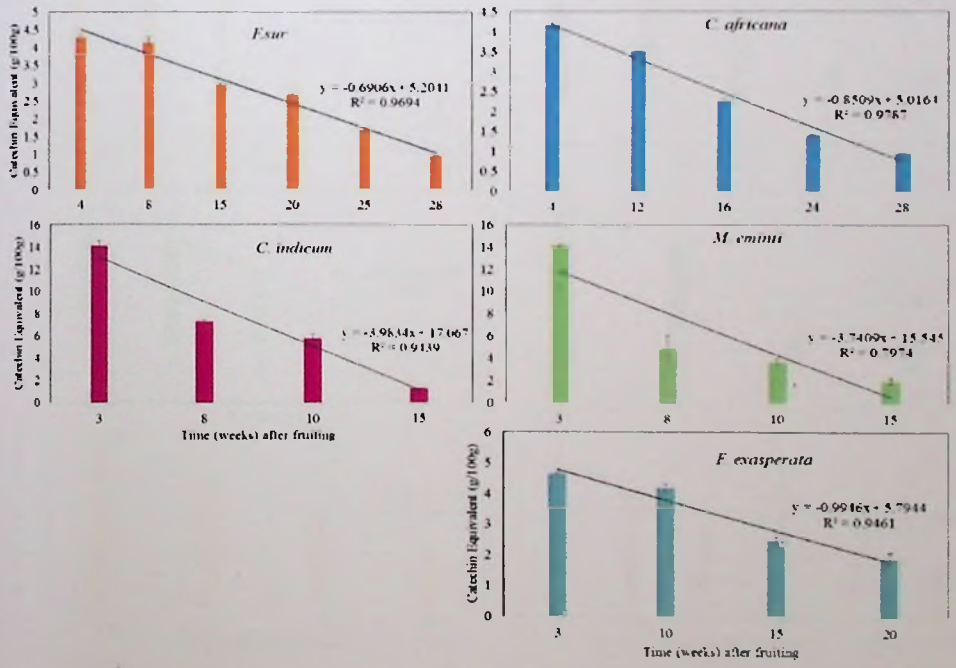


Figure 7.4 Tannin variations in fruit pulp at different stages of development for priority fruit trees commonly utilized as food in the fairly undisturbed portion of Mabira forest reserve.

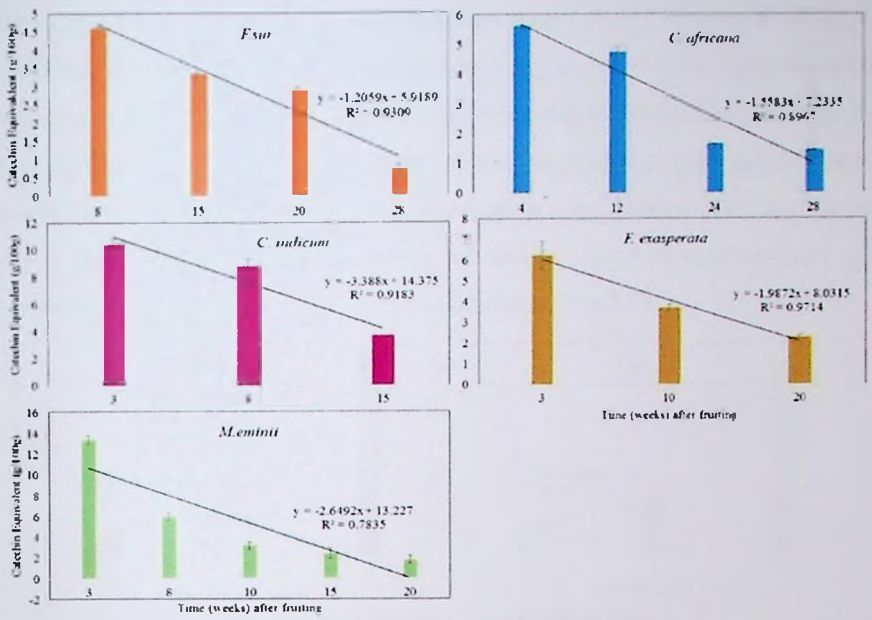


Figure 7.5 Tannin variations in fruit pulp at different development stages of priority fruit trees commonly utilized as food in the regenerating portion of Mabira forest reserve.

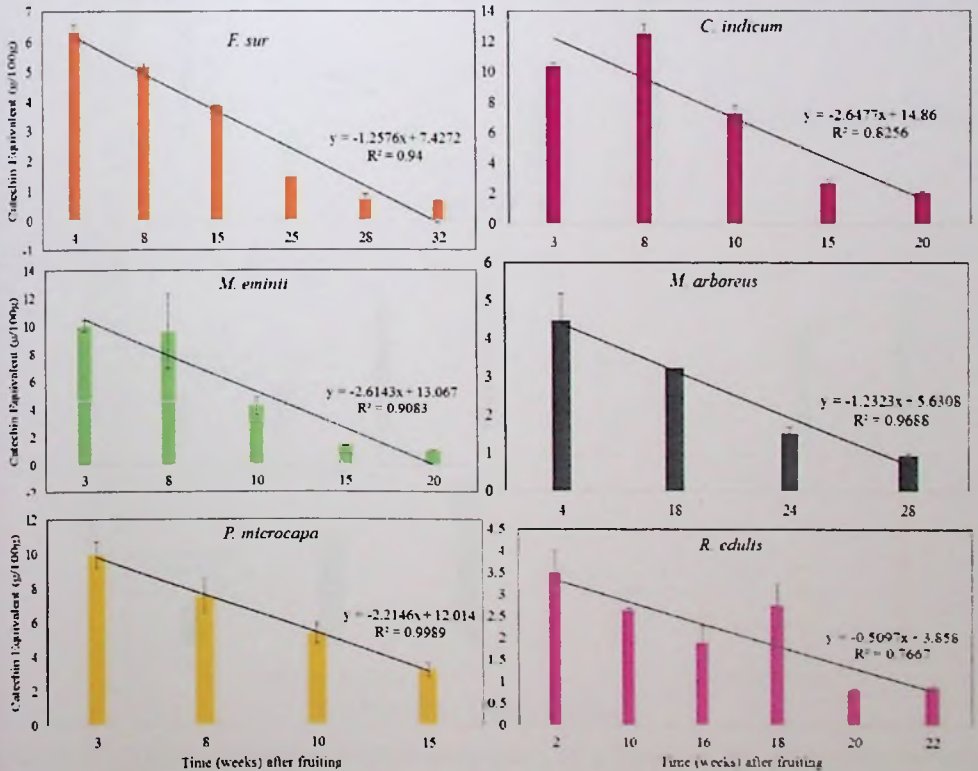
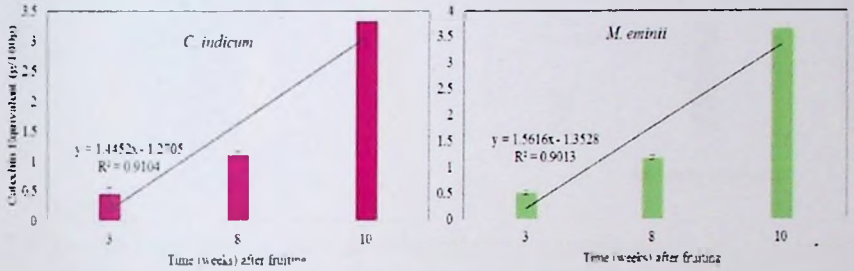
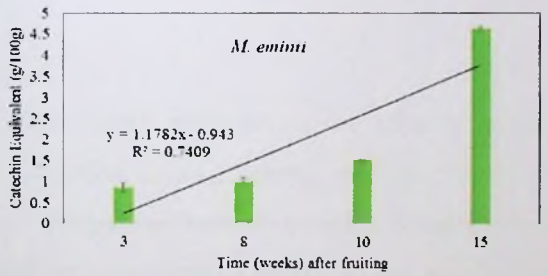


Figure 7.6 Tannin variations in fruit pulp at different development stages of priority fruit trees commonly utilized as food in the severely degraded Lwamunda forest reserve.

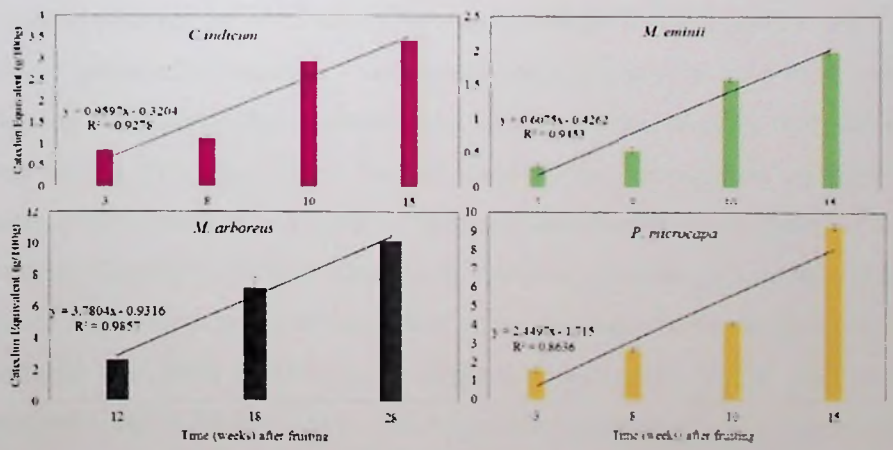
Mangabeys started consuming endosperms between weeks 3 and 10 after fruiting as observed in Table 7.3. When the tannin content exceeded 2.6g/100g and the pericarp hardened, they reverted to consumption of pulp whose tannin levels were declining to lower than 1g/100g. This was from week 20 to 32 depending on type of fruit. In severely degraded Lwamunda forest reserve where fruit resources were perpetually at low ebb, endosperm consumption was more prevalent than in both types of Mabira forest reserves. The level of tannins in endosperms seemed to increase with the fruit development regardless of fruit type and habitat (Fig 7.7).



A= Fruit trees from Mabira (M1)



B= Fruit tree from Mabira (M2)



C= Fruit trees from Lwamunda

Figure 7.7 Tannin variations in fruit endosperm at different stages of development for priority fruit trees (A, B, C) commonly utilized as food in the fairly undisturbed Mabira (M1), regenerating Mabira (M2) and Lwamunda forest reserves.

As expected, since the level of tannins increased in the endosperms with maturity, it would inevitably increase in the seeds (Fig. 7.8) regardless of the fruit type. Consumption of the seeds was predominantly observed in Lwamunda forest reserve. This was presumably due to lack of ripe fruit and generally prevailing food scarcity.

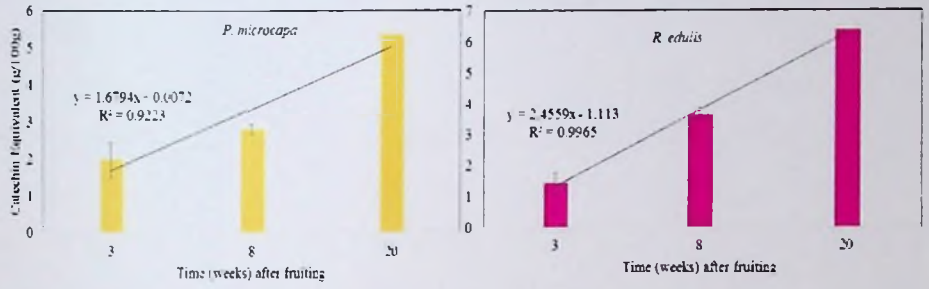


Figure 7.8 Tannin variations in seed at different development stages of a few priority fruit trees commonly utilized as food in the severely degraded Lwamunda forest reserve.

7.5 Discussion

Avoidance of fruit parts with levels of tannins exceeding 2.6g/100g threshold is undoubtedly a selection criteria among mangabeys inhabiting Mabira and Lwamunda forest reserves. Mangabeys tended to select fruit parts for consumption that did not exceed the threshold regardless of the fruit type and habitat. This was in agreement with other studies (Danish *et al.*, 2006; Ganzhorn, 1986; Glander, 1982) who noted that presence of undesirable secondary compounds played a crucial role in the selection of foods among primates. Other authors have observed other factors that influence food selection among primates. These include evolutionary disposition of fruit and taste (Chalmers, 1968), energetics (Chivers, 1986) and food availability (Olupot *et al.*, 1997). According to Ganzhorn (1986), apart from the concentration of tannins and alkaloids, selection of a food item was also dependent on availability of other foods and seasonality. We observed that food availability in degraded Lwamunda forest reserve was more compromised than in Mabira (M1) that was fairly undisturbed. It is therefore probable that mangabeys in Lwamunda had developed trade-off mechanisms to cope with habitat changes. The trade-off could entail consumption of food items with high levels of tannins but with high protein or lipids as a mitigation strategy to meet their daily dietary

requirements. However, considering that tannins are essentially anti-feedants, regular consumption of fruit parts with high levels of tannins may be a nutritional let-down. As such, primates consume small amounts of tannin-laden foods by diversifying food resource base (Glander, 1982). Alternatively some non-human primates ingested bouts of clay or limestone to neutralize plant toxins like tannins (Johns and Duquette, 1991; Kreulen, 1985). Klein *et al.*, (2008) reported that chimpanzees (*Pan troglodytes schweinfurthii*) of the Kibale National Park, Uganda, sometimes ingested soil shortly before or after consuming some plant parts such as leaves of *Trichilia rubescens*. This practice of soil ingestion was also reported by Krishnamani and Mahaney (2000) who identified the most plausible reasons why primates engage in geophagy namely; mineral supplementation, adsorption of toxins, treatment of diarrhoea and pH adjustment. Struhsaker *et al.*, (1997) reported that Red colobus monkeys consumed charcoal to effectively exploit the abundant food resource in form of young leaves of Indian almond and mango exotic tree species that were endowed with high digestible protein but laced with high total phenolic content. The benefits of charcoal eating are most likely due to the fact that charcoal adsorbs phenolics better than proteins. Although geophagy was not observed during the present study period, it is probable that mangabeys also engaged in this practice since consumption of unripe fruit was rife in Lwamunda and Mabira (M2) forest reserves. For the Mangabey to nutritionally benefit from the trade-off mechanism, it must balance the energy expended to detoxify the ingested tannins and energy acquired from consumption of protein or lipid. Since energetics or the economics of energy was beyond the scope of the present study, it was not possible to determine the energy balance. However, it appears energy acquired from trade-off mechanism was more than energy required for detoxification because during periods of fruit scarcity, mangabeys inhabiting severely degraded Lwamunda forest reserve were forced to consume unripe fruits to meet their dietary requirements. This food selection criterion based on trade-off mechanism was more evident in Lwamunda than in Mabira (M1) which was indicative of food scarcity.

Mangabeys may have also avoided consumption of fruit parts with unacceptable levels of tannins as a strategy to conserve energy for other physiological activities since

detoxification of foods with high levels of tannins and other secondary compounds is not cost-effective (Nabihamba, 1996). In the absence of preferred ripe fruit pulp with < 1g/100g of tannins, mangabeys would rather spend comparatively less energy to access fruit endosperm with low nutritive quality per unit volume (Wrangham *et al.*, 1998) than consume unripe fruit that would require detoxification. However, not all endosperms of fruits are nutritively poor; Verderane *et al.* (2013) reported that endosperms of palm nuts of catulé and piaçava species were rich in fats (60%) and carbohydrates (30%) and White (2011) noted that endosperms contained unavailable amino acids required by the seedling. Nonetheless, consumption of foods with high levels of condensed tannins compromises the nutritive quality of food resources and affects rates of digestibility and nutrient extraction (Doran-Sheehy *et al.*, 2006).

From a plant's perspective, synthesis of tannin molecules is energetically costly owing to their complex chemical structure (Sagers and Coley, 1995; Coley, 1986) so unless the external protection pressures are too high, plants invest in other less costly ecosystem activities. Since the production of secondary compounds including tannins is a deterrent mechanism employed by the plant to fend off folivorous and frugivorous pests (Howe and Jander, 2008; Bennett and Wallsgrove, 1994) prior to the intended use, complete avoidance of fruit parts with high levels of tannins is not likely to be a realistic strategy by mangabeys in Lwamunda or Mabira (M2) forest reserves especially during periods of food scarcity. As such, primates have devised strategies to overcome the severe impacts of secondary compounds in their diet. They produce salivary proline-rich proteins that bind tannins into complexes thereby ensuring that absorption of vital nutrients from the intestinal canal takes place (Sorensen and Dearing, 2003; Sorensen *et al.*, 2004). Alternatively, they regulate the intake of secondary compounds by a trade-off strategy with macro- nutrients (Schaefer *et al.*, 2003). A vivid example in the present study was the observed regular consumption of seeds in Lwamunda forest reserve despite their relatively high tannin content as they reached maturity. However, at times mangabeys reverted to consumption of fruit pulp instead of seed. Considering that Mangabey molars are quadrate, relatively long and bilophodont (Flannery, 2000), cracking hard fruit or tough pericarps, nuts and seeds (Marshall and Wrangham, 2007), should not hinder the

consumption of endosperm. So the reversion to pulp consumption could actually be attributed to unacceptable levels of tannins.

Indeed, according to other researchers (Chapman *et al.*, 2012; Wrangham *et al.*, 1998) mangabeys have developed tolerance to higher levels of tannins. They advanced that development of tolerance is likened to human children who if they encounter tannins in the diet regularly, their sensitivity wears off and they develop an improved ability to secrete protein-rich mucins from mucosal surfaces of the mouth which go into their saliva and serve to neutralize tannins (Reynolds, 2005)

The foraging pattern was evident during periods of food scarcity or seasonal variability of food resources especially among mangabeys inhabiting the severely degraded Lwamunda forest reserve. Mangabeys were compelled to consume endosperms picked out from unripe fruit through a labourous and time consuming process of biting and spitting the bitter pulp until they gained access to endosperm with low levels (< 0.6/100g) of tannins. Unripe fruit pulp is known to have high levels of tannins (Nathiya and Dorcus, 2012; Doran-Sheehy *et al.*, 2006; Wrangham *et al.*, 1998; Garber, 1987) and mangabeys were observed spitting out raw pulp when processing fruit to access endosperm. A similar behaviour was reported among the Chimpanzees of Budongo forest reserve, Uganda that devised a tannin-avoidance mechanism by rolling fig seeds into oral boli "wadges" and spitting them out because fig seeds contain higher levels of condensed tannins than pulp (Reynolds *et al.*, 1998).

It appears, Mangabey food choice was primarily determined by quantity and availability of food items as opposed to its quality attributes. Indeed, selection of a fruit part for consumption depended on general food availability. When food was abundant, mangabeys concentrated on consumption of ripe fruit with low tannin levels. However, during periods of food scarcity, mangabey diet consisted of unripe fruit and raided crops (Ogango, 2006). Figs were invariably consumed whole while *Canarium*, *Rheedia*, *Pseudospondias*, *Maesopsis* and *Myrianthus* were manipulated to access fruit endosperm. The food selection may also be species-specific (Wieczkowski, 2003). Some primate species like Chimpanzees (*Pan troglodytes*) prefer ripe fruit (Moscovice *et al.*, 2007;

Basabose and Yamagiwa 2002, Conklin-Brittain *et al.*, 1998) while mangabeys concentrate on ripe fruit when it is available but supplemented their omnivorous diet on regular basis. Hence, during periods of food scarcity, they utilize seed, unripe fruit and other forestry products.

We observed that during July to December 2006, there was literally no fruiting tree in Lwamunda forest reserve except a few trees of *F. sur* with 2 months old fruits and yet they were inedible. Since the nutritional quality of some endosperms was low (Wrangham *et al.*, 1998) and food was extremely scarce in Mabira (M2) and Lwamunda forest reserves, it was therefore not possible that those 2-3 trees with immature fruits could sustain a group of 10 mangabeys notwithstanding their competitors. To sustain the dietary requirements of mangabeys and other frugivores, there ought to have been other food resources which these forest fauna relied on for survival. Ogango (2006) observed that during periods of food scarcity in Lwamunda which were more frequent than in other habitats, mangabeys engage in crop-raiding. Fungo *et al.* (2013) also reported the highest crop-raiding in the maize-cassava mixtures in the villages that were close to the more disturbed zones of Central Mabira forest. According to Rode *et al.* (2006), raided food crops are selected based on their high rate digestibility, high energy and low secondary compounds.

7.6 Conclusion

Mangabeys are capable of detecting differences in tannin concentrations in fruit for consumption regardless of type or part or habitat as illustrated by the critical threshold. In incidences when consumption of seed becomes unavoidable, mangabeys seem to consider the quality of macro-nutrients contained therein and employ trade-off mechanism. In other words, because the seed is rich in protein, lipids and carbohydrates, the energy acquired through its consumption is more than the energy used for detoxication of the ingested tannins. Although Mabira and Lwamunda forest reserves are within the Mabira and Lwamunda, the micro-environments are totally different and therefore the influence of tannin levels on selection of fruit parts eaten by mangabeys varies according to food availability and seasonality.

7.7 Recommendations

This study on tannin levels in fruit/fruit parts should be repeated to include frequency of seed, endosperm and pulp consumption for priority fruit tree as well as fruits that were hardly utilized as food. Mechanisms of how mangabeys physiologically deal with the occasional tannin ingestion should be studied. The tannin threshold of 2.6g/100 should be explored in relation to different age groups among mangabeys and other primates.

7.8 Acknowledgments

We thank NUFU for funding this research and grateful to Jessica Rothman for her helpful comments on this manuscript. We thank NUFU for funding this research and grateful to our colleagues for helpful comments on this project and manuscript.

7.9 References

Baldwin L. A, Teleki G & Kavanagh M (1976). Field research on colobus, guenon, mangabey, and patas monkeys: an historical, geographical, and bibliographical listing. *Primates.* 17(2): 233-251.

Barnea A, Harborne J. B & Pannell C (1993). What parts of fleshy fruits contain secondary compounds toxic to birds and why? *Biochemical Systematics and Ecology* 21(4): 421–429.

Basabose, A. K & Yamagiwa, J. (2002). Factors affecting nesting site choice in chimpanzees at Tshibati, Kahuzi-Biega National Park: influence of sympatric gorillas. *International Journal of Primatology*, **23**(2), 263-282.

Bennett R. N & Wallsgrove R. M (1994). Secondary metabolites in plant defence mechanisms. *New Phytologist*, 127: 617– 633.

Boyle R, McLean S, Foley W. J & Davies N. W (1999). Comparative metabolism of dietary terpene, p-cymene, in generalist and specialist folivorous marsupials. *Journal of Chemical Ecology*, 25(9), 2109-2126.

Broadhurst R. B & Jones W. T (1978). Analysis of condensed tannins using acidified vanillin. *Journal of the Science of Food and Agriculture* 29(9): 788-794.

Chalmers N. R (1968). The visual and vocal communication of free inhabiting mangabeys in Uganda. *Folia primat* 9(0): 258-280

Chapman C. A, Rothman J.M & Lambert J. E (2012). Food as a selective force in Primates In PRIMATES MUST EAT to survive; the acquisition of food resources is thus among one of the most significant. *The Evolution of Primate Societies* 149-163. Eds; John C. Mitani, Josep Call, Peter M. Kappeler, Ryne A. Palombit, Joan B. Silk

Chapman C. A & Chapman L. J (2002). Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. Comparative Biochemistry and Physiology-Part A: *Molecular & Integrative Physiology* 133(3): 861-875.

Chapman C. A, Chapman L. J, Wangham R, Hunt K, Gebo D and Gardner . (1992). Estimators of fruit abundance of tropical trees. *Biotropica* **24** (4): 527-531.

Chivers, D. J. (1986). Current issues and new approaches in primate ecology and conservation. *Primate ecology and conservation*, 2, 3-18.

Cipollini M. L & Levey D. J (1997). Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *The American Naturalist*, 150(3): 346-372.

Coley P. D (1986). Costs and benefits of defence by tannins in a neotropical tree. *Oecologia* 70(2): 238-241.

Conklin-Brittain N. L, Wrangham R.W & Hunt K. D (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *International Journal of Primatology*, 19(6): 971-998.

Danish, L., Chapman, C.A., Hall, M.B., Rode, K.D. & Worman, C.O. (2006). The role of sugar in diet selection in redtails and red colobus monkeys. In Hohmann, G., Robbins, M. and Boesch, C. (Eds). *Feeding Ecology in Apes and Other Primates. Ecological, Physical and Behavioral Aspects* (pp. 473-487). Cambridge University Press.

Dearing M. D, Foley W. J & McLean S (2005). The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annual Review Ecology Evolution Systematics*, 36:169–89.

Doran-Sheehy DM, Shah NF & Heimbauer LA (2006). Sympatric western gorilla and mangabey diet: re-examination of ape and monkey foraging strategies. Cambridge Studies in Biological and Evolutionary Anthropology pp 49.

Eriksson O & Ehrlén J (1998). Secondary metabolites in fleshy fruits: are adaptive explanations needed? *The American Naturalist* **152** (6): 905-907.

Fashing JP (2001). Activity and ranging patterns of guerezas in the Kakamega forest: Intergroup variation and implications for intragroup feeding competition. *International Journal of Primatology* **22**(6): 549-577.

Flannery, S. (2000). "*Lophocebus albigena*" (On-line). Primate Info Net Fact Sheets. At http://animaldiversity.ummz.umich.edu/local/redirect.php/http://www.gisbau.uniroma1 .it/amd/amd004.html. Accessed September 16, 2005

Fungo B, Eilu G, Tweheyo M & Baranga D (2013). Forest disturbance and cropping mixtures influence crop raiding by red-tailed monkey and grey-cheeked mangabey around Mabira Forest Reserve, Uganda. *Journal of Ecology and the Natural Environment* **5**(2), 14-23.

Ganzhorn, J. U. (1986). Feeding behavior ofLemur catta andLemur fulvus. *International Journal of primatology*, 7(1), 17-30.

Garber, P.A. (1987). Foraging strategies among inhabiting primates. *Annual Review of Anthropology*, **16**(1987), 339-364.

Gargiullo M.B & Stiles E.W (1993). Development of secondary metabolites in the fruit pulp of Ilex opaca and Ilex verticillata. *Bulletin of the Torrey Botanical Club*. pp 423-430.

Glander, K. E. (1982). The impact of plant secondary compounds on primate feeding behavior. *American Journal of Physical Anthropology*, **25**(S3), 1-18.

Gombya-Ssembajjwe, W. (1999). Institutions and sustainable forest management. *Uganda Journal* **45**(1), 51-60.

Gonzalez F. J. & Gelboin H.V. (1994). Role of human cytochromes P450 in the metabolic activation of chemical carcinogens and toxins. *Drug metabolism reviews*, **26**(1-2): 165-183.

Gonzalez F. J. and Nebert D.W. (1990). Evolution of the P450 gene super family: animal-plant 'warfare', molecular drive and human genetic differences in drug oxidation. *Trends in Genetics*, **6**(0): 182-186.

Herrera, C. M. (1982). Defence of ripe fruit from pests: its significance in relation to plant-dispersers interactions. *The American Naturalist*. **120** (2): 218-241.

Howard, P. C., Butler, J., & Howard, P. (1991). Nature conservation in Uganda's tropical forest reserves. IUCN, Gland, Switzerland and Cambridge, UK with the financial support of WWF-International.

Howe G. A. & Jander G. (2008). Plant immunity to insect herbivores. *Annual Review of Plant Biology* 59, 41-66.

Jakubas W. J. , Karasov W. H. & Guglielmo C. G. (1993). Coniferyl benzoate in quaking aspen (Populus tremuloides): its effect on energy and nitrogen digestion and retention in ruffed grouse (*Bonasa umbellus*). *Physiological Zoology*, **66**(4): 580-601.

Johns, T., & Duquette, M. (1991). Detoxification and mineral supplementation as functions of geophagy. *The American journal of clinical nutrition*, **53**(2), 448-456.

Kizza, M., Rodhe, A., Xu, C. Y., Ntale, H. K., & Halldin, S. (2009). Temporal rainfall variability in the Mabira and Lwamunda in East Africa during the twentieth century. *Theoretical and applied climatology*, **98**(1-2), 119-135.

Klein, N., Fröhlich, F., & Krief, S. (2008). Geophagy: soil consumption enhances the bioactivities of plants eaten by chimpanzees. *Naturwissenschaften*, 95(4), 325-331.

Kraus T.E. , Dahlgren R. A. & Zasoski R. J. (2003). Tannins in nutrient dynamics of forest ecosystems-a review. *Plant and Soil*. **256**(1): 41-66.

Kreulen, D. A. (1985). Lick use by large herbivores: a review of benefits and banes of soil consumption. *Mammal Review*, **15**(3), 107-123.

Krief S, Hladik C. M., & Haxaire C. (2005). Ethnomedicinal and bioactive properties of plants ingested by wild chimpanzees in Uganda. *Journal of Ethnopharmacology*, **101**(1), 1-15.

Krishnamani, R., & Mahaney, W. C. (2000). Geophagy among primates: adaptive significance and ecological consequences. *Animal behaviour*, **59**(5), 899-915.

Lua Y. & Bennick A. (1998). Interaction of tannin with human salivary proline-rich proteins, *Archives of Oral Biology* **43**(9) 717–728.

Mack A. L. (2000). Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism? *Journal Biosciences* **25**(1): 93-97

Marshall, A.J. & Wrangham, R.W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*, **28**(6), 1219-1235.

Moscovice, L. R., Issa, M. H., Petrzelkova, K. J., Keuler, N. S., Snowdon, C. T., & Huffman, M. A. (2007). Fruit availability, chimpanzee diet, and grouping patterns on Rubondo Island, Tanzania. *American Journal of Primatology*, **69**(5), 487-502.

Nabihamba, E. (1996). Factors determining dietary choices among arboreal frugivores in Kibale forest in Western Uganda. Msc Thesis, Makerere University, Kampala.

Nathiya M and Dorcus D (2012). Preliminary phytochemical and antibacterial studies on Physalis minima Linn. *International Journal Current Science*, 24-30.

Norconk, M. A and Veres, M. (2011). Physical properties of fruit and seeds ingested by primate seed predators with emphasis on sakis and bearded sakis. *The Anatomical Record*, **294**(12), 2092-2111.

Ogango, A. (2006). *Crop Raiding by Mangabeys in Lwamunda forest reserve, Uganda*. A Research Project Submitted to the Zoology Department in Partial Fulfilment of the Requirements for a Degree in Bachelor of Science, Makerere University.

Olupot, W., Chapman, C. A., Waser, P. M., & Isabirye–Basuta, G. (1997). AJP 332. *American Journal of Primatology*, **43**, 65-78.

Reynolds V (2005). The Chimpanzees of the Budogo Forest: Ecology, behaviour and Conservation. Publ. Oxford University Press.

Reynolds, V., Plumptre, A. J., Greenham, J., & Harborne, J. (1998). Condensed tannins and sugars in the diet of chimpanzees (Pan troglodytes schweinfurthii) in the Budongo Forest, Uganda. *Oecologia*, **115**(3), 331-336.

Robbins C.T., Mole S, Hagerman A. E & Hanley T. A. (1987). Role of tannins in defending plants against ruminants: reduction in dry matter digestion? *Ecology* pp 1606-1615.

Rode K. D., Chapman C. A., McDowell L. R. & Stickler C. (2006). Nutritional Correlates of population Density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*) *Biotropica* 10: 1744

Sagers C. L & Coley P. D. (1995). Benefits and costs of defence in a Neotropical shrub. *Ecology*, 1835-1843.

Saini R. S. , Kumar P., Singh S., and Sharma J. R. (2009). Changes in quality characters during growth and development of lasora (Cordia myxa Roxb.) fruit. *Haryana Journal of Horticultural Sciences*, **38**(1/2), 9-13.

Schaefer H. M., Schmidt V. & Winkler H. (2003). Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos*, 102: 318–328.

Schwedhelm E., Maas R., Troost R. and Böger R. H. (2003). Clinical pharmacokinetics of antioxidants and their impact on systemic oxidative stress. *Clinical pharmacokinetics* **42**(5), 437-459.

Sorensen, J. S., McLister, J. D., & Dearing, M. D. (2005). Plant secondary metabolites compromise the energy budgets of specialist and generalist mammalian herbivores. *Ecology*, **86**(1), 125-139.

Sorensen J. S., Turnbull C. A., Dearing M. D. (2004). A specialist herbivore (*Neotoma stephensi*) absorbs fewer plant toxins than does a generalist (*Neotoma albigula*). *Physiol. Biochem. Zoology*. **77**(1):139–48.

Sorensen, J. & Dearing, M. (2003). Elimination of plant toxins by herbivorous woodrats: revisiting an explanation for dietary specialization in mammalian herbivores. *Oecologia*, **134**(1), 88-94.

Spuhler J. N & Jorde L. B. (1975). Primate phylogeny, ecology, and social behaviour. *Journal of Anthropological Research* **31**(4): 376-405.

Struhsaker, T. T., Cooney, D. O., & Siex, K. S. (1997). Charcoal consumption by Zanzibar red colobus monkeys: its function and its ecological and demographic consequences. *International Journal of Primatology*, **18**(1), 61-72.

Verderane M., Izar P., Visalberghi E. & Fragaszy D. M. (2013). Socioecology of wild bearded capuchin monkeys (*Sapajus libidinosus*): an analysis of social relationships among female primates that use tools in feeding. *Behaviour* 150: 659-689.

Waser PM (1975). Monthly variations in feeding and activity patterns of the Mangabey, *Cercocebus albigena* (Lydekker). *E. Afr. Wildl. Journal*. 13: 249-263

Wieczkowski, J. A. (2003). Aspects of the ecological flexibility of the Tana mangabey (*Cercocebus galeritus*) in its fragmented habitat, Tana River, Kenya.

Wrangham R. W., Conklin-Brittain N. L & Hunt K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology* **19**(6): 949-970.

Wiggins N. L, McArthur C, McLean S & Boyle R. (2003). Effects of two plant secondary metabolites, cineole and gallic acid, on nightly feeding patterns of the common brushtail possum. *Journal of Chemical ecology* **29**(6): 1447-1464

CHAPTER EIGHT

8 Effect of gaps on fruit availability for mangabeys in Mabira and Lwamunda forest reserves, Uganda

M. Masette, G. Isabirye-Basuta and D. Baranga.

Department of Biological Sciences, Makerere University, P.O. Box 7062, Kampala, Uganda

Abstract

The incessant felling of trees in Mabira and Lwamunda forests creates gaps which interfere with the functions of the ecosystem. This action undoubtedly, contributes to habitat loss and food scarcity for mangabeys. However, no attempt has been made hitherto to link gaps with food availability for primates and particularly mangabeys. The effect of gaps in the home ranges of 3 Mangabey social groups on fruit availability was examined by use phenological data collected over a period of 12 months (Jan-Dec 2006). The sizes of gaps were measured during the one month from June to July 2006 in three study sites with varying management histories. In each study site, an area of $1Km^2$ was surveyed for gaps using GPS while visual abundance score methods were used to determine fruit availability. Results indicated that as the size and number of gaps increased the number of trees utilized by mangabeys with edible fruits declined. In the severely degraded Lwamunda forest reserve, about 25.11% of the surveyed area was under gaps. In the fairly undisturbed Mabira (M1) and regenerating Mabira (M2) forest reserves, only 1.36% and 3.73% were under gaps respectively. On the other hand, there were about 10%, 9% and 4% of tree species with edible fruits in M1, M2 and Lwamunda respectively. By inference, fruit scarcity was more prevalent in severely degraded Lwamunda than the two Mabira habitats. This scenario implied that mangabeys in Lwamunda faced more dietary constraints and challenges than their counterparts in Mabira.

Key words: Deforestation, fruit scarcity, tropical forests, Uganda

8.1 Introduction

In a forest environment, gaps are normally associated with treefalls, standing dead trees and anthropogenic activities. Essentially, gaps assume a wide range of sizes from the small openings created by the death of single branches or trees to expanse of hectares attributed to catastrophic wild fires (Spies and Franklin, 1989) or anthropogenic activities like logging (Babaasa *et al.*, 2004) and encroachment for agricultural purposes. The loss of trees could have been caused by several inter-related factors like microclimatic changes and elevated wind turbulence (Laurance *et al.*, 1997) or logging (Curran *et al.*, 2004; Olupot, 2000; Johns, 1988) or simply natural tree mortality (Attiwill, 1994). Tree fall is part of autogenic change and it is fundamental to the development of structure and function of forest ecosystems.

Generally, large-sized gaps in the forest are partly associated with degradation attributed to anthropogenic activities. This is a worldwide human induced disturbance of habitat which has been partly attributed to technological advancement. In Uganda, tree loss has been largely driven by a combination of factors. They include human population growth, inequitable land, income disparity, skewed development policies and armed conflicts (Winterbottom and Eilu, 2006). These factors have led to rapid conversion of forested land to agriculture land in a bid to increase food production for an incessant population increase (Kayanja and Byarugaba, 2001), industrial inputs and human settlements (NEMA, 2006). The severity of forest degradation tended to increase with proximity to demand centres (Baranga, 2004) and Kampala being within reach of Mabira and Lwamunda forest reserves, degradation is exceptionally high in unprotected forests. Indeed, according to several observers (NEMA, 2012; Howard, 1991; Hamilton, 1984) forest degradation within the Mabira and Lwamunda has been on the rise since 1950s. This habitat disturbance has affected both the structure and composition of the forests therein and its fauna including primates like mangabeys. These and other related factors have synergistically imposed quantitative as well as qualitative changes in food availability with direct effect on fauna populations (Naughton-Treves *et al.*, 1998; Tweheyo *et al.*, 2005).

The level of forest degradation determines the area occupied by gaps and potential food

tree densities which in turn defines the quality and quantity of food items available to frugivorus primates. If so, the availability and quality of food in degraded forest with large area occupied by gaps would probably be lower than in relatively undisturbed forest reserves/habitats. Consequently, the primate feeding ecology and ranging patterns would differ with number and size of gaps such that mangabeys inhabiting degraded areas will have extended home ranges, reduced group size and high mortality rates among the vulnerable members of the group. The reverse would hold true for mangabeys in relatively undisturbed areas of the forests.

According to Kasenene (1987), low tree densities as a result of logging, invariably lessens food availability for primates. Low tree densities imply large and more gaps within a given forest (Skorupa, 1988) and tend to break the continuity of the tree canopy. Quite often, arboreal mangabeys are forced to climb down to forest floor and forage among herbaceous plants which are known to have high levels of condensed tannins (Schaefer *et al.*, 2003; Poulsen *et al.*, 2001). In most cases, primates shift to other habitats in search of food which inevitably increases travel costs. The consumption of tannin-laden food items and increased travel costs impinge on their nutritional status which has a bearing on reproduction and ultimately on their population densities.

Primates are known to be more sensitive to habitat disturbances (Olupot, 2000) than other forest fauna with the exception of butterflies (Akite, 2008) and birds (Plumptre *et al.*, 2001). Different species of primates respond to habitat changes differently. Some tend to have dietary shifts (Worman and Chapman, 2005; Waser, 1975), others engage in crop-raiding when gardens with domesticated crops are in close proximity (Strum, 2010; Hill, 2000). Mangabeys in particular have been known to change ranging patterns (Olupot *et al.*, 1997 and Waser, 1975). Homewood (1978) also observed that foraging behaviour increased when food was scarce and that the total distance travelled and area covered by the group increased in search of food. With prolonged habitat disturbance, Mangabey populations tended to decline (Chapman and Lambert, 2000).

Several studies have speculated on the inter-related factors which have ostensibly contributed to population declines among primates. Milton (1981) collected data on the reproductive parameters of *Ateles geoffroy* population for six and a half years. The author

noted that as much this primate adapted to primary resource base that was very low in protein and patchily distributed in space and time, the risk of increased predation probably contributed to population declines. Chapman *et al.* (2007) examined the effects of temporal variation in nutrition and parasitism on stress in endangered red colobus (*Procolobus* spp) monkeys in Kibale National Park, Uganda. They identified risk to parasitism and disease as one of the consequences of stress that is known to affect fecundity and mortality. Increased stress provides a warning of potential population declines. Worman and Chapman (2005) observed that a decline in food availability and quality corresponded with population declines in three frugivorous primate species (*Cercopithecus mitis*, *Cercopithecus ascanius* and *Lophocebus albigena*). According to Olupot *et al.*, (1994) reduced food availability led *L. albigena* to extend their home range. According to Freeland (1979 and Olupot (1999), foraging over large expanses of home range increases travel costs which in turn contributes to the onset of stress. Invariably, when a primate is stressed its body systems succumb to parasitism and disease (Mbora and McPeek, 2009; Chapman *et al.*, 2005). Once stress sets in, the body condition deteriorates and the nutritional status declines accordingly which may lead to local population extinction (Martínez-Mota *et al.*, 2007). Lee and Priston (2005) also cited conflicts between humans and non-human primates over habitats as one of the factors contributing to population declines among non-human primates.

None of the above responses have been established with respect to mangabeys inhabiting Mabira and Lwamunda forest reserves. Most available information relates to food availability in other forests (Olupot, 1998) to magnitude, mode and variations of sensitivity to forest degradation (Martínez-Mota *et al.*, 2007; Worman and Chapman, 2005; Poulsen *et al.*, 2001; Olupot, 2000; Chapman and Lambert, 2000; Medley, 1993). Undeniably, Mabira and Lwamunda forest reserves have been affected by incessant habitat disturbance and mangabeys may have adapted skills and various food acquisition mechanisms in order to compete and survive in a harsh environment. However, the manner in which they have responded to food availability is still unclear. Fundamental adaptations seem to have taken place with changes in population dynamics, home range, food availability, food selection, and food processing, dietary shifts, crop-raiding and

food trade-offs. However, this paper only examines effects of gaps created as a result of anthropogenic activities on food availability for mangabeys inhabiting Mabira and Lwamunda forest reserves in Uganda. As such, the number of gaps were probably underestimated because gaps created by treefalls and dead standing trees were not considered in this study. However, we hypothesized that the size of the gap and the proportion constituting gaps within a habitat may affect availability of fruit for mangabeys.

8.2 Methods and Materials

8.2.1 Study area

We studied Grey-checked mangabeys in Mabira (306 km^2, 0° 24`N and 0° 35`E and longitude 32° 52`N and 33° 07`E) and Lwamunda (67 km^2, - 0° 15′ N and 0° 23′ N longitude 32° 30′ E and 32° 43′ E) Forest Reserves, Uganda (Howard *et al.*, 1991) from June 2004 to March 2007. However, the data for this paper has been restricted to the period between January and December 2006. Recently, several researchers have conducted studies in the same forest reserves (Groves, 2007; Ogango, 2006; Baranga, 2004 and Obua, 1994) so the animals were habituated. However, earlier studies (Baldwin *et al.*, 1976; Chambers, 1968; Spuhler and Jorde, 1975; Waser, 1975) had been conducted in the same forests since 1965. Both forests being within the Mabira and Lwamunda, they have bimodal rainfall patterns varying between 1200-1500 mm annually and typically distributed between two rainy distinct seasons April-May and October-November (Kizza *et al.*, 2009). Mabira is located on undulating hills and valleys at an elevation of 1070–1340 m above sea level while Lwamunda is a riverine forest reserve surrounded by isolated flat-topped hills with steep slopes at an elevation of 1200 m (Howard *et al.*, 1991).

The gaps in the three forest reserves with varying histories of management were created by different natural occurrences and anthropogenic activities but only gaps created by the latter were considered in the present study. Sizes of anthropogenic-created gaps were measured along transects that were 100m apart using Garmin Channel XL GPS model. Only such gaps seen from transects were considered for the present study. The area

covered by the survey was 1 Km^2 for each study site. The GPS co-ordinates were interpreted using GIS software package.

Food availability for the three (3) groups of habituated mangabeys; one in Lwamunda and two in Mabira was determined by identifying and marking 10 individual trees of the top 10 priority fruit tree species commonly utilized by mangabeys in each study area. They included, *Ficus mucuso, Ficus exasperata, Ficus sur, Measopsis eminii, Celtis durandii, Celtis africana, Celtis mildbraedii, Canarium indicum, Antiaris toxicaria, Albizia grandibracteata, Treculia africana, Pseudospondias microcapa, Blighia unijugata, Myrianthus arboreus* and *Rheedia edulis*. For each of these priority fruit tree species, 10 individual trees were also marked and monitored. In total 300 trees; 100 in each study site were monitored on a monthly basis. Some fruit trees were common in the three sites while others were only available in particular sites. For example, *B.unijugata, M. arboreus, R. edulis, A. toxicaria* and *F. Sur* were only available in Lwamunda while all *Celtis* species not present in Lwamunda but occurred in Mabira.

Phenological data included fruiting cycles of marked priority fruit trees commonly utilized as food by mangabeys. Using a visual abundance score (Chapman *et al.*, 1992), fruit abundance, number of fruiting trees with edible or inedible fruits and fruitless trees was determined on a monthly basis. The level of fruit availability was indexed by the percentage of trees with edible ripe fruits in comparison with inedible fruit stages and fruitless trees within the range of each group.

8.2.2 Data analysis

The number of gaps was sequenced under regular gap size ranges and the frequency plotted against ranges and mean area under gaps. The percentage of the area covered by gaps in each respective study site was calculated from the formulated equation: -

A=gpa/tas x100

Where

A= percentage gap area covered in each study site

gpa = No of gaps x Mean gap area (m^2)

tas= total area surveyed (m^2)

Using SPSS version 17, a one way ANOVA was used to compare the mean monthly phenological fruit availability and abundance scores in the 3 forest types. The spatial and temporal patterns of fruit variability between forests were also analysed using the same package. However, fruit availability was determined by expressing the proportion of fruiting trees as percentage of all tagged trees regardless of species on a monthly basis.

8.3 Results

The number of gaps created by anthropogenic activities, sizes, frequency of occurrences and total area covered by gaps varied with type of forest. Whereas, gaps spread across all size ranges in Lwamunda, they were more concentrated in the low sized ranges in M1 and M2. The areas of gaps in Lwamunda were significantly bigger than gaps in both Mabira sites (t-test, $p < 0.05$). The area constituting gaps was two and half times larger in Lwamunda than the combined total of M1 and M2.

In the fairly undisturbed Mabira (M1) forest reserve, there were 10 gaps and the mean area under gaps was about 170.4m^2 (Fig 8.1). The area covered by gaps was about 1.4% which implied that 98.6% of the surveyed 1Km^2 had a fairly closed tree canopy. It was observed that the gaps in this study site were created as a result of tree falls.

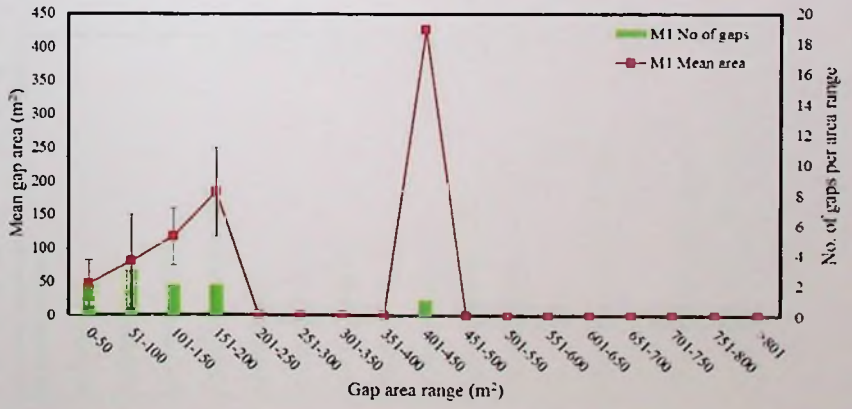


Figure 8.1 Variability of number of gaps and mean area under respective gap ranges in Mabira (M1) forest reserve.

In the Mabira portion that was regenerating (M2), there were 28 gaps with the mean area of about 96m^2 (Fig 8.2) which constituted 3.73% of the surveyed 1Km^2 area. It was observed that gaps in this study site were created both by logging and farming during the

two decades when prohibition to the forest was relaxed. At the time of the study, access to the forest for agricultural or logging purposes was prohibited. As such, there was dense undergrowth with a limited number of tall trees and discontinuous tree canopy.

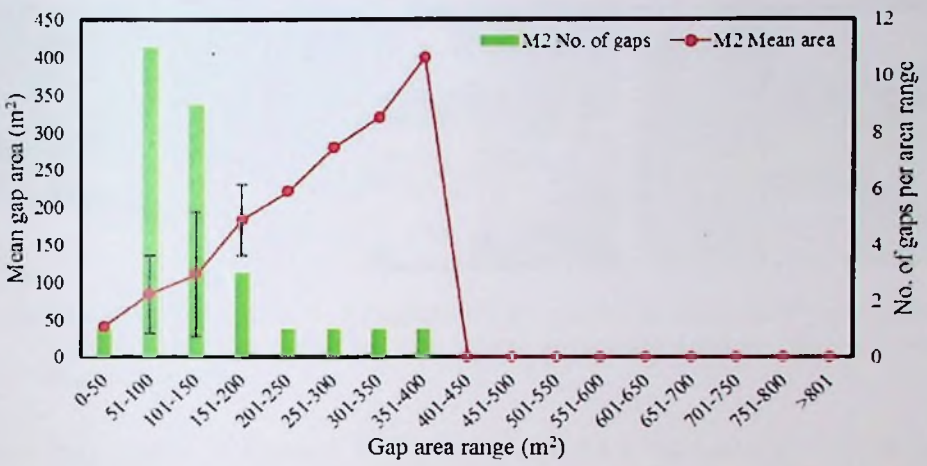


Figure 8.2 Variability of number of gaps and mean area under respective gap ranges in Mabira (M2) forest reserve.

In the severely degraded Lwamunda (LD), there were 53 gaps with a mean area of 423.79m^2 which consistituted 25.11% of the surveyed 1Km^2 area (Fig 8.3).

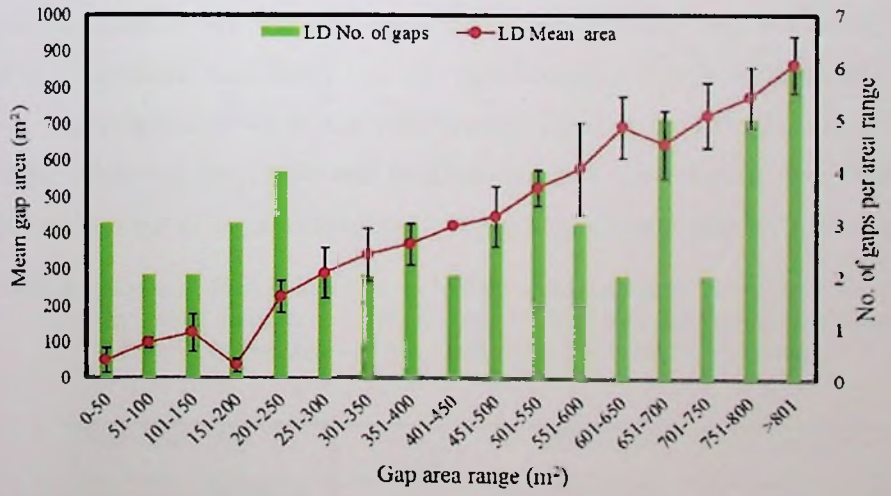


Figure 8.3 Variability of number of gaps and mean area under respective gap ranges in Lwamunda (LD) forest reserve.

It was observed that in LD. the gaps were created by tree falls. wanton logging and farming as shown in Fig 8.4. These factors may have serious repercussions on Mangabey foraging behaviour and nutrition.

Figure 8.4 The chronological level of degradation in Lwamunda forest reserve. Uganda. Large trees are felled for timber (a) then undergrowth cleared (b) and finally transformed into gardens (c).

The phenology results in Chapter 4, Fig 4.4.2 and 4.4.3 indicated that the number of fruiting trees with edible fruits or inedible varied with habitat type. However the statistical analysis using ANOVA (SAS statistical software) indicates that edibility was significantly different between M1 and LD while M2 showed cross-cutting character. (Table 8.1). This implied that it was not significantly different from M1 or LD although it was geographically next to M1. In other words, the number of fruits with edible parts or inedible fruits in M1 was not significantly different from M2, but significantly different from Lwamunda. Inedibility was not significantly different between M1 and M2 which was understandable but it was significantly different for LD. Overall M1 and M2 gave higher means in the edible and inedible category. Considering that Lwamunda had the highest number of large sized gaps, it appears gaps influenced food availability.

Table 8.1 Status of food availability in Mabira and Lwamunda forest reserves. 2006; symbolised by mean number of priority fruit trees commonly utilized as food by mangabeys. (*Figures in brackets are the coefficients. M1 being the reference*)

Fruit availability	*Mabira (M1)*	*Mabira (M2)*	*Lwamunda (LD)*	*p value*
Trees with edible fruits	10	9.0833 (-0.9167)	4.09 (-5.91)	0.0404
Trees with inedible fruits	19.83	23.493 (3.663)	5 (-14.83)	0.0003

8.4 Discussion

Since gaps are fundamental to the development of structure and function of forest ecosystems, they inevitably influence fruit availability and mobility of arboreal fauna including mangabeys. The gap size and frequency of occurrence observed in the present study appeared to influence fruit availability in the three habitats (Chapter 4). As the size of gaps increased, the number of fruit trees decreased in a habitat and therefore fruits available for mangabeys to consume sustainable declined accordingly. However, the effect of gap size was more pronounced in the severely degraded Lwamunda forest reserve than in Mabira 1 and 2. We suggest that the loss of canopy continuity created during wanton harvesting of trees and other gap dynamics like aggressive herb community delayed the vegetation recovery. This was in agreement with Chapman and Chapman (1997) when they assessed the regeneration of vegetation in logged and unlogged portions of Kibale National park forests. These and other factors probably have a negative impact on tree regeneration over time. According to Kasenene (1987), logging lowers tree densities which invariably lessen food availability for primates. Indeed, during the period of the present study, tree species like *Albizia*, *Pseudospondias*, *Canarium* and *Rheedia* were regularly felled for timber extraction which exacerbated fruit scarcity in Lwamunda forest reserve. Low tree densities imply large and more gaps within a given forest (Skorupa, 1988) and foraging in such habitats inevitably increases travel costs for primates. This impinges on their nutritional status that has a bearing on reproduction and ultimately on their population densities. However, there were some positive impacts ascribed to the presence of gaps in given habitats. For instance, fruit trees like *M.arboreus, B.unijugata* and *R.edulis* identified as preferred fruits by mangabeys (Chapter six of this thesis) thrived more in Lwamunda than in Mabira. According to Wiafe (2014) *M.arboreus* thrived in a slightly disturbed habitat while *F.sur* occurred more frequently in heavily disturbed Asenanyo moist Forest Reserve of Ghana. Some fruit trees like *F.sur* known to be a periphery or gap tree (Wiafe, 2014; Basuta, *unpublished data*) had more extended fruiting episodes and fruited more frequently in Lwamunda than in Mabira (M1) which had a continuous canopy. This was in agreement with Levy (1990) who compared trees under shade with trees in gaps and concluded that gaps played an important role in productivity of *M. centrodesma*.

About two decades ago, Barbour *et al.*, (1987) described Lwamunda as a tropical moist evergreen forest with closed canopies which was again echoed by Banana and Gombya-Ssembajjwe (2000) when elaborating the 1992 Uganda National Environmental Action Plan (NEAP). However, by 2007 the present study observed that most of the Lwamunda forest reserve had been transformed into farmland. The forest encroachment for agricultural purposes was probably attributed to increased human populations in Wakiso district (UBOS, 2014). This was in agreement with Tom-Dery and Schroeder, (2011) who reported high correlation between human population density and cumulative forest loss. Inescapably, the forest was fragmented without a continuous canopy. A decline in food availability and quality leads to extension of home range and the resultant high travel costs (Olupot, 1999; Freeland, 1979). During the study we observed mangabeys foraging in the undergrowth especially in Lwamunda forest reserve which implied the absence of food in the canopy. Food items available among the undergrowth like mushrooms and herbaceous fruits are known to have low nutrient quality and contain high levels of toxic secondary compounds. This imposed dietary shift is indicative of food scarcity according to Worman and Chapman (2005). The act of climbing down on the forest floor increases travel costs (Olupot, 1999), risk of predation (Milton 1981), risk to parasitism and disease (Mbora and McPeek, 2009; Chapman *et al.*, 2007) and exacerbates conflicts between humans and non-human primates over habitats (Lee and Priston, 2005). In most cases primates are forced to shift to another habitat in search of food since the available food is severely compromised in terms of quality and quantity.

On the contrary, the fewer and small sized gaps particularly in Mabira M1 implied that the canopy was essentially intact and arboreal mangabeys were rarely observed foraging on the forest floor. Although the gaps in M2 were fewer and relatively smaller in size, the forest canopy was not continuous. On several occasions, mangabeys were observed feeding on passion fruits, jackfruit and pineapples that had been abandoned by agricultural encroachers in early 1993 after imposition of the UNESCO Biosphere management strategy (Alpert, 1996). In both M1 and M2, there was potential for food availability as depicted by the total number of trees with edible and inedible fruits. However, the insignificant difference between M1 and M2 with regard to edibility and

inedibility was probably attributed to the similar micro-environments since they were in the same geographical area. Considering that most gaps in M1 and M2 were due to natural tree falls and natural forest responses to previous disturbances respectively, the apparent food scarcity was seasonal as opposed to anthropogenic activities. According to Banana and Gombya-Ssembajjwe (2000), the ability to regenerate by suckers and the coincidence of regenerative space and gregarious flowering are important components of forest response following disturbance. Theoretically, an open canopy allows in more light and therefore increases forest productivity (Taylor *et al.*, 1996) as demonstrated by the high number of fruiting trees. Protein content in leaves also increases with exposure to sunlight (Ganzhorn, 1995). However, Hartter and Southworth (2009) observed that productivity declined with deforestation or increase in gap size. This was evidently demonstrated in the present study by the high number of fruitless trees in severely degraded Lwamunda forest reserve (Chapter 4 of study). Physiologically, trees respond to stress by accumulating secondary compounds (Zhao *et al.*, 2005) and re-channelling energy resource to survival instead of reproduction (Roy, 2012). Theoritically, when a tree accumulates defensive secondary metabolites like tannins, it produces and retains more fruits because of limited number of pest. However, when the rate of tree felling outpaces fruit productivity, the dietary benefits to frugivores are equally diminished. This scenario was observed in Lwamunda forest reserve which perpetually exhibited fruit scarcity

8.5 Conclusion and Recommendations

8.5.1 Conclusion

Gaps created by anthropogenic activity cause irrepairable imbalance in forest ecosystems as illustrated by food scarcity in the severely degraded Lwamunda forest reserve. This tends to affect the quality and quantity of food and hence the dietary requirements of forest fauna including mangabeys. Consequently, mangabeys devised several strategies to meet their daily dietary requirements which included climbing down onto the forest floor and crop-raiding. These two strategies increased the risk of predation or death at the hands of humans and increased the travel costs. Nutritionally, mangabeys probably lost out more in a habitat with large gaps than a corresponding habitat with small sized gaps.

8.5.2 Recommendations

We recommend a policy or a strategy that will impose cessation of wanton tree felling in Lwamunda forest reserve for an extended period of time to allow regeneration process to take place. Thereafter, gap size and tree regeneration in the gaps should be monitored on a regular basis. Similarly, Mabira forest reserves should also be monitored to ensure continuation of the M2 recovery process from the past logging disturbance. We also suggest that the management strategy should be based on an ecological understanding of the processes that lead to creation of gaps. It should also include change in of social attitude to the law of the commons for maximum benefits from the forest, including timber, firewood, charcoal, medicinal portions and other environmental benefits.

8.6 Acknowledgement

The authors wish to express their gratitude to NUFU for funding for this study. National Council of Science and Technology for granting permission to work in Uganda forest reserves. Madina Namyalo for measuring gaps with GPS and NFA colleagues for deciphering GPS co-ordinates into area.

8.7 References

Akite, P. (2008). The effects of anthropogenic disturbances on the diversity and composition of the butterfly fauna of sites in the Sango Bay and Iriri areas, Uganda: Implications for conservation. *African Journal of Ecology*, **46**(1), 3–13.

Alpert, P. (1996). Integrated conservation and development projects. Examples from Africa. *BioScience*, **46**(11), 845-855.

Attiwill, P.M. (1994). The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and management*, **63**(2), 247-300.

Babaasa, D., Eilu, G., Kasangaki, A., Bitariho, R. & McNeilage, A. (2004). Gap characteristics and regeneration in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology*, **42**(3), 217–224.

Baldwin, L.A., Teleki, G. & Kavanagh, M. (1976). Field research on colobus, guenon, mangabey and patas monkeys: a historical, geographical and bibliographical listing. *Primates,* **17**(2), 233-251.

Banana, A.Y. & Gombya-Ssembajjwe, W. (2000). Successful Forest Management: The importance of security of tenure and rule enforcement in Ugandan forests. In Gibson, C.C., McKean, M.A. and Ostrom, E. (Eds), *People and Forests: Communities, Institutions, and Governance*, 1 Review (pp. 87-97). The MIT Press, Cambridge, Massachusetts, USA.

Baranga, D. (2004). Forest fragmentation and primate survival status in non-reserved forests of the Kampala area, Uganda. *African Journal of Ecology*, **42** (1), 70-77.

Barbour, M. G., Burk, J. H., & Pitts, W. D. (1987). Terrestrial Plant. *Ecology*, 2nd edn. *Benjamin/Cummings* Men Io Park.

Chalmers, N.R. (1968). The visual and vocal communication of free inhabiting Mangabeys in Uganda. *Folia Primatologica*, **9**(3-4), 258-280.

Chapman, C. A., Saj, T. L., & Snaith, T. V. (2007). Temporal dynamics of nutrition, parasitism, and stress in colobus monkeys: implications for population regulation and conservation. *American Journal of Physical Anthropology*, **134**(2), 240-250.

Chapman, C. A., Gillespie, T. R., & Goldberg, T. L. (2005). Primates and the Ecology of their Infectious Diseases: How will Anthropogenic Change Affect Host-Parasite Interactions?. *Evolutionary Anthropology: Issues, News, and Reviews*, **14**(4), 134-144.

Chapman, C. A., & Lambert, J. E. (2000). AJP 99007. *American Journal of Primatology*, 50, 169-185.

Chapman, C.A. & Chapman, L. J. (1997). Forest Regeneration in Logged and Unlogged Forests of Kibale National Park, Uganda. *Biotropica*, **29**(4), 396–412.

Chapman CA, Chapman LJ, Wangham R, Hunt K, Gebo D & Gardner . (1992). Estimators of fruit abundance of tropical trees. *Biotropica* **24** (4): 527-531.

Curran, L.M., Trigg, S.N., McDonald, A.K., Astiani, D., Hardiono, Y.M., Siregar, P., & Kasischke, E. (2004). Lowland forest loss in protected areas of Indonesian Borneo. *Science*, **303**(5660), 1000-1003.

Freeland, W.J. (1979). Mangabey (*Cercocebus albigena*). Social Organization and Population Density in Relation to Food Use and Availability. *Folia Primatologica*, **32**(1-2), 108-124.

Ganzhorn, J. U. (1995). Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology*, **76**(7), 2084-2096.

Groves, C.P. (2007). The Endemic Uganda Mangabey, *Lophocebus ugandae,* and other members of the albigena –group (*Lophocebus*). *Primate Conservation* **22**(1), 123-128

Hamilton, A.C. (1984). *Deforestation in Uganda*. Oxford University Press, Nairobi.

Hartter, J. & Southworth, J. (2009). Dwindling resources and fragmentation of landscapes around parks: wetlands and forest patches around Kibale National Park, Uganda. *Landscape Ecology*, **24**(5), 643-656.

Hill, C. M. (2000). Conflict of interest between people and baboons: crop raiding in Uganda. *International journal of primatology*, **21**(2), 299-315.

Homewood, K.M. (1978). Feeding strategy of the Tana mangabey (*Cercocebus galeritus galeritus*) (Mammalia: Primates) *Journal of Zoology*, **186**(3), 375–391.

Howard, P. C., Butler, J., & Howard, P. (1991). Nature conservation in Uganda's tropical forest reserves. IUCN, Gland, Switzerland and Cambridge, UK with the financial support of WWF-International.

Johns, A.D. (1988). Effects of "selective" timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica*, **20**(1), 31-37.

Kasenene, J.M. (1987). *The influence of mechanized selective logging, felling intensity and gap-size on the regeneration of a tropical moist forest in the Kibale Forest Reserve, Uganda*. Doctoral dissertation, Department of Botany and Plant Pathology, Michigan State University.

Kayanja, F.I.B, & Byarugaba, D. (2001). Disappearing forests of Uganda: The way forward. *Current Science*, **81**(8), 936-947.

Kizza, M., Rodhe, A., Xu, C. Y., Ntale, H. K., & Halldin, S. (2009). Temporal rainfall variability in the Mabira and Lwamunda in East Africa during the twentieth century. *Theoretical and applied climatology*, **98**(1-2), 119-135.

Laurance, W.F., Laurance, S.G., Ferreira, L.V., Rankin-de Merona, J.M., Gascon, C. & Lovejoy, T.E. (1997). Biomass collapse in Amazonian forest fragments. *Science*, **278**(5340), 1117-1118.

Lee, P.C. & Priston, N.E.C. (2005). Human Attitudes to Primates: Perceptions of Pests, Conflict and Consequences for Conservation. In Paterson, J.D. and Wallis, J. (Eds). *Commensalism and Conflict: The Primate-Human Interface* (pp. 1-23). American Society of Primatologist.

Levey, D.J. (1990). Habitat-dependent fruiting behaviour of an understorey tree, *Miconia centrodesma,* and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. *Journal of Tropical Ecology*, **6**(04), 409-420.

Martínez-Mota, R., Valdespino, C., Sánchez-Ramos, M. A., & Serio-Silva, J. C. (2007). Effects of forest fragmentation on the physiological stress response of black howler monkeys. *Animal Conservation*, 10(3), 374-379.

Mbora, D. N., & McPeek, M. A. (2009). Host density and human activities mediate increased parasite prevalence and richness in primates threatened by habitat loss and fragmentation. *Journal of Animal Ecology*, **78**(1), 210-218.

Medley, K. E. (1993). Primate conservation along the Tana River, Kenya: an examination of the forest habitat. *Conservation Biology*, **7**(1), 109-121.

Milton, K. (1981). Estimates of reproductive parameters for free-ranging *Ateles geoffroyi*. *Primates*, **22**(4), 574-579.

Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R. (1998). Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, **35**(4), 596-606.

NEMA. (2012). State of the Environment Report for Uganda 2012. National Environment Management Authority (NEMA), Kampala.

NEMA. (2006). State of environment report for Uganda 2004/5. National Environment Management Authority, Kampala.

Obua, J. (1994). Integrating Indigenous Knowledge in Conservation and Development of Forest Ecotourism in Mabira, Uganda. Department of Forestry, Makerere University.

Ogango, A. (2006). *Crop raiding by mangabeys in Lwamunda forest reserve, Uganda*. A Research Project Submitted to the Zoology Department in Partial Fulfilment of the Requirements for a Degree in Bachelor of Science, Makerere University.

Olupot, W. (2000). Mass differences among male Mangabey monkeys inhabiting logged and unlogged forest compartments. *Conservation Biology*, **14**(3), 833-843.

Olupot, W. (1999). Mangabey dispersal and conservation in Kibale National Park, Uganda. PhD Thesis, Purdue University.

Olupot, W., Waser, P.M. & Chapman, C.A. (1998). Fruit finding by mangabeys (*Lophocebus albigena*): Are monitoring of fig trees and use of sympatric frugivore calls possible strategies? *International Journal of Primatology,* **19**(2), 339-353.

Olupot, W., Chapman, C. A., Waser, P. M., & Isabirye–Basuta, G. (1997). AJP 332. *American Journal of Primatology*, 43, 65-78.

Olupot, W., Chapman, C. A., Brown, C. H., & Waser, P. M. (1994). Mangabey (*Cercocebus albigena*) population density, group size, and ranging: A twenty-year comparison. *American Journal of Primatology*, **32**(3), 197-205.

Poulsen, J.R., Clark, C.J. & Smith, T.B. (2001). Seasonal variation in the feeding ecology of the Grey-cheeked Mangabey (*Lophocebus albigena*) in Cameroon. *Ameicanr Journal of Primatology*, **54**(2), 91-105.

Roy, J. (2012). Response of plants to multiple stresses. In Winner, W.E. and Pell E.J. (Eds). Title of bookAcademic Press, pp 215

Roy, J., Winner, W.E. & Pell E.J. (Eds). (2012). Response of plants to multiple stresses. Academic Press. pp. 215

Schaefer HM, Schmidt V & Winkler H (2003). Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos*, 102: 318–328.

Skorupa, J. P. (1988). The effects of selective timber harvesting on rain-forest primates in Kibale Forest, Uganda (Doctoral dissertation, Ph. D dissertation, University of California, Davis, 1985. Snowdon, CT).

Spies, T.A. & Franklin, J.F. (1989). Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. *Ecology*, **70**(3), 543-545.

Spuhler, J.N. & Jorde, L.B. (1975). Primate phylogeny, ecology and social behaviour. *Journal of Anthropological Research,* **31**(4), 376-405.

Strum, S. C. (2010). The development of primate raiding: implications for management and conservation. *International Journal of Primatology*, **31**(1), 133-156.

Taylor, D.M., Hamilton, A.C., Whyatt, J.D., Mucunguzi, P. & Bukenya-Ziraba, R. (1996). Stand dynamics in Mpanga Research Forest Reserve, Uganda, 1968–1993. *Journal of Tropical Ecology*, **12**(04), 583-597.

Tom-Dery, D., & Schroeder, J. M. (2011). Tree species abundance and regeneration potential of semi-deciduous forest fragments of the Ashanti Region of Ghana. *Journal of the Botanical Research Institute of Texas*, 733-742.

Tweheyo, M., Hill, C. M., & Obua, J. (2005). Patterns of crop raiding by primates around the Budongo Forest Reserve, Uganda. *Wildlife Biology*, **11**(3), 237-247.

Waser, P.M. (1975). Monthly variations in feeding and activity patterns of the mangabey, *Cercocebus albigena* (Lydekker). *East African Wildlife Journal,* **13**(3-4), 249-264.

Wiafe, E. D. (2014). Tree Regeneration after Logging in Rain-Forest Ecosystem. *Research Journal of Biology*, 2, 18-28.

Winterbottom, B. & Eilu, G. (2006). *Uganda Biodiversity and Tropical Forest Assessment:* Final Report. USAID

Worman, C.O. & Chapman, C.A. (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *Journal of Tropical Ecology* **21**(6), 689-697.

Zhao, J., Davis, L.C. & Verpoorte, R. (2005). Elicitor signal transduction leading to production of plant secondary metabolites. *Biotechnology advances*, **23**(4), 283-333.

CHAPTER NINE

9 GENERAL DISCUSSION

9.1 Introduction

Generally, this study on feeding behaviour of mangabeys inhabiting the rapidly disappearing forest reserves of Mabira and Lwamunda (ML), provides information on (1) fruit selection drivers, (2) dietary adaptations in view of declining food resources (3) impacts of anthropogenic activities and teases of potential policy guidelines and strategies. The other cross-cutting variables include, fruit preferences, feeding behaviour, time spent feeding, group size and composition. This information is vital in understanding the dynamics underlying the observed Mangabey population declines in M&L forest reserves. Nevertheless, this study raises several pertinent issues regarding the future of these mangabeys. In order of importance, they include; habitat loss due to incessant anthropogenic activities and seasonal fruit variability that may have been influenced by deforestation. Habitat alteration seem to have contributed to the decline of fruit resources for mangabeys, influenced fruit availability and quality in terms of macro-nutrient composition as well as secondary metabolites. However, the three variables highlighted above seem to overlap and interact to define the nutritional ecology of mangabeys inhabiting M&L forest reserves.

9.2 Fruit selection drivers

There were several criteria used by mangabeys to select fruit for consumption. These fruit selection drivers were dictated by fruit availability, macro-nutrient content and levels of secondary metabolites and particularly tannins. Selection for fruit/fruit part(s) varied with availability and quality which appeared to the two principal criteria used by mangabeys to select the fruit part for consumption at a specific stage of development. The level of fruit development and nutritional content of respective fruits also played a part in selection of fruit type for consumption. The modalities of accessing fruit/fruit part(s) depended on its physical position on the tree branch and level of ripeness. Mangabey fruit selection criteria was based on fruit quality as predetermined by fruit ripeness, fruit

weight and different fruit parts consumed. Intrinsically, the mangabeys seemed to maximize intake of fruit parts with high protein and energy in form of sugars; avoid or regulate intake of fruit parts percieved to have high levels of plant secondary metabolites (tannins) and limit consumption of parts with high dietary fibre. This fruit selection criteria has been coroborated by Felton *et al.*, (2009) who reported that Spider monkeys normally applied traditional models in their foraging behaviour when food resources became a limiting factor. These included protein-leverage model which entailed maximization of available protein intake; preference for energy-dense foodstuffs; avoidance or regulation of tannin intake as it disappropriately affected protein intake and finally low-fibre intake model. As fruits ripened, toxic substances and chemical defences like secondary compounds decreased (Gargiullo and Stiles, 1993) which increased fruit selectivity by primates (Olupot, 1999; Waser, 1977).

9.2.1 Fruit availability

Frugivores rely on availability of fruits in the habitat for their dietary requirements. Fruit abundance did not translate into fruit availability because several fruit trees aborted during study period. Other studies have made similar observations (Pulido *et al.* 2010; Jones and Comita, 2008; Bos *et al.*, 2007; Owens, 1995; Bawa and Webb, 1984). It also tended to vary with seasons and habitats. Seasonality in frugivory refers to patterns of variation in fruit abundance (Buzzard, 2006). It was observed that during the wet season (February-June), almost every priority fruit tree species was in fruit and yet during the dry spells (July-September and December- January) very few priority trees were fruiting. It was noted that trees at the periphery of the forest reserve fruited more frequently than trees sheltered in the middle of the forest. This observation corroborated with other studies (Scarano, 2009; Ibarra-Manriquez and Oyama, 1992; Levey, 1988).

Although tropical forests typically show less seasonality than temperate or savannah habitats (Okecha and Newton-Fisher, 2006), there was seasonality in M&L forests reserves. Seasonality in these forest reserves is best described in terms of dry or wet spells characterized by low ($\leq$ 50mm) or high rainfall ($\geq$51mm) per month. The temporal variation of fruit availability seemed to be influenced by the amount of rainfall received

during the period of study (Uganda Metrological Department, 2008). This finding was in agreement with Moscovice *et al.*, (2007) who reported that tree fruit availability was positively correlated with rainfall. Most fruit trees in M&L forests reserves fruited after the long rains.

Fruit availability varied with habitat. In Lwamunda and Mabira (M2) that had extensive alteration or disturbance through logging or agricultural encroachment, fruit availability was low and erratic (Chapter 4 of this thesis). Consequently, the number of priority fruit trees commonly utilized by mangabeys as food were not available in all the three study habitats. The overall level of fruit abundance decreased from the fairly undisturbed Mabira to Lwamunda which was severely degraded. In the present study, variation in fruit abundance correlated with the level of forest disturbance. Noticeably, there was some relationships between nutrition and habitat disturbance. The phenology data of the present study showed that all priority fruit trees species commonly utilized as food by mangabeys fruited seasonally albeit at different times and frequency. Some trees like *F.sur* fruited almost every month in Lwamunda while others like *B.unijugata* and *T.africana* fruited biannually. This was in agreement with other studies (Potts and Lwanga, 2014; Chapman *et al.*, 1997). Other studies (Chapman *et al.*, 1999) also established positive correlation between number of fruiting trees and amount of rainfall but later on revised the claim. However, the major influence on fruit abundance in the three habitats was their management histories. Whereas the 1993 UNESCO management strategy (Alpert, 1996) was strictly enforcement of in Mabira forest reserve, it was relaxed in Lwamunda which might have contributed to its low number of trees in fruit. Differences in availability and abundance will lead mangabeys to consume different types of fruits at different levels of maturation (Pienkowski *et al.*, 1998; Ham, 1994). Mangabeys devised different fruit processing methods to access the selected fruit part at different stages of maturation and availability (Felton *et al.*, 2009; Leighton, 1993; Kinzey and Norconk, 1990; Herrera, 1982). Most of them preferred ripe fruit pulp but when it was not available, it appears mangabeys sought alternative food items like fruit endosperms which were accessed by fruit manipulation or processing. During periods of low fruit availability mangabeys shifted from a diet dominated by fruit to consumption of

endosperms, seeds, flowers, and young leaves as previously reported by other studies (Kimuyu *et al.* 2012; Poulsen *et al.*, 2001). Seed-eating was common in the three study sites but more prevalent in Lwamunda than Mabira (M1). Consumption of endosperms of unripe seeds was also associated with severely degraded Lwamunda during periods of food scarcity when 91% of the priority trees were fruitlessness.

It was observed during the present study that gap sizes also affected food availability. This was evident in the severely degraded Lwamunda forest reserve where tree densities were lower than in Mabira. According to Kasenene (1987), large gap sizes lessen food availability for primates. As a consequence, mangabeys were compelled to consume whatever was available including fruit endosperms. However, since endosperms were nutritionally inadequate, mangabeys engaged in crop-raiding to meet their daily dietary requirements (Fungo *et al.*, 2013; Ogango, 2006). In most cases, when food availability became a limiting factor, non-human primates are forced to shift to another habitat in search of high quality and plenteous food. Sometimes, change of habitats and foraging patterns imposes dietary shift which is indicative of food scarcity (Worman and Chapman, 2005).

In a habitat with low fruit availability, other forest fauna feeding on the same meagre food sources introduce stiffer competition following degradation (Lambert, 2005; Olupot *et al.*, 1998; Struhsaker, 1997). Foraging on a tree with reduced food resources exerts physiological pressure on the fruit tree. As a result, the fruiting cycle may be prolonged (Wright, 2005) or the fruiting tree aborts (Okullo *et al.*, 2004; Sage and Webster, 1987; Udovic and Aker, 1981). With reduced fruit resources, mangabeys changed their feeding habits as a coping mechanism to mitigate against fruit scarcity which was indicative of poor forest health. Low fruit scacity and undue stiff competition force mangabeys to resort to eating low quality foods like unripe fruit (Houle *et al.*, 2010) and fruit endosperms. The ability of mangabeys to process immature fruits for purposes of accessing low value endosperms and to raid domesticated crops buffers them from the detrimental effects of resource scarcity.

9.2.2 Fruit quality

Fruit quality refers to organoleptic attributes like colour, flavour, aroma, texture and taste (Causse *et al.*, 2002) but according to Schülke *et al.* (2006), it may also include digestibility and the rate at which fruit is harvested. When the fruit matured and ripened, its hue changed from different shades of green to a tint of red, orange and other bright colours depending on fruit species as it was also observed by Gargiullo and Stiles (1993). Most fruits are brightly coloured to attract dispersers including mangabeys (Izhaki, 1992). Whereas figs showed 7 stages, *Celtis* hardly showed significant colour change as it remained apple green from fruiting to consumption. Mangabeys showed preference along the ripening trend i.e. from bright maroon-red to pale yellow. From evolution standpoint, fruit ripening signals to potential seed dispersers by change in fruit colour (Mack, 2000) and usually exhibit bright colours that can be seen from a distance (Herrera, 1982). Size and sometimes colour changes were a function of fruit/seed maturity (Stickler and Chapman, *unpublished data*; Baranga, 1983). Generally animals including mangabeys have evolved taste preferences for sweet-tasting foods because the sugars contained therein provide readily available source of energy (Reynolds, 2005; Milton, 2004). The organoleptic attributes intensified as the fruit matured and ripened. These quality indices did not vary with habitat but with fruit type which influence choice (Wrangham *et al.*, 1993). Consumption of fruit at different stages of maturity and ripeness may be a factor which may influence fruit processing.

Astringency is associated with the taste attribute and causes puckering sensation in the mouth (Vidal *et al.*, 2004; Taira, 1995). The bitter and astringency detected in unripe fruit is due to the presence of plant secondary metabolites (PSMs) including tannins which form a complex when they precipitate salivary mucoproteins (Wrangham and Waterman, 1983). Plants develop tannins and other secondary metabolites in thousands (Balasundram *et al.*, 2006) for various reasons; Sometimes in response to stress (Zhao *et al.*, 2005) or level of herbivory (Kraus *et al.*, 2003; Dearing *et al.*, 2001 Coley, 1986) or against potential frugivores (Reynolds, 2005).

For reasons stipulated in Chapter 2 *section* 2.3 of this thesis, the levels of tannins in a given fruit/fruit part(s) can dictate their digestibility and the rate at which the preferred

fruit part is processed before ingestion by mangabeys. Consumption of large amounts of tannins and other PSMs can be harmful to the foraging primate hence the need for the development of mechanisms or strategies that can detect and regulate their intake. Mangabeys inhabiting M&L forests avoid consumption of fruits/fruit parts with high levels of tannins or trade-off with macro- nutrients like protein and fats. The avoidance behaviour could be a learned trait from the mother Mangabey or from past experience (Prescott, 2006; Hladik *et al.*, 2002; Dominy *et al.*, 2001). Complete avoidance of fruit parts with high levels of tannins and other PSMs in the diet is not likely to be a realistic strategy especially during periods of fruit scarcity in a severely degraded habitat like Lwamunda forest reserve. In such instances, mangabeys seem to have devised another strategy which could have regulated tannin intake. It involves a trade-off mechanism which allows consumption of unripe fruit with probably high levels of tannins but the desired protein content (Schaefer *et al.*, 2003). According to other studies (Sorensen and Dearing, 2003; Sorensen *et al.*, 2004), when frugivorous primates ingest unripe fruit, proline-rich proteins (PRPs) are secreted in their saliva which inactivates the tannins by forming complexes. Apparently, these complexes prevent interaction with other biological compounds and also disallows tannin absorption from the intestinal canal (*ibid*). Thereafter, the complexes can be eliminated from the body by biotransformation of lipophilic PSMs (Boyle *et al.*, 2000) prior to excretion through urine.

In the present study, the level of tannins varied with fruit, part of the fruit and stage of development but not type of habitat. This was probably attributed to the ecological similarities and climatic conditions obtaining in three study sites within the Lake Victoria Crescent (Obua and Agea, 2010). It appears the level of tannins and other ante-feedants influenced choice of fruit/part consumed by mangabeys regardless of fruit type, habitat and season. This observation has been corroborated with other studies (Lambert, 2013; Chapman *et al.*, 2012; Wrangham *et al.*, 1998; Garber, 1987). Mangabeys did not consume fruit parts that exceeded the threshold of 2.6g/100g catechin equivalents of tannins regardless of habitat and degree of disturbance. This observation was also reported by Yamashita (2008) when studying the chemical properties of the diets of two lemur species of south western Madagascar.

The detection of the tannin threshold is probably a learnt foraging behaviour observed from the mother Mangabey (Basuta, *unpublished data*; Rapaport and Brown, 2008). If mangabeys detected bitterness and astringency in the fruit/fruit part before ingestion, it probably caused a burning sensation in the mouth that triggered a trigeminal stimulation which in turn caused the repulsion of the fruit/fruit part. These sequences of events that regulate intake of PSMs were also reported by other studies (Chapman *et al.* 2012; Dearing *et al.*, 2005; Sorensen *et al.*, 2005; Jakubas *et al.*, 1993). As such, mangabeys seemed to select parts at a specific stage of fruit development when the tannin level was below the threshold. They included fruit endosperms and ripe pulp with the average level of tannins; $\leq$ 0.6 g/100g. As the fruit matured and ripened, there seemed to be a transfer of tannins from the pulp to endosperm that was rapidly developing into seed. The level of tannins in immature and ripe fruit pulp was 8.0 g/100g and 1.6 g/100g on average respectively (Table 7.2). On the contrary, tannin levels in endosperm increased from 0.5 g/100g to 3.6 g/100g in mature seed on average (Figs 7.8-7.10).

The tannin reversal has to do with protection against pests including seed dispersers (Cipollini and Stiles, 1992; Wrangham and Waterman, 1983; Herrera, 1982). When the fruit is immature, the pulp is highly defended with ante-feedants but when it ripens, the tannin levels decline (Waterman, 1984) fruit becomes attractive (Schaefer and Schmidt, 2004; Lambert and Garber, 1998) and palatable to frugivorous seed dispersers (Petre *et al.*, 2013; Poulsen *et al.*, 2001; Milton, 1984). On the contrary, when the seed matures, the level of ante-feedant increases and it becomes unpalatable to the would-be dispersers (Gautier-Hion *et al.*, 1985). This unpalatability ensures germination of the seed and propagation of the species. In respect to this reversal, mangabeys switched from eating endosperms to consumption of ripe pulp. This observation is in agreement with other studies (Harborne, 2001; Tutin *et al.*, 1996; Waterman, 1984). Undeniably, tannin levels appear to play a significant role in diet selection of mangabeys in M&L forest reserves. Other studies have also concluded likewise (Lawler *et al.*, 1999; Reichardt *et al.*, 1991). In severely disturbed Lwamunda forest reserve, the level of tannins in a given fruit part was higher than in the same fruit part from Mabira (M1) which was fairly undisturbed.

This was probably due to the physiological response to stress obtaining in a severely degraded Lwamunda forest reserve.

During periods of food scarcity, mangabeys regularly foraged among the herbaceous undergrowth on the forest floor in Lwamunda and M2. Van Schaik *et al.* (1993) reported herbaceous plants were characterized by low quality due to presence of high tannin levels (Waser, 1975). Consumption of low quality and tannin laden foods by mangabeys contributed to their poor body condition (McCabe *et al.* (2013). This is because detoxifying tannins required high levels of energy (Nabihamba,1996) and yet the available food supply was inadequate. The feeding behaviour was more prevalent in the severely degraded Lwamunda and M2 than M1 which correlated with level of habitat alteration. Apart from herbaceous plants on forest floor, many unripe fruits also contain high levels of secondary compounds. Plants manufacture secondary metabolites presumably for protection against attacks by frugivores that do not disperse the seeds (Dai and Mumper, 2010). The secondary compounds may be toxic or non-toxic depending on the evolutionary relationship between plant defence mechanisms and potential seed dispersers (Levey and Cipollini, 1998).

From the perspective of the fruiting tree, the frugivores or other dispersers play a critical propagation role. As such, fruits have been evolving mechanisms to ensure that animals eat them at the right time and not before. In the present study, the choice to process the fruit or not was probably dependent on the perceived low levels of secondary compounds in preferred fruit parts. For instance, processing of *C. indicum M. eminii*, *P. microcapa* and *B. unijugata* to access endosperm or ripe pulp or aril was based on the notion that tannin thresh-holds were less than 2.6g/100g catechin equivalent.

9.2.3 Macro-nutrient content

Quality in this regard, denotes nutrient composition of food and other cellular metabolites like secondary compounds that influence fruit edibility. Based on Schülke *et al.* (2006) definition, food quality constitutes nutrient content, digestibility and the rate at which food is harvested and processed. Such an extended definition seems necessary because intense feeding competition and risk-prone foraging may constrain primates in terms of

time and energy. For optimal nutritional benefits therefore frugivores must handle and process fruits efficiently which is determined by the level of seed or fruit maturity and the digestive tract of the frugivore (Milton, 1979). The availability of macro-nutrient contained in the seed or fruit varies with level of development, season, type of tree species and location in the canopy (Houle *et al.*, 2007. Although frugivorous primates least understand the intricate nutrient composition of food, they extensively utilize sensory perceptions to make efficient decisions about spatiotemporal distribution of food (Dominy *et al.*, 2001). The nutrient composition of a food includes macro as well as micro-nutrients. Since the role of micro-nutrients is yet to be evaluated as a food selection criterion among the frugivorous primates (Chapman, *unpublished data*), this study concentrated on determination of macro-nutrients; proteins and carbohydrates in form of sugars and fats.

Previous nutritional studies (Matsumoto-Oda and Hayashi, 1999; Milton, 1979) in non-human primates have indicated that protein content is positively correlated with food selection and conversely fibre and condensed tannins are negatively correlated. Nevertheless, proteins, fats and carbohydrates can be converted into energy for mobility, reproduction and other physiological activities in living organisms. Like all other forest fauna, mangabeys must garner sufficient energy and nutrients from their habitat to achieve the stated physiological obligations and food acquisition. However, they should typically avoid expending energy through unnecessary travel while foraging for the most nutritious foods within their home range (Chapman *et al.*, 2012). The dietary requirements of mangabeys inhabiting M&L forest reserves seemed to be influenced by quality properties and quantity of available fruit resources.

Essentially, carbohydrates are the principal source of energy (Potter and Hotchkiss, 1995). However, fruits have relatively small amounts of carbohydrates compared to the energy requirements for arboreal mangabeys. Ripe fruit have readily available digestible sugars (Gaulin and Gaulin, 1982) hence the mangabeys prefer their consumption as opposed to any other fruit part. Based on the results of the present study, mangabeys regularly consumed seeds and endosperms in Lwamunda probably as a primary a source of energy; however these were found to be rich in proteins as opposed to sugars. This

suggests that although mangabeys ate endosperms during periods of food scarcity, there was an alternative source of carbohydrates which supplemented their daily dietary requirements. Indeed Ogango (2006) who was conducting his study on crop-raiding concurrently with the present study in Lwamunda forest reserve, observed that mangabeys incessantly raided cultivated food crops like cassava, sweet potatoes, bananas and pineapples. It is therefore probable that these domesticated crops were the alternative sources of carbohydrate eaten by mangabeys during periods of food scarcity in addition to wild fruit endosperms.

Protein is an essential food for body building, repair and constituent part of body fluids (Potter and Hotchkiss, 1995) and plays a crucial role in reproduction (McCabe, 2012). Each primate species has a protein threshold below which it cannot maintain bodily functions (Milton 1979; Milton, van Soest & Robertson, 1980). Since fruits are poor sources of protein (Rode *et al.*, 2006), frugivores including mangabeys usually supplement their frugivorous diet with foods known to have protein for example young leaves (Baranga, 1983), flower buds (Conklin-Brittain *et al.*, 2002) and other animals (Janson and Chapman, 1999). It was therefore not surprising that mangabeys inhabiting LVB forests regularly consumed endosperms with protein content varying between 5-10% depending on type of fruit.

Generally, primates have relatively low requirements for protein since the nutrient demands for growth and reproduction are spread out over time (Oftedal *et al.*, 1991). However, most of them maintain a daily protein intake but allow total energy intake to vary as a function of the composition of available food items (Felton *et al.*, 2009). On a daily basis, they tend to choose foods from more than one category of food resources to get the balanced essential nutrients and required energy (Milton, 1984). Except perhaps during weaning periods, they do not need to seek out high nutrient density foods (Oftedal *et al.*, 1991).

Fat primarily provides energy for primates (Reiner *et al.*, 2014; McCabe *et al.*, 2013; Fietz and Ganzhorn, 1999; Conklin-Brittain *et al.*, 1998). Of the ten (10) priority trees utilized by mangabeys in the present study, only ripe fruit of *Celtis* species and *Blighia* aril were the main source of fat in the Mangabey diet. Ripe *Blighia* aril had higher fat

content of 25% (on wet weight basis) than any other part of the same fruit while ripe whole *C. mildbraedii* that ripened in January to March registered similar fat content to *Celtis durandii*. This was in agreement with O'Driscoll Worman and Chapman (2005) who reported the highly variable lipid content of 0.3–30.8% (dry matter) for ripe *Celtis durandii* fruit. However, since *Blighia* and *Celtis* species were seasonal fruits, they could not have possibly been the main sources of fat in the Mangabey diet. In the absence of these fruits, mangabeys probably sought alternative food source to meet their dietary fat requirements. It is probable that pupae of insects or small mammals provided alternative source of fat (Raubenheimer and Rothman, 2013; Hernandez, 2011; Bravo, 2008; Janson and Chapman, 1999). In the present study, mangabeys were observed consuming insect pupae from ripe fig fruits; probably to supplement their dietary fat requirements. Some primates, for example fat-tailed dwarf lemur (*Cheirogaleus medius*) have devised other means of fat supplementation. They tend to accumulate fat deposits by either lowering standard metabolism thereby minimizing energy expenditure or increasing the efficiency of food assimilation which maximizes energy intake (Fietz and Ganzhorn, 1999). It is probable that mangabeys are engaged in a similar form of supplementation but since its determination was beyond the scope of this study, it is not possible to prove this assumption. Wild fruits normally have low fat values compared to domesticated oil crops (Potter and Hotchkiss, 1995) but Howe and Kerckhove (1981) reported that wild nutmeg (*Virola surinamensis*) had an average of 63% fat content. Other primates and particularly mountain gorilla (*Gorilla beringei*) consume a diet with low fat content compared to humans (Reiner *et al.*, 2014).

Like other primates, mangabeys require energy for mobility and other physiological activities. The energy is mostly generated from carbohydrates, lipids and sometimes from proteins (Potter and Hotchkiss, 1995). However, the amount of energy available to primates from ingested foods will depend both on the composition of the food and the extent to which various constituents, including fibre fractions, are digested (Oftedal *et al.*, 1991). Ripe fruits are a high-energy resource rich in non-structural carbohydrates and simple sugars (Garber, 1987). It was evident that when available, mangabeys preferred ripe fruit pulp as readily available energy source. This was collaborated with other studies

(Jordano, 2000; Chivers and Raemaekers, 1986). However, ripe fruit was not always available in Lwamunda and in the regenerating portion of Mabira (M2). In such cases, mangabeys ate unripe and particularly fruit endosperms as a source of protein and carbohydrate or sugars.

The energy provided by fruits ingested by mangabeys inhabiting LVB forest reserves did not vary significantly across study sites (ANOVA, $p > 0.05$) but varied between type of fruits (Table 6.2). Mangabeys gained more energy when they consumed seasonal fruits like *Blighia*, *Celtis*, *Rheedia*, *Myrianthus* and *Pseudospondias* species than when they ate fall back fruit (FBF) species (figs, *Canarium* and *Maesopsis*). On average, seasonal fruit provided 4.35Kcal/g compared to 3.76Kcal/g provided by fallback fruits. Since the seasonal fruits were available for less than six months of the study duration, reliance on FBFs for energy was not unrealistic. Based on the work conducted by Ogango (2006) at the same time with the present study, mangabeys actually relied on domesticated fruits and crops. According to other studies (Amarteifio and Mosase, 2006; Maghembe *et al.*, 1994) domesticated fruits are rich in macro as well as micro-nutrients.

Generally, fibre, protein and fat content varied more greatly than gross energy between and within the tree fruit species, fruit parts and developmental stages of fruits commonly utilized as food by mangabeys inhabiting M&L forest reserves. This observation was also made by other studies (Ryan *et al.*, 2013; Houle *et al.*, 2007; Chapman *et al.*, 2003; Dearing and Cork, 1999). Results of the present study also indicated that FBFs generally had high fibre content and low protein content. As such, they were not nutritionally adequate for mangabeys. However, they had comparable sugar content with seasonal fruits which were not always available. Habitat alterations also affect fruit ripeness, size and nutritional content of fruit and seed (Khan *et al.*, 2005). Consequently, other factors come into play; for instance, fruit choice, quality, quantity, nutrient composition and location of fruit in the same tree (Houle *et al.*, 2014).

9.3 Dietary adaptations

In view of the declining food resources in Mabira and Lwamunda forest reserves, mangabeys have developed coping mechanisms to meet their dietary requirements from a resource-poor habitat. From the present study, at least three interlinked adaptations were

identified. They included, fruit processing or manipulation, avoidance of fruit parts with tannins above a particular threshold and reliance on fall-back fruits (FBFs). Other studies that were concurrently conducted with the present study (Ogango, 2006) identified crop-raiding as one of the strategic adaptations during food scarcity. Unfortunately, these identified dietary adaptations require expenditure of energy which mangabeys can ill afford in a resource-poor habitat and yet they have to strike a balance between starvation and survival. Although, dietary shifts are usually associated with nutritional trade-off as a strategy to increase energy or protein intake (Schaefer *et al.*, 2003), in the present study it was indicative of forest health.

Fruit manipulation or processing by mangabeys entails active discarding of fruit parts deemed undesirable prior to accessing those desirable fruit parts. This adaptative and selective strategy is intended to maximize the intake of protein and energy; avoid or regulate intake of secondary metabolites like tannins and limit the consumption of parts with high dietary fibre according to Felton *et al.*, (2009). However, in the severely degraded habitat like Lwamunda forest reserve, it was not always possible to abide by this prescribed feeding behaviour using macro-nutrient content as selection criteria. As a strategy to maximize food intake against a backdrop of low and erratic fruit resources, mangabeys employed different foraging methods. Generally, primates practice various forms of food processing that modifies the physical structure of food to increase intake rates and passage time as well as maximizing nutrient absorption (Hohmann, 2009). However, they have to overcome several adaptation obstacles by the plant prior to accessing vital nutrient foods. The deterrents may include hardened pericarps, thorns and size that may be too large for the intending frugivores (Leighton and Leighton, 1983).

When ripe fruit was in short supply, mangabeys processed unripe fruit. During the >18 months (or 76%) period of study that coincided with periods of food scarcity, mangabeys consumed endosperms of specific fruit tree species at different stages of development. They included *M. eminii*, *C. indicum*, *M. arboreus* and *P. microcapa* but *B. unijugata* was manipulated for its seed at earlier stages and aril when the fruit was ripe. However, this foraging behaviour was not observed in all habitats. It was more frequent in severely degraded Lwamunda, rarely in Mabira (M2) and absent in Mabira (M1). Accessing

endosperms is elaborate and requires more energy than accessing ripe pulp. Generally, acquisition of food items that supply adequate dietary requirements from a resource-poor habitat is time and energy consuming. So mangabeys engage in this kind of activity only when the food resources within the home range become a limiting factor. As such, the degree of fruit processing seemed to vary with fruit abundance but also with seasonality in M&L forests reserves. It appears therefore that food scarcity as a consequence of habitat degradation was a precursor of fruit processing behaviour among mangabeys inhabiting Lwamunda and regeneration portion of Mabira forest reserves. It also appears that other inter-related factors could have influenced fruit processing among mangabeys for example nutrient content of fruit/fruit as noted by other researchers (Worman and Chapman, 2005; Waser, 1977).

The second dietary adaptation strategy employed by mangabeys as a mitigation measure against food scarcity was the observed selectivity and preferences for specific fruit parts. Similar observations have been made by other authors (Bowler and Bodmer, 2011; Marshall and Wrangham, 2007; Glander, 1982). The avoidance of certain fruit parts by mangabeys observed during fruit processing was intended to minimize the ingestion of fruits with tannin levels above the threshold (2.6g/100g). On several ocassions, however it was observed that during periods of food scarcity in Lwamunda and Mabira-M2, mangabeys often climbed down to the forest floor and foraged among herbaceous plants known to have high levels of antfeedants including tannins. It was not therefore entirely true that mangabeys avoided tannin-laden foods but they traded-off with other nutrient components like proteins (Sorensen *et al.*, 2005). According to Nabihamba (1996) detoxifying of tannins is an energy consuming activity which may subsequently contribute to the poor body condition of the respective primate.

The third dietary adaptation starategy was the consumption nutrient deficient fall-back fruits (FBFs) because they contained high levels of tannins and low protein content. FBFs therefore are nutritionally poor and symbolized energy imbalance in the mangabey diet (Ehlers-Smith *et al.*, 2013). During periods of food scarcity, mangabeys consumed fall-back fruits because they were available for most of the study period as coroborated with other studies (Marshall and Wrangham, 2007; Lambert *et al.*, 2004). Coincidentally,

during periods of fruit scarcity, the preferred fruits with relatively high levels of protein, sugars and fat were conspicously absent from the three study sites. For some undocumented reason, the tannin content of most FBFs pulps was close to the threshold of 2.6g/100g catechin equivalent. In such circumstances, it appears mangabeys engaged in trade-off mechanism to meet their daily dietary requirements. According to Schaefer *et al.*, (2003) trade-off mechanisms entailed ingesting one bout of endosperms with high protein content and small amounts fruit pulp with relatively high tannin levels. This type of foraging behaviour was also observed in other frugivores (Norconk and Conklin-Brittain, 2004) where White-Faced Sakis (*Pithecia pithecia*) accepted a trade-off for food items that were fibrous or astringent if they were also rich in lipids. It is also probable that mangabeys have some adaptations for reducing the effects of tannins on protein digestibility (Kendrick *et al.*, 2009) which are yet to be studied in detail.

Based on phenological studies (Chapter 4), one or two of these FBFs were available at any one time. These were mainly figs (*F. sur* and *F. mucuso*). Even when they were available, only a few individual trees were in fruit at any one time. Hence, they could not have possibly sustained mangabeys especially in Lwamunda during the study period. It is therefore probable that mangabeys supplemented their daily dietary requirements with another food source. Ogango (2006) who was concurrently studying crop-raiding phenomenon among mangabeys in Lwamunda forest reserve and later on Fungo *et al.*,(2013) in Mabira forest confirm the speculation that the alternative food source which was domesticated crops like maize, sweet potato, bananas and fruits.

9.4 Impacts of anthropogenic activities on Mangabey nutritional ecology

Habitat alteration attributed to anthropogenic activities (Onderdonk and Chapman, 2000) which include encroachment for agricultural purposes, logging for timber and other forestry products. These activities essentially create gaps in the habitat and breakage of tree canopy which impact on foraging behaviour as well as ranging patterns of mangabeys. At a micro level, these habitat alterations impact negatively on the nutritional ecology of mangabeys with regard to food quantity, availability and quality. Other studies have observed similar scenarios. For example Olupot (1999) reported that habitat degradation had direct impacts on the nutritional ecology of mangabeys in Kibale

National Park forest reserve.

The gaps of different sizes were created in Mabira (M2) and Lwamunda, had disastrous consequences on Mangabey mobility and nutrition. They reduced food diversity and quantity for mangabeys hence the adoption of fruit processing as a coping mechanism. Wide gaps between fruit trees created discontinuity of the canopy which implied that the arboreal mangabeys had to climb down before climbing up another tree. The act of climbing down onto the forest floor increased travel costs for the arboreal mangabeys (Olupot, *et al.*, 1997) and undoubtedly increased their risk of predation or death by human primates. A decline in food availability leads to extension of home range and increases travel costs (Olupot, 1999; Freeland, 1979). Loss of continuous tree canopies as observed in the severely degraded Lwamunda forest reserve affected the mobility and foraging patterns of mangabeys. This may have contributed to the merger of two groups of mangabeys observed at the beginning of the study. Subsequently, their home ranges overlapped and enlarged which may have increased their energy budgets as they foraged for food. These activities were time consuming and subjected mangabeys to stiff competition for meagre fruit resources. Nevertheless primates must strike a balance between meeting dietary requirements and predator avoidance (Chapman *et al.*, 2012).

About 40 years ago, Waser (1975) listed priority fruits in the diet of mangabeys inhabiting Central Uganda and Lwamunda forest reserves. The list seemed to have changed as highlighted in Chapter 4 of this thesis. The reduction in biodiversity and change in the list of priority fruits and feeding habits can only be attributed to several factors. From observations made during this study, the most obvious contributory factor to reduced biodiversity was habitat disturbance caused by increased anthropogenic pressure. Indeed, in 1969, the population of Uganda was about 9.535 million with a population density of 40 persons/ Km^2 (Lwasa, 2007). By 2014, it had increased to about 35 million with a population density of 152 individuals /Km^2 (UBOS, 2014). With a population annual growth rate of 3.24 and birth rate of 44.17 births for every 1000 individuals (UBOS, 2014), the 2014 population has almost quadrupled the 1969 population. This population increase has greatly contributed to habitat loss for mangabeys and other forest fauna. The other factor that may have contribute to the change in

Mangabey priority fruit list, could have been climatic variability that may have caused tree mortality associated with climate-induced physiological stress (Allen *et al.*, 2010), changes in fruiting patterns (Chapman *et al.*, 2005), and spatiotemporal variation in forest structure (Chapman *et al.*, 1997).

Apart from gap creation due to incessant logging and opening up of forests for agricultural purposes, there are other inter-related myriad of factors that influence fruit availability. The results of the present study identified some of them which included seasonality, fruiting cycles of individual fruit trees, their location in the forest reserve, and competition with other frugivores. Other studies have cited additional factors which may affect fruit availability and abundance. They include, soil fertility (Martin, 1991; Chapin *et al.*, 1986), location of fruit within the tree canopy (Houle *et al.*, 2007) and micro-environments (Wright, 2005; Wright and van Schaik, 1994). In the absence of anthropogenic disturbances as observed in M1, mangabeys experience a wider and potentially more consistent food resource base than their counterparts in Lwamunda forests with inconsistent food resources which probably contributed to fruit scarcity and subsequent initiation of fruit processing.

In the present study, the overarching criterion for diet selection was fruit quality. As the level of habitat disturbance increased, fruit quality declined. The interlinked factors; seasonality, number and sizes of gaps, inter and intra competitions ultimately affect diet composition, food consumption rates, activity time budgets and travel patterns and travel costs (Kaplin *et al.*, 1998; Poulsen *et al.*, 2001). Essentially, consumption of low quality foods, high travel costs and aggressive competition for meagre food resources impinges on the nutritional status of primates. This has a bearing on their reproduction and ultimately on their population densities (Olupot, 1999). Knowledge of the correlation between activity budget and travel patterns provides an insight into habitat use.

9.5 Potential guidelines for policy formulation to conserve mangabeys

There were several policy guidelines identified in this study that could be formulated into viable policies. Knowledge of priority fruits commonly utilized by mangabeys, fall back and seasonal fruits is a viable tool for formulation of a policy that regulates felling of trees like *B. unijugata*, *M. arboreus*, *Celtis* spp, *P. microcapa* and *R. edulis* in M&L

forest reserves. Considering that food for mangabeys was more abundant during the two months after a wet season than during the dry spells, prohibition of trees felling should be strictly enforced during the two- months- window period to ensure sustainability of the species. Similarly, felling of fall-back tree species like figs, *C. indicum* and *M. eminii* should be prohibited during the dry spells because they contribute to the Mangabey diet during periods of food scarcity. Thereafter, should there be dire need for forestry products that necessitates felling of trees; selective logging should be practiced. Knowledge of seasonality, availability and quality of food for the mangabeys can also form another policy guideline on the type of crops that can be grown by subsistence farmers at the forest interface. Hockings and Humle (2009) suggested growing of unpalatable crops like chilli, sisal and tea. Alternatively, the growing of early maturing agricultural crops like beans should be synchronized with high availability of wild preferred fruits like *B. unijugata, R. edulis*, *M. arboreus* and *P. microcapa*. This may require close collaboration between subsistence farmers at the interface, agricultural staff, forest rangers and academicians or a copy of this thesis. According to Lee and Priston (2005) collaboration of major stakeholders is the basis for solving conflicts between human communities and non-human primates.

Knowledge of gap sizes in the three study sites is another clear policy guideline. About fifteen years ago, Banana and Gombya-Ssembajjwe (2000) alluded to the fact that the open-access policy and inability to enforce ideal management practices in Lwamunda forest reserve, could lead to a local fuelwood shortage, substantial forest degradation and loss of useful biotic resources. Ever since that proclamation was made, the status quo has not changed and by 2014, most of Lwamunda forest had been transformed into farmland. However, the status quo can be reversed by re-planting of the preferred fruit tree species highlighted above. The replanting programme can be extended to M2 regenerating Mabira forest reserve. This concept is not entirely new in Uganda and specifically in M&L forest reserves because the 1980 Man and Biosphere program under UNESCO (Alpert, 1996) proposed and implemented a similar management strategy and it had relatively positive results that have caused the regeneration of Mabira (M2) forest reserve. In western Uganda, a similar exercise was conducted in a portion of Kibale

National Park which had also been severely degraded in the 1970s. Omeja *et al.* (2011) reported that it was replanted in 1995 with five native tree species and by 2010, 39 tree species had naturally regenerated in the restored area in addition to the five originally planted species. This implies that intensive replanting is a plausible option for restoration of previously degraded protected forests provided the people living within the proximity own the restoration process. Failure to develop workable strategies and policies that will ensure conservation of the forests, may result in the extinction of the Mangabey species within the M&L forest reserves.

9.6 Potential conservation strategies for mangabeys in M&L forests

Comprehension of the nutritional ecology of mangabeys is a vital tool for the development of conservation strategies. Johns and Skorupa (1987) predicted that by 2010, most of the world's rain forests would be reduced to logged or otherwise disturbed patches and that the ability of primates to survive in such areas would form a basis for formulating conservation strategies. As predicted, all forests within LVB have been reduced to patches, it is imperative that viable strategies are developed and implemented to conserve their degraded habitat. The information on Mangabey coping mechanisms and threats to their survival can provide a basis for the proposed conservation strategy. This will not only guarantee a balanced diet of high quality food resources for mangabeys but it will also spare them from imminent extinction (Isabirye-Basuta and Lwanga, 2007). Knowledge of adaptive mechanisms used by mangabeys to nutritionally survive in a degraded habitat provides valuable insight into the formulation process of conservation strategies for both primates and forests (Onderdonk and Chapman, 2000).

Factors that influence food availability for mangabeys also form a basis for development of an effective management strategy. In Kibale National Park where similar studies were conducted (Onderdonk and Chapman, 2000; Olupot, 1999; Olupot *et al.*, 1997; Waser, 1977) and critical data generated, conservation effort has borne fruit. It is envisaged that with this information, similar strategies can be put in place for the long-term management and conservation effort of M&L forests and their fauna including mangabeys. With incessant loss of habitat due to anthropogenic pressure and absence of feasible management strategies, the future of mangabeys in Mabira and Lwamunda forest reserves

appears to be bleak unless NFA in collaboration with other government agencies come up with an action plan that will bar anthropogenetic activities in the remaining forest fragments. In Lwamunda forest reserve where enchroachment by human communities inhabiting the interface has continued unbated, the absence of such a strategy will lead to widespread conflicts between humans and non-human primates. Conflicts between forest fauna and humans inhabiting at the interface have been reported over time (Lee and Priston, 2005; Hill, 2000). They normally revolve around crop raiding and unless the conflicts are amicably resolved, the incidences of crop raiding are bound to increase. This will undermine the food and nutritional security of the already impoverished subsistence farmers.

Appropriate management strategies that take into account the concerns of human communities living at the forest interface. For example, if they can be encouraged to co-manage the forest resources, it is possible for Lwamunda forest reserve to recover from the current obliterated state to a regenerated form in the long-term. Alternatively, a plan for selective logging as opposed to total prohibition of forest encroachment should be instituted as strategy to conserve mangabeys and other forest fauna and flora in the Mabira and Lwamunda for the foreseeable future. Considering that degradation in Lwamunda has continued unabated for the last two decades, an effective management strategy that balances the nutritional requirements of mangabeys and concerns of the people in the adjacent villages, can lead to recovery of the forest reserve. This will not only provide a habitat for mangabeys and other forest fauna but it will also undoubtedly improve the livelihoods of human communities within proximity of the forest reserve. However, as long as human population continue to increase incessantly, forest reserves will continue to be exploited for agricultural land, timber, firewood and other forestry products.

The invisaged policies and strategies for conservation of M&L forest reserves should factor-in the concerns and aspirations of the communities living at the interface of these forest reserves for ownership. By so doing, the rate of habitat loss will be slowed down and undoubtedly, the Mangabey population will recover from current threatened status. Skorupa (1986) recommended a similar long-term conservation plan for the 7 primate

species in Kibale National Park forest reserve. About three decades down the road, the plan seems to have worked and the seven species are thriving. Factors that influence fruit choice and the relationship between habitat degradation and food/fruit availability provide sufficient information for designating borderlines between forest fauna and humans. A successful and comprehensive conservation strategy will benefit both the human at the habitat interface and non-human primate populations. This will reduce the incidences of conflicts between the two sets of primates. In this regard, human communities at the interface should be sensitized on the importance of mangabeys and other forest fauna in forest regeneration process to ease implementation of conservation strategies.

Another viable option for Mangabey conservation plan may be eco-tourism or formation of parks; whereby designated areas within Mabira and Lwamunda reserves are demarcated with touristic trails to allow viewing of forest ecosystems without wanton damage. This is not a farfetched proposition because other 12 protected areas have already been gazetted as tourist areas (Musinguzi *et al.*, 2014) and being used as source of revenue. The construction of eco-tourism trails was also proposed by Kroeker-Maus (2014) using metageography of enclavisation approach to benefit both human and non-human primates. The formation of parks was also suggested by Hartter *et al.* (2010). While working in Albertine Rift forests, Bush (2009) suggested another approach which can be tested in M&L. This integrated approach ensures conservation of mangabeys and at the same time ensures poverty alleviation among the poor households adjacent to forest reserves. In addition, it will improve the biodiversity of fauna and flora that will attract and boost eco-tourism trade. Community participation in the conservation and development programmes is an effective way of law enforcement and protection of natural resources. Being a "new" species (Groves, 2007) in Uganda, conservation of *L. ugandae* would enhance the biodiversity in these highly fragmented and degraded LVB forests. With political instability in the Democratic Republic of Congo and South Sudan where several species of primates are regularly hunted as protein source for human consumption, the envisaged conservation strategies would protect mangabeys from cross-border trade in bush meat (Bowen-Jones and Pendry (1999).

9.7 References

Alpert, P. (1996). Integrated conservation and developmental projects. Examples from Africa. *BioScience*, **46** (11), 845-855.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzbergerg, T., Riglingh, A., Breshearsi, D., Hoggj, D.E.H. (Ted), Gonzalezk P., Fenshaml, R., Zhangm, Z., Castron, J., Demidovao, N., Jong-Hwan, L., Allardq, G., Runningr, SW., Semercis, A. & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**(4), 660-684.

Amarteifio, J.O. & Mosase, M.O. (2006). The chemical composition of selected indigenous fruits of Botswana. *Journal of Applied Sciences and Environmental Management*, **10**(2), 43-47.

Balasundram, N., Sundram, K. & Samman, S. (2006). Phenolic compounds in plants and agri-industrial by-products: Antioxidant activity, occurrence, and potential uses. *Food chemistry*, **99**(1), 191-203.

Banana, A.Y. & Gombya-Ssembajjwe, W. (2000). Successful Forest Management: The importance of security of tenure and rule enforcement in Ugandan forests. In Gibson, C.C., McKean, M.A., Ostrom, E. (Eds), People and Forests: Communities, Institutions, and Governance, 1 Review (pp 87-97). MIT Press, Science.

Baranga, D. (1983). Changes in chemical composition of food parts in the diet of colobus monkeys. *Ecology*, **64** (4), 668-673

Bawa, K.S. and Webb, C.J. (1984). Flower, fruit and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. *American journal of botany*, **71** (5), 736-751.

Becker, C.D. & Ostrom, E. (1995). Human ecology and resources sustainability: The importance of institutional diversity. *Annual Review of Ecology and Systematics*, **26**(1995): 113-133.

Bos, M.M., Steffan-Dewenter, I. & Tscharntke, T. (2007). Shade tree management affects fruit abortion, insect pests and pathogens of cacao. *Agriculture, ecosystems and environment*, **120**(2), 201-205.

Bowen-Jones, E. and Pendry, S. (1999). The threat to primates and other mammals from the bush meat trade in Africa, and how this threat could be diminished 1. *Oryx*, **33**(3), 233-246.

Bowler, M. & Bodmer, R.E. (2011). Diet and food choice in Peruvian red uakaris (Cacajao calvus ucayalii): selective or opportunistic seed predation? *International Journal of Primatology*, **32**(5), 1109-1122.

Boyle, R., McLean, S., Foley, W.J., Moore, B.D., Davies, N.W. & Brandon, S. (2000). Fate of the dietary terpene, p-cymene, in the male koala. *Journal of Chemical Ecology*, **26**(5), 1095-1111.

Bravo, S.P. (2008), Seed Dispersal and Ingestion of Insect-Infested Seeds by Black Howler Monkeys in Flooded Forests of the Parana River, Argentina. *Biotropica*, **40**(4), 471-476. Doi: 10.1111/j.1744-7429.2008.00400.x

Bush, G. K. (2009). The economic value of Albertine Rift Forests; applications in policy and programming.

Buzzard, P. J. (2006). Ecological partitioning of Cercopithecus campbelli, C. petaurista, and C. diana in the Tai Forest. *International Journal of Primatology*, **27**(2), 529-558.

Causse, M., Saliba-Colombani, V., Lecomte, L., Duffe, P., Rousselle, P. & Buret, M. (2002). QTL analysis of fruit quality in fresh market tomato: a few chromosome regions control the variation of sensory and instrumental traits. *Journal of experimental botany*, **53**(377), 2089-2098.

Chapin III, F.S., Vitousek, P.M. & Van Cleve, K. (1986). The nature of nutrient limitation in plant communities. *American naturalist*, **127**(1), 48-58.

Chapman, C.A., Rothman, J.M. & Lambert, J.E. (2012). P RIMATES MUST EAT to survive; the acquisition of food resources is thus among one of the most significant se. *The Evolution of Primate Societies*. Edited by John C. Mitani, Josep Call, Peter M. Kappeler, Ryne A. Palombit, and Joan B. Silk. *Chapter* 7, 149-162.

Chapman, C.A., Chapman, L.J., Struhsaker, T.T., Zanne, A.E., Clark, C.J. & Poulsen, J.R. (2005). A long-term evaluation of fruiting phenology: importance of climate change. *Journal of Tropical ecology*, **21**(1), 31-45.

Chapman, C.A., Chapman, L.J., Rode, K.D., Hauck, E.M. & McDowell, L.R. (2003). Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal of Primatology*, **24**(2), 317-333.

Chapman, C. A., Wrangham, R. W., Chapman, L. J., Kennard, D. K., & Zanne, A. E. (1999). Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*, **15**(02), 189-211.

Chapman, C.A., Chapman, L.J., Wrangham, R., Isabirye-Basuta, G. & Ben-David, K. (1997). Spatial and temporal variability in the structure of a tropical forest. *African Journal of Ecology*, **35**(4), 287-302.

Chivers, D.J. & Raemaekers, J.I. (1986). Natural and synthetic diets of Malayan gibbons. In Else, J.G. (Ed). *Primate ecology and conservation*. Selected Proceedings of the 10th Congress of the International Primatological society held in Nairobi, Kenya. July 1984.

Cipollini, M.L. & Stiles, E.W. (1992). Antifungal activity of ripe ericaceous fruits: Phenoliz-acid interactions and palatability for dispersers. *Biochemical Systematics and Ecology*, **20**(6), 501-514.

Coley, P.D. (1986). Costs and benefits of defence by tannins in a neotropical tree. *Oecologia*, **70**(2), 238-241.

Conklin-Brittain, N.L., Wrangham, R.W. & Smith, C.C. (2002). A two-stage model of increased dietary quality in early hominid evolution: the role of fiber. In Unger, P. and Teaford, M. (Eds). *Human Diet: Its Origin and Evolution* (pp. 61-76). Bergin & Garvey, Westport.

Conklin-Brittain, N.L., Wrangham, R.W. & Hunt, K.D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *International Journal of Primatology*, **19**(6), 971-998.

Dai, J & Mumper, R. J. (2010). Plant phenolics: extraction, analysis and their antioxidant and anticancer properties. *Molecules*, **15**(10), 7313-7352.

Dearing, M.D., Foley, W.J. & McLean, S. (2005). The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annual review of ecology, evolution, and systematics*, **36**(1), 169-189.

Dearing, M.D., Mangione, A.M. & Karasov, W.H. (2001). Plant secondary compounds as diuretics: an overlooked consequence. *American Zoologist*, **41**(4), 890-901.

Dearing, M.D. & Cork, S. (1999). Role of detoxification of plant secondary compounds on diet breadth in a mammalian herbivore, Trichosurus vulpecula. *Journal of Chemical Ecology*, **25**(6), 1205-1219.

Dominy, N.J., Lucas, P.W., Osorio, D. & Yamashita, N. (2001). The sensory ecology of primate food perception. *Evolutionary Anthropology*, **10**(5), 171–186.

Ehlers Smith, D.A., Husson, S.J., Ehlers Smith, Y.C. & Harrison, M.E. (2013). Feeding ecology of red langurs in Sabangau tropical peat-swamp forest, Indonesian Borneo: extreme granivory in a non-masting forest. *American Journal of primatology*, **75**(8), 848-859.

Felton, A.M., Felton, A., Raubenheimer, D., Simpson, S.J., Foley, W.J., Wood, J.T. & Lindenmayer, D.B. (2009). Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioral Ecology*, **20**(4), 685-690.

Fietz, J. & Ganzhorn, J.U. (1999). Feeding ecology of the hibernating primate Cheirogaleus medius: how does it get so fat?. *Oecologia*, **121**(2), 157-164.

Freeland, W.J. (1979). Mangabey (*Cercocebus albigena*) social organization and population density in relation to food use and availability. *Folia primatologica,* **32**(-2), 108-124

Fungo, B., Eilu, G., Tweheyo, M. & Baranga, D. (2013). Forest disturbance and cropping mixtures influence crop raiding by red-tailed monkey and grey-cheeked mangabey around Mabira Forest Reserve, Uganda. *Journal of Ecology and the Natural Environment*, **5**(2), 14-23. doi: 10.5897/JENE11.028

Garber, P.A. (1987). Foraging strategies among living primates. *Annual review of Anthropology*, **16**(1), 339-364.

Gargiullo MB & Stiles EW (1993). Development of secondary metabolites in the fruit pulp of Ilex opaca and Ilex verticillata. *Bulletin of the Torrey Botanical Club*. pp 423-430.

Gaulin, S.J. & Gaulin, C.K. (1982). Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. *International Journal of Primatology*, **3**(1), 1-32.

Gautier-Hion, A., Duplantier, J.M., Quris, R., Feer, F., Sourd, C., Decoux, J.P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J.M. (1985). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia*, **65**(3), 324-337.

Glander, K.E. (1982). The impact of plant secondary compounds on primate feeding behaviour. *American Journal of Physical Anthropology*, **25**(3), 1–18. doi: 10.1002/ajpa.1330250503

Groves, C. P. (2007). The endemic Uganda mangabey, *Lophocebus ugandae*, and other members of the albigena-group (*Lophocebus*). *Primate Conservation*, **22**(1), 123-128.

Ham, R.M. (1994). *Behaviour and ecology of grey-cheeked mangabeys (Cercocebus albigena) in the Lope Reserve, Gabon*. eTheses from School of Natural Sciences legacy departments, University of Stirling.

Harborne, J.B. (2001). Twenty-five years of chemical ecology. *Natural product reports*, **18**(4), 361-379.

Herrera, C.M. (1982). Defence of ripe fruit from pests: its significance in relation to plant-disperser interactions. *American Naturalist*, **120** (2), 218-241.

Hernandez, A. (2011). Internal dispersal of seed-inhabiting insects by vertebrate frugivores: a review and prospects. *Integrative zoology*, **6**(3), 213-221.

Hill, C. M. (2000). Conflict of interest between people and baboons: crop raiding in Uganda. *International journal of primatology*, **21**(2), 299-315.

Hladik, C.M., Pasquet, P. and Simmen, B. (2002). New perspectives on taste and primate evolution: the dichotomy in gustatory coding for perception of beneficent versus noxious substances as supported by correlations among human thresholds. *American Journal of Physical Anthropology*, **117**(4), 342-348.

Hockings, K., & Humle, T. (2009). Best practice guidelines for the prevention and mitigation of conflict between humans and great apes (No. 37). IUCN.

Hohmann, G. (2009). The diets of Non-human Primates: Frugivory, food manipulation and food sharing. In Hublin, J-J. and Richards, M.P. (Eds), *The Evolution of*

Hominin Diets: Integrating Approaches to the study of Palaeolithic subsistence (pp. 1-14). Springer Science and Business media B. V.

Houle, A., Conklin-Brittain, N.L. & Wrangham, R.W. (2014). Vertical stratification of the nutritional value of fruit: Macronutrients and condensed tannins. *American journal of primatology*, **76**(12), 1207-1232.

Houle, A., Chapman, C.A. & Vickery, W.L. (2010). Intratree vertical variation of fruit density and the nature of contest competition in frugivores. Behavioral Ecology and Sociobiology, **64**(3), 429-441. DOI 10.1007/s00265-009-0859-6

Houle, A., Chapman, C.A. & Vickery, W.L. (2007). Intratree variation in fruit production and implication for primate foraging. *International Journal of Primatology*, **28**(6), 1197-1271.

Howe, H.F. & Kerckhove, G.A.V. (1981). Removal of wild nutmeg (Virola surinamensis) crops by birds. *Ecology*, **62**(4),1093-1106.

Ibarra-Manriquez, G. & Oyama, K. (1992). Ecological correlates of reproductive traits of Mexican rain forest trees. *American Journal of Botany*, **79** (4), 383-394.

Isabirye-Basuta, G.M. & Lwanga, J.S. (2008). Primate populations and their interactions with changing habitats. *International Journal of Primatology*, **29**(1), 35-48.

Izhaki, I. (1992). A comparative analysis of the nutritional quality of mixed and exclusive fruit diets for Yellow-vented Bulbuls. *Condor*, 912-923.

Jakubas, W.J., Karasov, W.H. & Guglielmo, C.G. (1993). Ruffed grouse tolerance and biotransformation of the plant secondary metabolite coniferyl benzoate. *Condor*, **95**(3), 625-640.

Janson, C.H. & Chapman, C.A. (1999). Resources and primate community structure. In Fleagle, J.G., Janson, C.H. and Reed, K.E. (Eds), *Primate communities* (pp. 237-267). Cambridge University Press, Cambridge.

John, A.D. & Skorupa, J.P. (1987). Responses of rain forest primates to habitat disturbance: A Review. *International Journal of Primatology*, **8**(2), 157-191.

Jones, F.A. & Comita, L.S. (2008). Neighbourhood density and genetic relatedness interact to determine fruit set and abortion rates in a continuous tropical tree

population. *Proceedings of the Royal Society of London B: Biological Sciences*, **275**(1652), 2759-2767.

Jordano, P. (2000). Fruits and frugivory. In Fenner, M. (Ed), *Seeds: the ecology of regeneration in plant communities,* 2 Edition (Pp. 125-166). CABI Publishers, Wallingford, UK.

Kasenene, J.M. (1987). *The influence of mechanized selective logging, felling intensity and gap-size on the regeneration of a tropical moist forest in the Kibale Forest Reserve, Uganda.* Doctoral dissertation, Department of Botany and Plant Pathology, Michigan State University.

Kaplin, B.A., Munyaligoga, V. & Moermond, T.C. (1998). The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*), *Biotropica*, **30**(1), 56-71

Kendrick, E.L., Shipley, L.A., Hagerman, A.E. & Kelley, L.M. (2009), Fruit and fibre: the nutritional value of figs for a small tropical ruminant, the blue duiker (Cephalophus monticola). *African Journal of Ecology*, **47**(4), 556–566. doi: 10.1111/j.1365-2028.2008.00985.x

Khan, M.L., Bhuyan, P. & Tripathi, R.S. (2005). Effects of forest disturbance on fruit set, seed dispersal and predation of Rudraksh (*Elaeocarpus ganitrus* Roxb.) in northeast India. *Current Science*, **88**(1), 133-142.

Kimuyu, D.M., Wahungu, G.M. & Otieno, D.O. (2012). Seed dispersal by Tana River mangabeys in fragmented gallery forests. *Open Journal of Ecology* **2**(1), 12-20

Kinzey, W.G. & Norconk, M.A. (1990). Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology*, **81**(1), 5–15.

Kraus, T.E., Dahlgren, R.A. & Zasoski, R.J. (2003). Tannins in nutrient dynamics of forest ecosystems-a review. *Plant and Soil*, **256**(1), 41-66.

Kroeker-Maus, D. (2014). The Protected Area as Enclave: Towards New Geographies of Tourism and Conservation. *Geography Compass*, **8**(11), 796-807.

Lambert, J.E. (2013). Evolutionary Biology of Ape and Monkey Feeding and Nutrition. Handbook of Paleoanthropology. pp 1-27

Lambert, J.E. (2005), Competition, predation, and the evolutionary significance of the cercopithecine cheek pouch: The case of *Cercopithecus* and *Lophocebus*. *American Journal of Physical Anthropology*, **126**(2), 183-192. doi: 10.1002/ajpa.10440

Lambert, J. E., Chapman, C. A., Wrangham, R. W., & Conklin-Brittain, N. L. (2004). Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology*, **125**(4), 363-368.

Lambert, J.E. & Garber, P.A. (1998). Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology*, **45**(1), 9-28.

Lawler, I. R., Eschler, M., Schliebs, D. M., & Foley, W. J. (1999). Relationship between chemical functional groups on Eucalyptus secondary metabolites and their effectiveness as marsupial antifeedants. *Journal of Chemical Ecology*, **25**(11), 2561-2573.

Lee, P.C. & Priston, N.E.C. (2005). Human Attitudes to Primates: Perceptions of Pests, Conflict and Consequences for Conservation. In Paterson, J.D. and Wallis, J. (Eds). *Commensalism and Conflict: The Primate-Human Interface* (pp. 1-23). American Society of Primatologist.

Leighton, M. & Leighton D.R. (1983). Vertebrate responses to fruiting seasonality within Bormean rainforest. *British Ecological Society,* **2**(1983), 181-196.

Levey, D. J & Cipollini, M. L. (1998). A glycoalkaloid in ripe fruit deters consumption by Cedar Waxwings. *The Auk*, 359-367.

Levey, D.J. (1988). Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology*, **69** (4), 1076-1089.

Lwasa, S. (2007). Population, urban development and the environment in Uganda: the case of Kampala city and its environs. Pg 5

Mack, A. L. (2000). Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism?. *Journal of Biosciences*, **25**(1), 93-97.

Maghembe, J.A., Kwesiga, F., Ngulube, M., Prins, H. & Malaya, F.M. (1994). Domestication potential of indigenous fruit trees of the miombo woodlands of southern Africa. In Leakey, R.R.B. and Newton, A.C. (Eds), *Tropical trees:*

Potential for domestication and rebuilding of forest resources (pp. 220-229). HMSO, London, UK.

Martin, C. (1991). Ecological Niches in Undisturbed and Disturbed Forest. In *The Rainforests of West Africa.* Birkhäuser Basel. (pp. 110-133).

Marshall, A.J. & Wrangham, R.W. (2007). Evolutionary Consequences of Fallback Foods. *International Journal of Primatology*, **28**(6), 1219-1235

Matsumoto-Oda, A. & Hayashi, Y. (1999). Nutritional aspects of fruit choice by chimpanzees. *Folia Primatology,* **70**(3), 154-162.

McCabe, G.M., Fernández, D. & Ehardt, C.L. (2013), Ecology of reproduction in Sanje mangabeys (*Cercocebus sanjei*): Dietary strategies and energetic condition during a high fruit period. *American Journal of Primatology*, **75**(12), 1196–1208. doi: 10.1002/ajp.22182

McCabe, G.M. (2012). *Reproductive ecology of the Sanje mangabey in the Udzungwa Mountains, Tanzania.* PhD Dissertation, The University of Texas at San Antonio.

Milton, K. (2004). Ferment in the family tree: Does a frugivorous dietary heritage influence contemporary patterns of human ethanol use?. *Integrative and Comparative Biology*, **44**(4), 304-314.

Milton, K. (1984). The role of food-processing factors in primate food choice. In Rodman, P. and Cant, J. (Eds), *Adaptations for foraging in nonhuman primates*, (pp 249-279). Columbia University Press, New York.

Milton, K., van Soest, P.J. & Robertson, J.B. (1980) Digestive efficiencies of wild howler monkeys. *Physiological Zoology*, **53**(4), 402–409.

Milton, K. (1979) Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *American Naturalist*, **114**(3), 363-378.

Moscovice, L. R., Issa, M. H., Petrzelkova, K. J., Keuler, N. S., Snowdon, C. T., & Huffman, M. A. (2007). Fruit availability, chimpanzee diet, and grouping patterns on Rubondo Island, Tanzania. *American Journal of Primatology*, **69**(5), 487-502.

Musinguzi, D., Tukamushaba, E. K., Katongole, C., & Obua, J. (2014). 19 Rainforest primate tourism in Uganda. *Rainforest Tourism, Conservation and Management: Challenges for Sustainable Development*, 275.

Nabihamba, E. (1996). Factors determining dietary choices among arboreal frugivores in Kibale forest in Western Uganda. Msc Thesis, Makerere University, Kampala.

Norconk, M.A. & Conklin-Brittain, N.L. (2004). Variation on frugivory: The diet of Venezuelan white-faced sakis. *International Journal of Primatology*, **25**(1), 1-26.

Obua, J. & Agea, J.G. (2010). Forests and Forestry in Uganda. *Degraded forests in Eastern Africa: management and restoration. F. Bongers and T. Tennigkeit. London, Earthscan Ltd*, 65-88.

O'Driscoll, W.C. & Chapman, C.A. (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. Journal of tropical ecology, **21**(06): 689-697.

Oftedal, O.T., Whiten, A., Southgate, D.A.T. & Van Soest, P. (1991). The Nutritional Consequences of Foraging in Primates: The Relationship of Nutrient Intakes to Nutrient Requirements and Discussion. Philosophical Transactions of the Royal Society B: *Biological Sciences*, **334**(1270), 161-170. DOI: 10.1098/rstb.1991.0105

Ogango, A. (2006). *Crop raiding by mangabeys in Lwamunda forest reserve, Uganda*. A Research Project Submitted to the Zoology Department in Partial Fulfilment of the Requirements for a Degree in Bachelor of Science, Makerere University.

Okecha, A.A. & Newton-Fisher, N.E. (2006). The diet of olive baboons (*Papio* anubis) in the Budongo Forest Reserve, Uganda. In Newton-Fisher, N.E., Notman, H., Peterson, J.D. and Reynolds, V. (Eds), *Primates of Western Uganda* (pp. 61-73). Springer, New York.

Okullo, J. B. L., Hall, J. B., & Obua, J. (2004). Leafing, flowering and fruiting of Vitellaria paradoxa subsp. nilotica in savanna parklands in Uganda. *Agroforestry Systems*, **60**(1), 77-91.

Olupot, W. (1999). *Mangabey dispersal and conservation in Kibale National Park, Uganda.* PhD Thesis, Purdue University.

Olupot, W., Waser, P.M. & Chapman, C.A. (1998). Fruit finding by mangabeys (*Lophocebus albigena*): Are monitoring of fig trees and use of sympatric frugivore calls possible strategies? *International Journal of Primatology*, **19**(2), 339-353.

Olupot, W., Chapman, C. A., Waser, P. M., & Isabirye–Basuta, G. (1997). AJP 332. *American Journal of Primatology*, 43, 65-78.

Omeja, P.A., Chapman, C.A., Obua, J., Lwanga, J.S., Jacob, A.L., Wanyama, F. & Mugenyi, R. (2011). Intensive tree planting facilitates tropical forest biodiversity and biomass accumulation in Kibale National Park, Uganda. *Forest Ecology and Management*, **261**(3), 703-709.

Onderdonk, D.A. & Chapman, C.A. (2000). Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *International Journal of Primatology*, **21**(4), 587-611.

Owens, J.N. (1995). Constraints to seed production: temperate and tropical forest trees. *Tree Physiology*, **15**(7-8), 477-484.

Petre, C., Tagg, N., Haurez, B., Beudels-Jamar, R., Huynen, M.C. & Doucet, J.L. (2013). Role of the western lowland gorilla (*Gorilla gorilla gorilla*) in seed dispersal in tropical forests and implications of its decline. *Biotechnology, Agronomy, Society and Environment,* **17**(3), 517-526.

Pienkowski, M. W., Watkinson, A. R., Kerby, G., Naughton-Treves, L. I. S. A., Treves, A., Chapman, C., & Wrangham, R. (1998). Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, **35**(4), 596-606.

Potts, K.B. & Lwanga, J.S. (2014), Floristic heterogeneity at Ngogo, Kibale National Park, Uganda and possible implications for habitat use by chimpanzees (*Pan troglodytes*). *African Journal of Ecology*, **52**(4), 427–437. doi: 10.1111/aje.12137

Potter N.N. & J.H. Hotchkiss (1995). Constituents of Foods: Properties and significance. In Food Science 5th Edition. pp. 30. Published by Chapman and Hall

Poulsen, F.E., Clark, C.J. & Smith, T.B. (2001). Seasonal variation in the feeding ecology of the grey-cheeked Mangabey (*Lophocebus albigena*) in Cameroon. *American Journal of Primatology*, **54**(2), 91-105.

Prescott, M. (2006). Primate sensory capabilities and communication signals: implications for care and use in the laboratory. National Centre for the Replacement, Refinement and Reduction of Animals in Research. (pp. 1-6).

Pulido, F., García, E., Obrador, J.J. & Moreno, G. (2010), Multiple pathways for tree regeneration in anthropogenic savannas: incorporating biotic and abiotic drivers into management schemes. *Journal of Applied Ecology*, **47**(6), 1272-1281.

Rapaport, L.G. & Brown, G.R. (2008). Social influences on foraging behaviour in young nonhuman primates: Learning what, where, and how to eat. *Evolutionary Anthropology*, **17**(4), 189-201.

Raubenheimer, D. & Rothman, J.M. (2013). Nutritional ecology of entomophagy in humans and other primates. *Annual review of entomology*, **58**(2013), 141-160.

Reichardt, P. B., Chapin Iii, F. S., Bryant, J. P., Mattes, B. R., & Clausen, T. P. (1991). Carbon/nutrient balance as a predictor of plant defense in Alaskan balsam poplar: potential importance of metabolite turnover. *Oecologia*, **88**(3), 401-406.

Reiner, W.B., Petzinger, C., Power, M.L., Hyeroba, D. & Rothman, J.M. (2014). Fatty acids in mountain gorilla diets: Implications for primate nutrition and health. *American Journal of Primatology*, **76**(3), 281-288.

Reynolds, V. (2005). *The Chimpanzees of the Budogo Forest: Ecology, behaviour and Conservation*. Oxford University Press.

Rode, K.D., Chiyo, P.I., Chapman, C.A. & McDowell, L.R. (2006). Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behaviour. *Journal of Tropical Ecology,* **22**(4), 441-449.

Ryan, A.M., Chapman, C.A. & Rothman, J.M. (2013). How do differences in species and part consumption affect diet nutrient concentrations? A test with red colobus monkeys in Kibale National Park, Uganda. *African Journal of Ecology*, **51**(1), 1-10.

Sage, T. L & Webster, B. D. (1987). Flowering and fruiting patterns of *Phaseolus vulgaris* L. *Botanical Gazette*, 35-41.

Scarano, F.R. (2009). Plant communities at the periphery of the Atlantic rain forest: rare-species bias and its risks for conservation. *Biological Conservation*, **142**(6), 1201-1208.

Schaefer, H.M. & Schmidt, V. (2004). Detectability and content as opposing signal characteristics in fruits. Proceedings of the Royal Society of London B: *Biological Sciences*, **271**(5), 370-373.

Schaefer, H.M., Schmidt, V. & Winkler, H. (2003). Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos* **102**(2), 318–328.

Schülke, O., Chalise, M.K. & Koenig, A. (2006). The importance of ingestion rates for estimating food quality and energy intake. *American Journal of Primatology*, **68**(10), 951-965. Doi: 10.1002/ajp.20300

Skorupa, J. P. (1986). Responses of rainforest primates to selective logging in Kibale Forest, Uganda: a summary report. In Primates (pp. 57-70). Springer New York.

Sorensen, J.S., Heward, E. & Dearing, M.D. (2005). Plant secondary metabolites alter the feeding patterns of a mammalian herbivore (*Neotoma lepida*). *Oecologia*, **146**(3), 415-422.

Sorensen J, S, Turnbull C. A, Dearing M. D (2004). A specialist herbivore (*Neotoma stephensi*) absorbs fewer plant toxins than does a generalist (*Neotoma albigula*). *Physiology Biochemistry and Zoology*. 77(1):139–48.

Sorensen, J & Dearing, M. (2003). Elimination of plant toxins by herbivorous woodrats: revisiting an explanation for dietary specialization in mammalian herbivores. *Oecologia*, **134**(1), 88-94.

Struhsaker, T.T. (1997). *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. Florida University Press, Gainesville.

Taira, S. (1995). Astringency in persimmon. *In Fruit analysis*. Springer Berlin Heidelberg. (pp. 97-110).

Tutin, C.E., Parnell, R.J. & White, F. (1996). Protecting seeds from primates: Examples from Diospyros spp. in the Lopé reserve, Gabon. *Journal of Tropical Ecology*, **12**(3), 371-384.

UBOS (Uganda Bureau of Statistics) (2014). *National Population and Housing Census*. Provional Results. Revised Edition November 2014

Udovic, D & Aker, C. (1981). Fruit abortion and the regulation of fruit number in Yucca whipplei. *Oecologia*, **49**(2), 245-248.

Uganda Metrological Department (2008). Weather and climate database

Van Schaik, C.P., Terborgh, J.W. & Wright, S.J. (1993). The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics,* **24**(1993), 353-377.

Vidal, S., Francis, L., Noble, A., Kwiatkowski, M., Cheynier, V. & Waters, E. (2004). Taste and mouth-feel properties of different types of tannin-like polyphenolic compounds and anthocyanins in wine. *Analytica Chimica Acta*, **513**(1), 57-65.

Waser, P.M. (1977). Feeding, Ranging and Group size in the Mangabey *Cercocebus albigena*. In Clutton-Brocks, T.H. (Ed), *Primate Ecology* (pp. 183-222). Academic Press, London.

Waser, P.M. (1975). Monthly variations in feeding and activity patterns of the mangabey, *Cercocebus albigena* (Lydekker). *East African Wildlife Journal,* **13**(3-4), 249-264.

Waterman, P.G. (1984). Food acquisition and processing as a function of plant chemistry. In *Food acquisition and processing in primates.* Springer US. (pp. 177-211).

Worman, C.O. & Chapman, C.A. (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *Journal of Tropical Ecology* **21**(6), 689-697

Wrangham, R.W., Conklin-Brittain, N.L. & Hunt, K.D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, **19**(6), 949-970.

Wrangham, R. W., Gittleman, J. L., & Chapman, C. A. (1993). Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behavioral ecology and Sociobiology*, **32**(3), 199-209.

Wrangham, R.W. & Waterman, P.G. (1983). Condensed tannins in fruits eaten by chimpanzees. *Biotropica*, **15** (3), 217-222.

Wright, S.J. (2005). Tropical forests in a changing environment. *Trends in Ecology & Evolution*, **20**(10), 553-560.

Wright, S.J. & Van Schaik, C.P. (1994). Light and the phenology of tropical trees. *American Naturalist*, **143**(1), 192-199.

Yamashita, N. (2008). Chemical properties of the diets of two lemur species in south-western Madagascar. *International Journal of Primatology*, **29**(2), 339-364.

Zhao, J., Davis, L.C. & Verpoorte, R. (2005). Elicitor signal transduction leading to production of plant secondary metabolites. *Biotechnology advances*, 23(4), 283-333

CHAPTER TEN

10 CONCLUSIONS AND RECOMMENDATIONS

10.1 General Conclusions

During this study, mangabeys inhabiting the LVB forest reserves were observed to utilize certain priority fruits as food. These included *Blighia unijugata*, *Maesopsis eminii*, *Myrianthus arboreus*, *Rheedia edulis Canarium indicum*, *Celtis* species (*C. durandii*, *C. africana* and *C. Mildbraedii*), *Antiaris toxicaria*, *Pseudospondias microcapa*, *Treculia africana*, *Albizia grandibracteata* and figs (*F.sur*, *F. exasperata* and *F. mucuso*). This list seems to have changed over a period of 50 years probaly due to anthropogenic activities and climatic variability. Among these priority fruits, *B. unijugata M. arboreus*, *R. edulis Celtis* species and *P. microcapa* were preferred fruits due their relatively high macro-nutrient. The remaining fruits on the list were categorized as fallback fruits (FBFs) because of their low nutrient content.

Essentially, the nutritional requirements of M&L mangabeys revolved around availability of food resources and its quality. Although FBFs constituted 75% of priority fruit trees and were available for most of the study period (>18 months on average), their nutritive quality was poor. Since the preferred fruits were only available for $\leq$ 6 months, the available fruit resources could not sustain the dietary requirements of mangabeys especially during periods of low fruit availability. This implied that mangabeys foraged alternative food resources to cope with fruit scarcity. Hence, the initiation of the fruit processing behaviour to access low quality endosperms. The contribution of endosperms and FBFs to the Mangabey diet during periods of fruit scarcity seemed to be still inadequate especially in the severely degraded Lwamunda forest reserve. It is therefore probable that mangabeys raided domesticated crops to supplement their daily diet. It appears fruit processing and reliance on FBFs is a consequence of low food availability and an adaptative and selective strategy to acquire food items in a resource-poor habitat. It may also be indicator of poor habitat health.

Generally, fruit availability varied with fruit tree species, seasonality and type of habitat. More trees fruited during the beginning and throughout the wet season (February-June) than during the dry spells (July-September and December-January). Fruit abundance did not translate into fruit edibility because immature fruits (1-2 weeks after flowering) of all priority tree species were not utilized as food by mangabeys. Endosperms of relatively unripe fruit (3- 18 weeks after flowering) depending on type of tree species were regularly consumed. Ripe fruit pulp (>20-32 weeks after flowering) were the most preferred part of the fruit because of its readily available sugars. With regard to *B.unijugata*, the aril was the most preferred fruit part because of its high fat content. The severely degraded Lwamunda forest reserve with a coefficient of 16 had more fruitless trees than either fairly undisturbed Mabira (M1) or regenerating M2 forest reserves.

It appears mangabeys were capable of detecting differences in tannin concentrations in fruit for consumption regardless of type or part or habitat as illustrated by the determined threshold of 2.6g/100g catechin equivalent. In incidences when consumption of seed becomes unavoidable, mangabeys seem to consider the quality of macro-nutrients contained therein and employ trade-off mechanism. In other words, because the seed is rich in protein, lipids and carbohydrates, the energy acquired through its consumption is more than the energy used for detoxication of the ingested tannins. Although Mabira and Lwamunda forest reserves are within the Mabira and Lwamunda, the micro-environments are totally different and therefore the influence of tannin levels on selection of fruit parts eaten by mangabeys varies according to food availability and seasonality. Large sized gaps cause irrepairable imbalance in forest ecosystems and contributes immensely to food scarcity in the habitat where they occur. Consequently, mangabeys incurred high energy cost in terms of travel and fruit processing which could definitely affect their nutritional status.

With this acquired knowledge of the inter-relationship between the Mangabey nutritional ecology and forest disturbance with its spatiotemporal variations, it is possible to formulate a viable forest management strategy for M&L forests. This allows management of a forest as a renewable resource which can be utilized sustainably to retain species

diversity and richness for the continued benefit of communities inhabiting the forest interface and Ugandans at large. Undoubtedly, the management strategy is desperately needed to ensure protection and sustainable utilization of the M&L forest reserves and conservation of its fauna. Furthermore, knowledge of the nutritional content of Mangabey priority fruit items enriches the understanding of the interaction between other forest fauna with respect to food selection and its quality status.

10.2 General Recommendations

To advance the field of nutritional ecology and gain a better understanding of dietary selection and foraging strategies among primates, it will be useful to analyse food items from the species of interest and, if possible, the actual plant from which the animal fed. With regard to Mangabey diet, it would be prudent to consider the nutritional content of specific fruit/fruit part consumed at a particular stage of development as a pre-requisite to understanding its nutritional ecology. This is because the nutrient content varies with fruit maturity and fruit part. It was observed in the present study that mangabeys frequently ate fruit endosperms, seeds, pulps and *Blighia* aril. However, due to time constraint it was not possible to establish the frequency of each fruit part in Mangabey diet. Subsequent studies should take into account frequency of fruit part consumption and by what age and gender of Mangabey. Similarly, the frequency of fallback and preferred fruits in the Mangabey diet should be established to underscore their importance and correlation with altered or disturbed habitats.

Information generated on fr uit availability, fallback and preferred fruit tree species, tannin levels and gap sizes should be used as a basis for development of credible strategies and policies for conservation of M&L forest reserves by the management of National Forest Authority (NFA) and Uganda Wildlife Authority. They may include but not limited to regulation (timing) of tree felling, selective logging as opposed to total prohibition of forest encroachment and prevention of Mangabey hunting for cross-border trade in bush meat. This will enhance the biodiversity and sustainability of fruit tree species that will ensure availability of quality fruit for mangabeys.

This study should be repeated with increased study sites, groups and sample size of monitored tree species. For correlation between fruit abundance and fruit processing, the latter should be quantitatively assessed. More time should be allotted to experimental design. For example, frequency of sampling for seasonal fruits like *B. unijugata*, *M. arborea*, *Celtis* spp, *P. microcapa* and *R. edulis* should be increased from monthly to weekly to improve on statistical confidence. Now, that it is known that mangabeys select fruits based on the level of ripeness, a chroma meter should be used to differentiate between the developmental stages of fruits instead of human sensorial detection. The experimental design should also include feeding scores, feeding bouts and weight of consumed part for each developmental fruit stages. The study should also include other secondary metabolites like terpenoids and alkaloids, energetics and population dynamics, tree species inventory and tree follow for in-depth understanding of other frugivores that utilize the same fruit tree. To find out whether the feeding behaviour was age or gender specific, the number of fruit tree species monitored should be reduced from ten to probably two or three. Studies on domesticated types of foods and particularly seasonal nutrient variations of different fruit/root components should be conducted. The generated information would provide a basis for evaluation of Mangabey responses to anthropogenic habitat disturbance as it was also noted by Chapman, *et al.* (2012).

The number of trees per unit area with their corresponding dbh, canopy size and cover should have been determined on a monthly basis. This information would have been useful when calculating the rate of tree loss or creation of gaps and growth rate. Data on distance travelled by male/female, young/ adult/juvenile per day should have been determined to confirm the hypothesis that as the gap size increased and canopy discontinued, the distance travelled by mangabeys increased. Faecal matter should have been analysed to determine the actual amount of food assimilated per unit bout of fruit ingested. Admittedly, this line of research would have required a controlled environment probably in captivity and an experimental design that correlates fruit fruit part consumed by a specific animal and the defecated feacal matter

Based on the chemical composition of fruits preferred by mangabeys, farmers living at forest interface should be advised on types of crops they should grow near the forest to avoid conflicts with non-human primates. They should be unpalatable like chilli, sisal and tea or early maturing like beans without readily available sugars. To ensure compliance to the proposed strategy, there should be close collaboration between subsistence farmers, agricultural staff, forest rangers and academicians. Community participation in the conservation and development programmes is an effective way of law enforcement and protection of natural resources.

Since Lwamunda was decimated by the end of the present study, it should be replanted and certain areas gazetted for eco-tourism like it was done in Mabira several years ago by NFA and UWA. The development of tourist areas or formation of parks will allow viewing of forest ecosystems without wanton damage. This will ensures poverty alleviation among the poor households adjacent to forest reserve and it will improve the biodiversity of fauna and flora to attract and boost eco-tourism trade.

Mangabeys should be considered as one of indicators of forest health because they were sensitive to habitat alterations as previously observed (Olupot, 2000). When the health status of the habitat was poor and incapable of sustaining them like Lwamunda, they engaged in aggressive fruit processing.

Further studies and particularly seasonal nutrient variations of different fruit/fruit parts should be conducted on wild as well as domesticated types of foods. Mangabey population dynamics should also be done to establish the relationship between their statuses with food availability results generated by this study. Finally, in view of the rapid disappearance of forests in Uganda, there is need to conduct similar studies for extended periods of time for comparison and in-depth understanding of nutritional ecology of mangabeys and other forest fauna.