Habitat use and nutrition of chimpanzees in an anthropogenic landscape: A case study in Bossou, Guinea, West Africa

Photos © Nicola Bryson-Morrison 2012-2013

Nicola Bryson-Morrison

July 2017

School of Anthropology and Conservation, University of Kent, Canterbury

Thesis submitted for the degree of Doctor of Philosophy in

Biological Anthropology

Word count: 57,038

ACKNOWLEDGMENTS

Thank you to my supervisor, Tatyana Humle, for her inspiration and guidance, and of course her unwavering support no matter what problem I presented her with. Above all else, I am forever grateful for her belief in me and my work. I am extremely thankful to Professor Matsuzawa for supporting my research and for allowing me the opportunity to work at Bossou. I would also like to thank the Kyoto University Primate Research International Team, and in particular Professor Yamakoshi, Kimberley Hockings, Naruki Morimura, Hiroyuki Takemoto, Kathelijne Koops, Gaku Ohashi, and Christopher Martin for their helpful insights and discussions on the ecology and behaviour of chimpanzees.

I would like to express my gratitude to Andy Beer for his invaluable guidance and support on the nutritional aspects of this research. I thank the Royal Zoological Society Scotland, Edinburgh Zoo and Sparsholt College technical staff, in particular Roy Niblett, for helping me with the nutritional analyses. I would also like to thank the staff and chimpanzees of Budongo Trail at Edinburgh Zoo for allowing me a practise run of my behavioural data collection protocol before the “real thing”. I am thankful to Joseph Tzanopoulos for his help with GIS methods and map development. The statistics helpdesk, and in particular Rachel McCrea and Owen Lyne, provided valuable support on statistical analyses.

This work would not have been possible without the remarkable chimpanzees of Bossou. I thank them for tolerating my presence and for giving me so many memorable experiences. A special thank you goes to all of the staff of the Kyoto University Primate Research Institute

(KUPRI) in Bossou and especially the guides Vincent, Henry, Gouanou, Jules, Lawe, and Boniface. I would not have been able to conduct this research without their in-depth knowledge of the chimpanzees and the forest. Their brilliant sense of humours and camaraderie made me feel instantly at home. I am also deeply grateful to all of the wonderful villagers of Bossou for making me feel so welcome during my stay. I would like to thank the Institut de Recherche Environmentale de Bossou and the Direction Nationale de la Recherche Scientifique et Technologique for granting me permission to conduct this research. A big thanks also to the “Nimba students” Lucy D’ Auvergne, Wren Edwards, Justin Caraway, Maegan Fitzgerald, and Pauline Le Sommer for the adventures, laughs, movie nights, and chocolate.

This thesis is dedicated to my husband, Alistair Morrison, and our beautiful little boy, Ash. Words cannot express how grateful I am for the unconditional love and support they have given me throughout this PhD. I would like to thank Mum and Dad for always encouraging me to follow my dreams and never give up, and my sister, Debbie Bryson, for introducing me to the world of captive chimpanzees. Also a big thank you to my colleagues past and present, Stefano Kaburu, Lia Betti, Carin Tunaker, Kelly Greenway, Caroline Bennett, and many others, for providing insightful discussions and much needed tea breaks and pub nights.

Support was provided for this study by a graduate teaching scholarship by the School of Anthropology and Conservation at the University of Kent, a MEXT #24000001 to T

Matsuzawa, and research grants from Sigma-Xi the Scientific Research Society and Copenhagen Zoo, Copenhagen, Denmark.

AUTHORS DECLARATION

All chapters in this thesis were written by N. Bryson-Morrison. My supervisor, T. Humle, made editorial suggestions and comments on all chapters. N. Bryson-Morrison conceived all chapters, conducted all fieldwork and carried out all data analyses. In Chapter 3, the map was developed by J. Tzanopoulos and N. Bryson-Morrison using GPS information provided by T. Humle (cultivated fields) and N. Morimura (roads and footpaths). A. Beer and R. Niblett assisted N Bryson-Morrison with nutritional analyses. N. Bryson-Morrison wrote all research papers (i.e. Chapter's 2, 3, 4, and 5) with collaborative input from all co-authors.

PUBLISHED THESIS CHAPTERS

Chapter 2 was published on the 22 June 2016:

Bryson-Morrison, N., Matsuzawa, T. & Humle, T. (2016). Chimpanzees in an anthropogenic landscape: examining food resources across habitat types at Bossou, Guinea, West Africa. *American Journal of Primatology* 78: 1237-1249

Chapter 3 was published on the 30 January 2017:

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T. & Humle, T. (2017). Activity and habitat use of chimpanzees (*Pan troglodytes verus*) in the anthropogenic landscape of Bossou, Guinea, West Africa. *International Journal of Primatology*: doi:10.1007/s10764-016-9947-4

Chapter 4 is currently in preparation for journal submission:

Bryson-Morrison, N., Beer, A., Matsuzawa, T. & Humle, T. The macronutrient composition of wild and cultivated plant foods consumed by chimpanzees inhabiting the anthropogenic landscape at Bossou, Guinea, West Africa

Chapter 5 is currently in preparation for journal submission:

Bryson-Morrison, N., Beer, A., Matsuzawa, T. & Humle, T. The role of crops in primate diets: examining sex differences, seasonality, and macronutrient balancing in the diets of chimpanzees (*Pan troglodytes verus*) inhabiting a forest-agricultural mosaic

ABSTRACT

Human population increases and an expanding agricultural frontier are driving tropical deforestation. As a result, many primates are increasingly found outside of protected areas in highly-disturbed environments in close proximity to humans. A better understanding of primate species adaptability to human pressures and the ability of anthropogenic landscapes to support viable populations in the long-term is critical for effective conservation efforts. By focusing on the chimpanzee (*Pan troglodytes verus*) community in the anthropogenic landscape of Bossou, Guinea, West Africa, I aimed to 1) empirically describe the composition and availability of chimpanzee resources across fine spatial scales, 2) examine chimpanzee use and activity budget across available habitat types and in relation to anthropogenic pressures and risks, 3) determine the macronutrient composition of wild and cultivated chimpanzee foods, and 4) investigate chimpanzee macronutrient intake and balancing from wild and cultivated foods.

To examine objective 1, I undertook quadrat vegetation surveys and phenology surveys to spatially and temporally quantify chimpanzee food resources in all available habitat types. Bossou is largely composed of regenerating forest and the scarcity of large fruit bearing trees is offset by a high diversity of wild and cultivated chimpanzee food species. Moraceae (mulberries and figs) is the dominant family, trees of which produce drupaceous fruits favoured by chimpanzees. The oil palm, which provides the chimpanzees with year-round food resources, occurs at high densities throughout Bossou. Mature and secondary forests are the most important habitat types for food species availability. Overall, these results emphasise the importance of examining ecological characteristics of an anthropogenic

landscape as each available habitat type is unlikely to be equally important in terms of spatial and temporal availability of resources.

To examine objective 2, I conducted behavioural follows to record chimpanzee activities and habitat use across all forest and highly disturbed habitat types, and foraging locations in non-cultivated habitat in relation to anthropogenic pressures i.e. cultivated fields and roads and paths. Chimpanzees preferentially use forest habitat types for travelling and resting and highly disturbed habitat types for socialising. The availability of wild fruit and crops influences seasonal habitat use for foraging. The chimpanzees rely heavily on a small patch of mature forest, rich in food species and with low human presence, irrespective of season and activity. The chimpanzees avoid foraging in non-cultivated habitat within 200 m of cultivated fields, with no effect of habitat type or season, suggesting an influence of associated risk. Nevertheless, they did not actively avoid foraging close to roads and paths. These results reveal chimpanzee reliance on different habitat types and the influence of human-induced pressures on their activities.

To examine objective 3, I used standard wet chemistry procedures to estimate the macronutrient content of wild and cultivated chimpanzee foods. The composition of wild fruit, leaves and pith are consistent with previous reports for primate diets. Cultivars are generally higher in carbohydrates and lower in fibre than wild foods, while wild foods are higher in protein. Oil palm food parts are rich in energy, carbohydrates, protein, lipids and/or fermentable fibre fractions; adding nutritional support for the importance of oil palms for chimpanzees in anthropogenic landscapes. These results build on current understanding of chimpanzee feeding ecology and nutrition within forest-agricultural mosaics and provide further empirical evidence that cultivars offer primates energetic benefits over most wild plant foods.

To examine objective 4, I used the macronutrient composition of foods and recorded chimpanzee intakes of wild and cultivated foods during focal follows. Diet composition and macronutrient intakes vary little between the sexes; however females have higher total foods (i.e. wild and cultivated combined), digestible fibre (NDF), and protein intakes when controlling for metabolic body mass. There are no differences in wild or cultivated food intake between seasons; however lipid and protein intake from cultivars, and most likely oil palm food parts, is higher during the fruit scarce season. The chimpanzees maintain their proportional intake of protein while allowing carbohydrate and lipid intakes to vary. Furthermore, they were able to achieve a consistent balance of protein to non-protein (carbohydrates, lipids, and NDF) energy across the year. These results suggest the chimpanzees suffer little seasonal constrains in food quality or availability and are able to combine their consumption of available wild and cultivated foods to achieve a balanced diet.

Overall, this thesis provides new insights into the ecology of anthropogenic landscapes, the influence of human pressures on chimpanzee habitat use and behaviours, and the role of cultivars in chimpanzee foraging strategies and in allowing them to meet their nutritional requirements. Such information is important for informing conservation initiatives aimed at balancing the needs of people and chimpanzees that share space and resources within anthropogenic landscapes.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

Chapter 1 INTRODUCTION

1.1 HUMAN-INDUCED ENVIRONMENTAL PRESSURES

Human population increases and human activities are impacting the earth’s ecosystems on such a scale that we are now in a new epoch, the “Anthropocene” (Steffen et al, 2011). Human-induced environmental change and the subsequent loss of species have reached unprecedented levels over the last 50 years (Millennium Ecosystem Assessment, 2005). Human pressures on the environment are numerous and varied, including habitat degradation and fragmentation, overexploitation of natural resources, the introduction of exotic species, pollution, and climate change (Millennium Ecosystem Assessment, 2005). Loss of habitat from human land-use activities, such as agriculture, logging, livestock farming, mining, and infrastructures such as roads, are the biggest threat to survival for many terrestrial species (Sala et al, 2000), including non-human primates (hereafter ‘primates’) (Chapman & Peres, 2001; Estrada, 2013). Indeed, it is estimated that 60% of the world’s primate species are in danger of extinction from human-induced pressures, of which tropical deforestation driven by agricultural expansion is the primary threat (Estrada et al, 2017).

The continued decline of forested areas coupled with an ever expanding human population means that many primates are increasingly found in highly-disturbed environments in close proximity to humans and human activity. Such environments, often termed as human-dominated, or anthropogenic, are typically fragmented mosaic landscapes with past and continuing direct human alteration of ecological processes (Ellis et al, 2006). Anthropogenic landscapes are characterised by a matrix of managed and unmanaged land types, including remnant patches of forest, successional habitat/fallow areas, agricultural fields and plantations, and human infrastructures such as roads and clusters of buildings for human settlement. Many primate species occur outside of formally protected areas and the need for examining anthropogenic landscapes for conserving populations has become apparent in recent years (Chapman & Peres, 2001; Schwitzer et al, 2011). Furthermore, primate populations residing in anthropogenic landscapes are potentially excellent models for unravelling adaptability and responses to environmental changes, and an increasing number of primate studies and conservation activities are now focusing on these human-dominated environments (e.g. Benchimol & Peres, 2013; Chapman et al, 2005; Cowlishaw & Dunbar, 2000; Halloran et al, 2014; Irwin et al, 2010). However, empirical data on biodiversity in forest-agricultural mosaics in primate range countries, particularly across Africa, are lacking (Blanco & Waltert, 2013; Norris et al, 2010; Trimble & van Aarde, 2014).

1.2 THE STATUS OF CHIMPANZEES

Less than 28% of great ape species populations are found within protected areas (Hickey et al, 2013; Wich et al, 2014; Lanjouw et al, 2015) and this, along with intrinsic species characteristics, such as slow life histories and low population densities, puts them at particularly high risk of extinction from human-induced pressures (Purvis et al, 2000). Certainly, all great ape species are listed as Endangered or Critically Endangered by the International Union for Conservation of Nature and all are declining in numbers, including chimpanzees (*Pan troglodytes*) (IUCN, 2016).

Chimpanzee populations across their range in West, Central and East Africa are declining due to illegal hunting, epidemic diseases, and widespread habitat loss (Humle et al, 2016). Chimpanzees occur in a variety of habitats including moist lowland forests, swamp forest, montane forest, and savannah-woodland (Oates, 2011). However, rapid human population growth and agricultural expansion into forested areas has severely impacted chimpanzee habitat, and populations are increasingly found in forest-agricultural mosaics and highly impacted fallow-agricultural-oil palm matrixes (Humle et al, 2016). This is particularly true for West Africa, where the majority of forested areas are now dominated by forest-agricultural mosaics (Norris et al, 2010), and as much as 80% of chimpanzee populations are located outside of protected areas in land managed for human needs (Kormos et al, 2003). As such, increasing our current understanding of the suitability of these unprotected anthropogenic landscapes for chimpanzees, as well as chimpanzee responses to habitat changes, is of paramount importance for conservation efforts outside protected areas.

1.3 CHIMPANZEES IN ANTHROPOGENIC LANDSCAPES

All great apes display high levels of behavioural and ecological flexibility, and chimpanzees in particular show a degree of adaptability in response to anthropogenic change (Hockings & Humle, 2009). Chimpanzees in forest-agricultural mosaics that face no hunting pressure can adjust their behaviours, foraging strategies, grouping patterns, and range use in response to human presence and activities (Hockings et al, 2015). Chimpanzees often incorporate agricultural crops into their diets. They are also known to adapt their behaviour and foraging strategies in response to perceived and actual risks posed by potential human presence and the measures used by farmers to deter them from feeding on cultivars. For example, feeding party sizes are larger, contain more males, and are more cohesive when foraging on cultivars compared to wild foods (Hockings et al, 2012). Furthermore, when feeding on cultivars, chimpanzees vocalise less (Wilson et al, 2007) and forage at night to reduce the risk of detection by humans (Krief et al, 2014). Chimpanzees also use human-made roads and footpaths that dissect their home range, adapting their grouping patterns and behaviour before and during road-crossings (Cibot et al, 2015; Hockings, 2011) and show awareness of the potential dangers posed by snares by deactivating them upon detection (Ohashi & Matsuzawa, 2011) and removing snares from the limbs of other individuals (Amati et al, 2008; Boesch & Boesch-Achermann, 2000).

Nevertheless, chimpanzees show signs of anxiety when faced with anthropogenic pressures (Hicks et al, 2012; Hockings, 2011; Hockings et al, 2006), including evidence of chronic stress, measured using the endocrine stress marker cortisol, in populations residing in forest fragments in close proximity to humans (Carlitz et al, 2016). Prolonged exposure to increased levels of anxiety and stress have negative impacts on fitness (Sapolsky et al, 2000), including decreased immune response (Sternberg et al, 1992), reduced fertility (Arck et al, 2001; Cocks, 2007), and reduced growth (Santos et al, 2000). Perceived and actual risks to chimpanzees from human presence and activities can be numerous, and the adaptive behaviours chimpanzees display in response to anthropogenic pressures can often exacerbate these risks. For example, foraging on cultivars is risky because of potential negative interactions with humans seeking to protect their crops (e.g. Brncic et al, 2010; Hill 2000, 2005; Hockings et al, 2009; Hockings & Sousa, 2013; McLennan, 2013; Tweheyo et al, 2005). Particularly as crop protection methods can be as extreme as lethal control, and farmers may respond to repeated chimpanzee incursions into their fields with retaliatory killings (Hockings & McLennan, 2016). Chimpanzees also face substantial risks from collisions with vehicles when crossing roads (Cibot et al, 2015; McLennan & Asiimwe, 2016). Aggression by chimpanzees towards local people can also occur, particularly on footpaths and in agricultural fields adjacent to forest, and is often in response to surprise encounters or provocation by humans (Hockings et al, 2015), although rare incidences of predatory behaviour towards children has also been documented (Wrangham et al, 2000). Furthermore, people's tolerance and perception of their chimpanzee neighbours are predominantly driven by social, cultural and economic factors that significantly influence the intensity and degree of human-induced risks and negative interactions faced by chimpanzees in anthropogenic landscapes (Hill & Webber, 2010).

Yet, there is currently limited knowledge on the extent of chimpanzee ecological and behavioural adaptability to anthropogenic pressures, as well as the ability of disturbed environments to support populations in the long-term (Hockings et al, 2015; Humle, 2015). Empirical data on the ecological characteristics of anthropogenic landscapes are lacking, and determining the ecological patterns of specific chimpanzee resources across fine spatial scales is necessary to increase understanding of the suitability of such landscapes as viable long-term habitat for resident populations. Furthermore, there is need for a better understanding of the influences anthropogenic disturbances have on chimpanzee habitat use and activities. Such information would provide invaluable insights into chimpanzee reliance on specific habitat types, as well as their ability to respond and adapt to habitat change and potential risks associated with human presence and pressures (Palminteri & Peres, 2012; Porter et al, 2007).

Additionally, there is a current lack of understanding of the drivers behind crop consumption by chimpanzees (Hockings & McLennan, 2012), despite the prevalence of cultivar-foraging and its potentially harmful effects on chimpanzee-human coexistence. This lack of knowledge hinders conservation initiatives aimed at reducing negative interactions between people and chimpanzees, particularly as effective mitigation strategies require evidence-based management (Thirgood & Redpath, 2008). The decision by chimpanzees to forage on cultivars will depend on a variety of factors including type, availability, and proximity of cultivated resources, habitat quality and wild food availability, and perceived risks associated with cultivar-foraging (Reynold, 2005; Hockings et al, 2009; Naughton-Treves et al, 1998; McLennan, 2013). Furthermore, chimpanzees may be attracted to cultivars that provide rich sources of easily digestible carbohydrate energy compared to wild foods (McLennan & Ganzhorn, 2017). However, to date, no published studies have examined the ability of chimpanzees to meet their nutritional requirements within anthropogenic landscapes, and the potential role of cultivars in fulfilling these requirements.

Various models have been used to explain primate diet selection, including energy/protein maximisation, toxin/fibre minimisation and nutrient balancing (reviewed in Felton et al, 2009a). Recent advances in nutritional ecology have highlighted the use of nutritionally explicit frameworks for a better understanding of how foraging decisions and food intakes relate to nutrient and energy requirements (Raubenheimer et al, 2015; Righini, 2017). The geometric framework for nutrition allows the nutritional composition of selected foods and dietary intakes to be quantified in order to determine primate nutritional responses and regulation (Raubenheimer et al, 2015). Examining consumption of wild and cultivated foods in a nutritionally explicit way is necessary for providing new insights into chimpanzee foraging strategies and food-related decision making within highly-disturbed environments. It is vital to determine the extent to which crop consumption is driven by a need to fulfil specific nutritional requirements in order to inform the development of appropriate conservation efforts. Particularly, land-use management aimed at protecting or regenerating important wild foods as well as mitigation strategies that balance the needs of both people and chimpanzees that share space and resources within anthropogenic landscapes.

See Chapter 2 for more details on the behavioural and ecological responses of different primate species to anthropogenic landscapes.

1.4 STUDY SITE AND CHIMPANZEE POPULATION

There are a number of reasons why the anthropogenic landscape that surrounds the village of Bossou in Guinea, West Africa and the resident chimpanzee (*P. t. verus*) population make an excellent case study for examining chimpanzee responses and adaptability to human-induced pressures. First, Bossou is one of only two long-term chimpanzee field sites in West Africa and it has been rated as the most heavily impacted of all six long-term chimpanzee research sites (Wilson et al, 2014). Second, over thirty-five years of research has been conducted at Bossou which has produced a wealth of knowledge on many aspects of chimpanzee behaviour, ecology, life history, and population dynamics (Matsuzawa et al, 2011). Third, the long history of research and conservation efforts has built good relations with local villagers and as a result the people’s cultural and social beliefs and past and present land use practices are well understood (Matsuzawa et al, 2011; Sugiyama & Koman, 1992; Yamakoshi, 2005). Lastly, the chimpanzees are well habituated to researcher presence, which enables an in-depth examination of various aspects of their behaviour and ecology, such as dietary intake, which would be near impossible for unhabituated populations residing in anthropogenic landscapes. Overall, the Bossou chimpanzees offer a unique and important opportunity for conducting research aimed at informing conservation efforts for other populations within human-impacted environments.

1.4.1 Site description

Bossou is situated in the south-eastern forest region of the Republic of Guinea, West Africa (latitude 7°38’71.7’N and longitude 8°29’38.9’W) and is isolated from the nearest stretch of continuous mature forest in the Nimba Mountain range by approximately 6 km of savannah (Fig. 1.1). The Nimba Mountain range spans the borders with Côte d’Ivoire and Liberia, and the Guinean portion of the massif was designated as a Biosphere Reserve in 1980 and also encompasses the Bossou landscape (Fig. 1.1) (Humle, 2011). The climate in this region is classified as tropical wet seasonal (Richards, 1996), with a short dry season from November to February and a distinct rainy season from March to October (Hockings et al, 2009; Humle, 2011; Takemoto, 2002; Yamakoshi, 1998). Monthly precipitation can vary between 0 mm in the dry season to over 700 mm in the wet season (Humle, 2011). Temperatures can range from 12 °C to 43 °C, with the greatest difference in daily minima and maxima temperatures in the dry season (Humle, 2011).

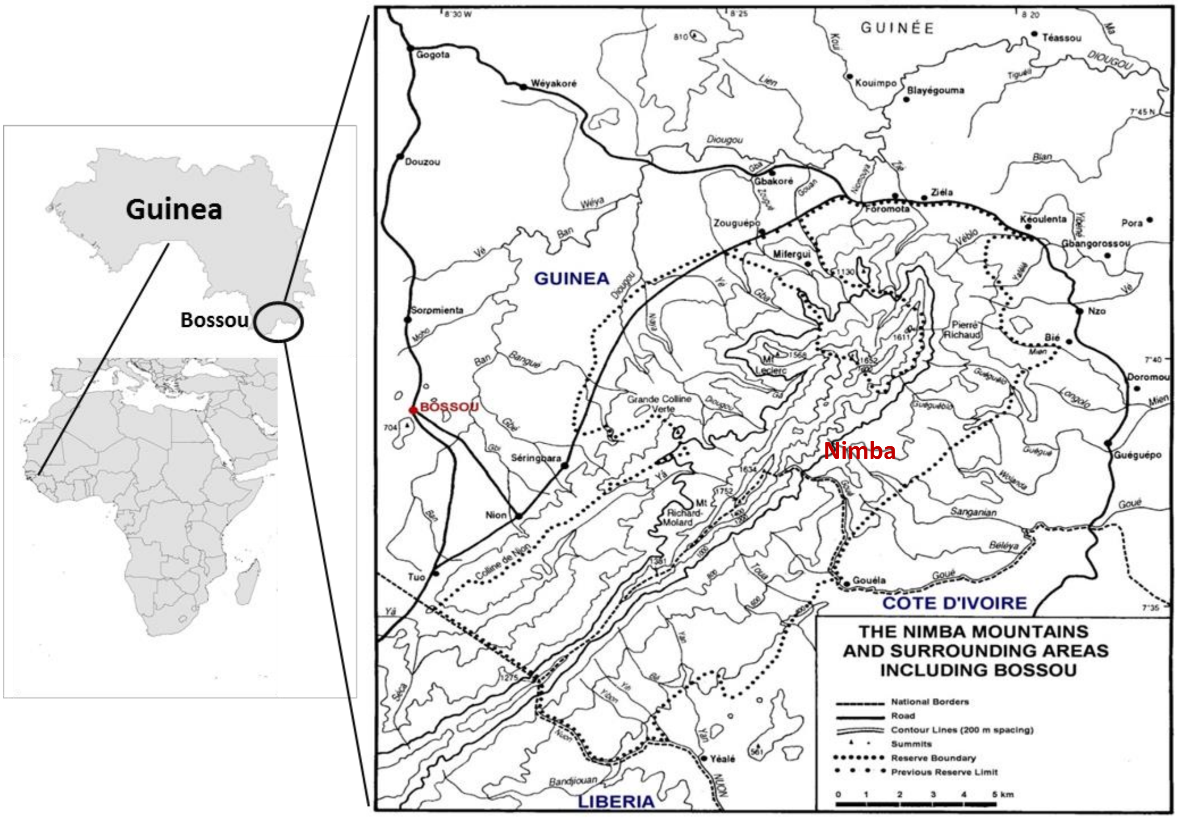

Figure 1.1 Map showing the location of Bossou in relation to the Nimba Mountains range in the Republic of Guinea, West Africa (Map drawn by T. Humle, N. Garnier and L. Martinez)

The village of Bossou is surrounded by four small hills (70-150 m high) and the landscape is a highly heterogeneous patchy mosaic of primary, riverine and secondary forest, coffee plantations, cultivated fields, and fallow areas of varying successional stages (Hockings et al 2009; Sugiyama & Koman, 1992; Yamakoshi, 1998). The remnant patch of mature forest measures < 1 km^2 and is located on the summit of the largest hill, Gban (Humle, 2011).

Secondary forest is the most dominant forest type, and there is a high occurrence of wild or semi-domesticated oil palm trees (*Elaeis guineensis*) throughout the landscape.

1.4.2 Human Impact

Around 2,500 people live in Bossou, and despite the reserve status local people are predominantly subsistence farmers and continue to practise traditional slash and burn agriculture within and around the four small hills. Generally, a mix of crops are grown in agricultural fields, such as important subsistence foods like rice (*Oryza* sp.) and cassava (*Manihot esculenta*), and fruit and vegetables including maize (*Zea mays*), okra (*Hibiscus esculentus*), banana (*Musa sinensis*) and pineapple (*Ananasa comosus*) (Hockings et al*.* 2009). In addition to coffee trees (*Coffea* sp.), most coffee plantations contain cultivated fruit tree orchards such as orange (*Citrus sinensis*), mandarin (*Citrus reticulata*), mango (*Mangifera indica*), papaya (*Carica papaya*) and cacao (*Theobroma cacao*), as well as banana plants. The prevalence of cash crops at Bossou, such as coffee, rubber (*Hevea brasiliensis*) and pineapple has increased in recent years (Matsuzawa et al, 2011). Local people also rely heavily on the oil palm, predominantly for domestic and commercial palm oil production (Yamakoshi, 2005).

Human-made roads and footpaths are found throughout the landscape. The larger of the two dirt roads (approximately 12 m wide) serves as a main thoroughfare from Liberia to the forest region of Guinea and is frequently used by vehicles and pedestrians (Hockings, 2011). The smaller road (approximately 3 m wide) runs to nearby villages and is used by pedestrians and motorcycles (Hockings, 2011). Small paths dissect all four hills and are used by local people for access to forest and agricultural areas.

Although the chimpanzees are not hunted, there is frequent illegal poaching, using guns and traps, of other mammals, including red-flanked duiker *(Cephalophus rufilatus)* and cane rat *(Thrynomys swinderianus)*. As a result there are relatively few large mammal species left in the forested areas around Bossou.

1.4.3 Human-chimpanzee coexistence

Bossou village is home to the Manon people who hold chimpanzees sacred as one of their animal totems and believe that the chimpanzees are the reincarnation of their ancestors (Kortlandt, 1986; Yamakoshi, 2011). These beliefs protect the chimpanzees from being hunted, killed, or eaten (Yamakoshi, 2005). Local villagers also believe that their ancestors' souls reside on the sacred hill of Gban; beliefs which have helped maintain the small patch of mature forest found at the summit (Kortlandt, 1986). These strong cultural beliefs have maintained a relatively peaceful coexistence between people and chimpanzees for many generations (Yamakoshi, 2005). However, people and chimpanzees regularly come into close proximity on roads, footpaths, and agricultural areas and many villagers, particularly women and children, are afraid of the chimpanzees (Hockings, 2007; Pers. obs.). The chimpanzees do occasionally exhibit aggressive behaviour towards people, and physical attacks on local villagers, and predominantly children, in areas of high human presence have occurred at a rate of every 1-2 years since records began in 1995 (Hockings et al, 2010). The chimpanzees regularly feed on cultivars and are known to forage on crops at any time of day, including on occasions when local people are present (Hockings, 2007). Chimpanzee incursions into agricultural fields are rarely tolerated and farmers frequently chase them away using noise and/or by throwing stones (Hockings et al, 2009).

1.4.4 The Bossou chimpanzees

The Bossou chimpanzees spend most of their time within a 6 km^2 core area which encompasses the four small hills that surround the village of Bossou (Humle, 2011). The chimpanzees occasionally travel to nearby forested areas using the few remaining riverine forest corridors, which extends their home range to approximately 15 km^2 (Humle, 2011).

A comprehensive list of over 200 different plant species and 246 plant parts consumed by the chimpanzees has been compiled over the years (Humle et al, 2011) and represents around 30% of available species (Sugiyama & Koman, 1992). The chimpanzees spend an average of 61% of their annual feeding time consuming fruit (Yamakoshi, 1998). Leaves, and pith from terrestrial herbaceous vegetation (THV) and oil palm fronds are the next most important food items (Yamakoshi, 1998; Takemoto, 2002; Hockings et al, 2009). Flowers, seeds, nut kernel, palm heart, bark, roots, tubers, mushrooms, and algae are also consumed. The chimpanzees also occasionally eat animal products including termites, ants, insect eggs, larvae, bird eggs, honey and tree pangolin (*Manis tricuspis*) (Sugiyama & Koman, 1992). Wild fruit availability is highly seasonal and tends to peak during the dry season (Yamakoshi, 1998; Hockings et al, 2009). During fruit scarce periods, the chimpanzees rely on food parts from oil palms, pith from THV, and fruits from the aseasonal umbrella tree (*Musanga cercropoides*). The chimpanzees also feed on 17 different fruit and non-fruit crop species (Hockings et al, 2009), and cultivars account for a relatively large proportion of feeding time (6.4-14%: Hockings et al, 2009; Takemoto, 2002). The chimpanzees forage more on cultivars when wild fruits are scarce, particularly succulent fruits such as oranges, although they consume some crops, such as rice pith and maize, regardless of wild fruit availability (Hockings et al, 2009).

The chimpanzee community size ranged between 12-13 individuals during this study (March 2012 - April 2013) with 4 adult males (age range: 14 - 55) and 6 adult females (age range: 15 - 56). One infant male (< 1 year old) and one juvenile male (5 years old) were present throughout. The one adolescent female (8 years old) disappeared from the group half-way through the study period. The Bossou chimpanzees exhibit less fission-fusion than other known communities (Hockings et al*,* 2012), often traveling and foraging in larger parties than expected relative to community size (Matsuzawa et al, 2011).

1.5 THESIS STRUCTURE

This research aimed to provide new insights into the ecology of anthropogenic landscapes and the chimpanzees that reside within them to build on current knowledge of chimpanzee adaptability to human pressures and the ability of disturbed environments to support populations in the long-term. Specifically, my objectives were:

1. To empirically describe the composition and availability of chimpanzee resources across fine spatial scales
2. To examine chimpanzee habitat use and activity budget across available habitat types and in relation to anthropogenic pressures and risks

3. To determine the macronutrient composition of wild and cultivated chimpanzee foods and compare these findings to recently reported results for a chimpanzee population in an anthropogenic environment in East Africa
4. To investigate chimpanzee macronutrient intake and balancing from wild and cultivated foods

In this thesis, the four objectives were examined in separate chapters written as independent research papers.

Chapter 2 aimed to quantify the structure, composition and diversity of chimpanzee plant food resources across all forested and highly disturbed habitat types in the core area, and to compare the suitability of the different habitat types for foraging by examining food availability. Quadrat vegetation surveys, covering more than 70% of the core area, were used to determine the floristic heterogeneity, diversity and distribution of chimpanzee plant resources. Phenology surveys of 67 chimpanzee food species and 1073 individual trees were used to assess temporal food availability bi-weekly over 1 year.

Chapter 3 had two main aims. First, to determine the chimpanzees overall and seasonal patterns of habitat use within their core area with respect to foraging, travelling, resting, and socialising. Second, to examine the influences of risky areas i.e. cultivated fields and human-made roads and paths, on foraging in non-cultivated habitat. The habitat composition and resource availability of the landscape described in Chapter 2 were used along with behavioural follows to examine chimpanzee use and preferences of all forested and highly disturbed habitat types overall and for specific activities. Feeding event locations with respect to anthropogenic areas were determined by recording all feeding events with a handheld GPS during behavioural follows. These GPS feeding event points were mapped in relation to all cultivated fields, roads and paths using QGis.

Chapter 4 aimed to build on existing knowledge of primate diets in anthropogenic landscapes by estimating the macronutrient composition of wild and cultivated plant foods consumed by the chimpanzees. These were compared with recently published results for wild and cultivated foods that constituted the diet of the chimpanzee community at Bulindi, Uganda (McLennan & Ganzhorn, 2017). The macronutrient composition of all oil palm food parts (except flowers) deemed important for chimpanzees were also described. Food samples were collected during feeding bout observations and were dried in a dehydrator. In the UK, samples were ground and analysed using standard wet chemistry procedures to estimate macronutrient content.

Chapter 5 explored the nutritional role of crops in primate diets. Specifically, this study examined sex and seasonal differences in chimpanzee macronutrient and food intakes from wild and cultivated foods and used the geometric framework of nutrition to investigate proportional contributions of macronutrients to the diet and nutrient balancing. The macronutrient composition of wild and cultivated foods detailed in Chapter 4 were used along with feeding bout data collected during continuous focal follows to estimate chimpanzee food and macronutrient intakes across sexes and seasons. Three-way right-angled mixture triangles were plotted to observe the contribution of protein, carbohydrates and lipids to energy intake. Bivariate plots were used to examine the balanced intake of protein vs. non-protein energy (carbohydrates + digestible fibre + lipids).

1.6 REFERENCES

Amati, S., Babweteera, F. and Witting, R. (2008). Snare removal by a chimpanzee of the Sonso community, Budongo Forest (Uganda). *Pan AfricanNews* 15: 6-8.

Arck, P. C., Rose, M., Hertwig, K., Hagen, E., Hildebrandt, M., & Klapp, B. F. (2001). Stress and immune mediators in miscarriage. *Human Reproduction* 16: 1505-1511.

Millennium Ecosystem assesment (2005). Ecosystems and human well-being. Island Press, Washington, DC.

Benchimol, M. and Peres, C.A. (2013). Anthropogenic modulators of species–area relationships in Neotropical primates: a continental-scale analysis of fragmented forest landscapes. *Diversity and Distributions* 19:1339–1352.

Blanco, V. and Waltert, M. (2013). Does the tropical agricultural matrix bear potential for primate conservation? A baseline study from Western Uganda. *Journal for Nature Conservation* 21: 383-393.

Boesch, C. and Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. Oxford University Press, USA.

Brncic, T., Amarasekaran, B. and McKenna, A. (2010). Sierra Leone national chimpanzee census. *Tacugama Chimpanzee Sanctuary, Freetown, Sierra Leone.*

Carlitz, E. H., Miller, R., Kirschbaum, C., Gao, W., Hänni, D. C., and van Schaik, C. P. (2016). Measuring hair cortisol concentrations to assess the effect of anthropogenic impacts on wild chimpanzees (Pan troglodytes). *PloS one* 11: e0151870.

Chapman, C.A., Gillespie, T.R. and 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* 14:134–144.

Chapman, C.A. and Peres, C.A. (2001). Primate conservation in the new millennium: the role of scientists. *Evolutionary Anthropology* 10:16–33.

Cibot, M., Bortolamiol, S., Seguya, A., and Krief, S. (2015). Chimpanzees facing a dangerous situation: A high-traffic asphalted road in the Sebitoli area of Kibale National Park, Uganda. *American Journal of Primatology* 77: 890–900.

Cocks, L. (2007). Factors affecting mortality, fertility, and well-being in relation to species differences in captive orangutans. *International Journal of Primatology* 28: 421-428.

Cowlishaw, G. and Dunbar, R. (2000). *Primate conservation biology*. University of Chicago Press.

Ellis, E.C., Wang, H., Xiao, H.S., Peng, K., Liu, X.P., Li, S.C., Ouyang, H., Cheng, X. and Yang, L.Z. (2006). Measuring long-term ecological changes in densely populated landscapes using current and historical high resolution imagery. *Remote Sensing of Environment* 100: 457-473.

Estrada, A. (2013). Socioeconomic Contexts of Primate Conservation: Population, Poverty, Global Economic Demands, and Sustainable Land Use. *American Journal of Primatology* 75:30–45.

Estrada, A., Garber, P.A., Rylands, A.B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K.A.I., Nijman, V., Heymann, E.W., Lambert, J.E. and Rovero, F. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances* 3: e1600946.

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

Gabriel, D. (2013). Habitat use and activity patterns as an indication of fragment quality in a strepsirrhine primate. *International Journal of Primatology* 34: 388-406.

Guzmán, A., Link, A., Castillo, J.A. and Botero, J.E. (2016). Agroecosystems and primate conservation: Shade coffee as potential habitat for the conservation of Andean night monkeys in the northern Andes. *Agriculture, Ecosystems & Environment* 215: 57-67.

Halloran, A.R., Cloutier, C.T., Monde, S. and Sesay, P.B. (2014). The Tonkolili Chimpanzee Project in Sierra Leone: implications for chimpanzee conservation strategies in anthropogenic landscapes. *African Primates* 9: 15-22.

Hickey, J.R., Nackoney, J., Nibbelink, N.P., Blake, S., Bonyenge, A., Coxe, S., Dupain, J., Emetshu, M., Furuichi, T., Grossmann, F. and Guislain, P. (2013). Human proximity and habitat fragmentation are key drivers of the rangewide bonobo distribution. *Biodiversity and conservation* 22: 3085-3104.

Hicks, T., Roessingh, P. and Menken, S. (2012). Reactions of Bili-Uele chimpanzees to humans in relation to their distance from roads and villages. *American journal of primatology* 74: 721-733.

Hill, C. (2000). Conflict of interest between people and baboons: crop raiding in Uganda. *International Journal of Primatology* 21: 299-315.

Hill, C. (2005). People, crops and primates: a conflict of interests. *Commensalism and conflict: The human-primate* i*nterface. Norman, Oklahoma: American Society of Primatologists*: 40-59.

Hill, C.M. and Webber, A.D. (2010). Perceptions of nonhuman primates in human–wildlife conflict scenarios. *American Journal of Primatology* 72:919–924.

Hockings, K.J. (2007). *Human-Chimpanzee Coexistence at Bossou, the Republic of Guinea: A Chimpanzee Perspective.* University of Stirling.

Hockings, K.J. (2011). Behavioral flexibility and division of roles in chimpanzee road-crossing. In: Matsuzawa, T., Humle, T. and Sugiyama, Y. eds. *The Chimpanzees of Bossou and Nimba*. London: Springer, 221–229.

Hockings, K.J. (2011). The Crop-Raiders of the Sacred Hill. In: Matsuzawa, T., Humle, T. and Sugiyama, Y. eds. *The Chimpanzees of Bossou and Nimba*. London: Springer, 211–220.

Hockings, K., Anderson, J. and Matsuzawa, T. (2006). Road crossing in chimpanzees: a risky business. *Current Biology* 16: R668-R670.

Hockings, K.J., Anderson, J.R. and 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* 71:636–646.

Hockings, K., Anderson, J. and Matsuzawa, T. (2012). Socioecological adaptations by chimpanzees, Pan troglodytes verus, inhabiting an anthropogenically impacted habitat. *Animal Behaviour* 83: 801-810.

Hockings., K.J. and Humle, T. (2009). *Best Practice Guidelines for the Prevention and Mitigation of Conflict between Humans and Great Apes.* Gland, Switzerland: IUCN/SSC Primate Specialist Group.

Hockings, K. and McLennan, M. (2012). From forest to farm: systematic review of cultivar feeding by chimpanzees–management implications for wildlife in anthropogenic landscapes. *PLoS One* 7: e33391.

Hockings, K. and McLennan, M. (2016). Problematic Primate Behaviour in Agricultural Landscapes: Chimpanzees as 'Pests' and 'Predators'. *Ethnoprimatology*. Switzerland: Springer, 137-156.

Hockings, K.J., McLennan, M.R., Carvalho, S., Ancrenaz, M., Bobe, R., Byrne, R.W., Dunbar, R.I., Matsuzawa, T., McGrew, W.C., Williamson, E.A. and Wilson, M.L. (2015). Apes in the Anthropocene: flexibility and survival. *Trends in Ecology & Evolution* 30: 215-222.

Hockings, K. and Sousa, C. (2013). Human-chimpanzee sympatry and interactions in Cantanhez National Park, Guinea-Bissau: current research and future directions. *Primate Conservation* 26: 57-65.

Hockings, K.J., Yamakoshi, G., Kabasawa, A. and Matsuzawa, T. (2010). Attacks on local persons by chimpanzees in Bossou, Republic of Guinea: Long-term perspectives. *American Journal of Primatology* 72:887–896.

Humle, T. (2011). Location and Ecology. In: Matsuzawa, T., Humle, T. and Sugiyama, Y. eds. *The Chimpanzees of Bossou and Nimba*. London: Springer,13–21.

Humle, T. (2015). The dimensions of ape-human interactions in industrial agricultural landscapes. *State of the apes: Industrial agriculture and ape conservation*, Cambridge University Press.

Humle T., Koops K. and Cherif P. (2011). Appendix B: Plant food list of Bossou chimpanzees. In: Matsuzawa T, Humle T, Sugiyama Y, editors. *The chimpanzees of Bossou and Nimba. London*: London, Springer, 406–411.

Humle, T., Maisels, F., Oates, J.F., Plumptre, A. and Williamson, E. (2016). *Pan Troglodytes*.: http://www.iucnredlist.org/details/15933/0 [Accessed: 21 February 2017].

Irwin, M.T., Wright, P.C., Birkinshaw, C., Fisher, B.L., Gardner, C.J., Glos, J., Goodman, S.M., Loiselle, P., Rabeson, P., Raharison, J.L. and Raherilalao, M.J. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation*

143: 2351-2362.

Kormos, R., Boesch, C., Bakarr, M.I. and Butynski, T.M. (2003). *West African chimpanzees: status survey and conservation action plan.* IUCN/SSC Primate Specialist Group. Gland, Switzerland and Cambridge, UK: IUCN.

Kortlandt, A. (1986). The use of stone tools by wild-living chimpanzees and earliest hominids. *Journal of Human Evolution* 15:77–132.

Krief, S., Cibot, M., Bortolamiol, S., Seguya, A., Krief, J.M., and Masi, S. (2014). Wild chimpanzees on the edge: nocturnal activities in croplands. *PLoS One* 9: e109925.

Lanjouw, A., Rainer, H. and White, A. (2015). Apes overview. *State of the Apes: Industrial Agriculture and Ape Conservation*. Cambridge University Press, 164-192.

Matsuzawa, T., Humle, T. and Sugiyama, Y. (2011). *The Chimpanzees of Bossou and Nimba*. London: Springer.

Mckinney, T. (2011). The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced Capuchins (Cebus capucinus). *American Journal of Primatology* 73: 439–448.

McLennan, M. (2013). Diet and feeding ecology of chimpanzees (Pan troglodytes) in Bulindi, Uganda: foraging strategies at the forest–farm interface. *International Journal of Primatology* 34: 585-614.

McLennan, M. and Asiimwe, C. (2016). Cars kill chimpanzees: case report of a wild chimpanzee killed on a road at Bulindi, Uganda. *Primates* 57: 377-388.

McLennan, M. and Ganzhorn, J. (2017). Nutritional Characteristics of Wild and Cultivated Foods for Chimpanzees (Pan troglodytes) in Agricultural Landscapes. *International Journal of Primatology*: doi: 10.1007/s10764-016-9940-y.

McLennan, M. and Plumptre, A.J. (2012). Protected apes, unprotected forest: composition, structure and diversity of riverine forest fragments and their conservation value in Uganda. *Tropical Conservation Science* 5*:* 79-103.

Norris, K., Asase, A., Collen, B., Gockowksi, J., Mason, J., Phalan, B. and Wade, A. (2010). Biodiversity in a forest-agriculture mosaic–The changing face of West African rainforests. *Biological Conservation* 143: 2341–2350.

Oates, J. (2011). Primates of West Africa: a field guide and natural history. Arlington VA: Conservation International.

Ohashi, G. and Matsuzawa, T. (2011). Deactivation of snares by wild chimpanzees. *Primates* 52: 1-5.

Palminteri, S. and Peres, C.A. (2012). Habitat selection and use of space by bald-faced sakis (*Pithecia irrorata*) in southwestern Amazonia: lessons from a multiyear, multigroup study. *International Journal of Primatology* 33:401–417.

Pienkowski, M. W., Watkinson, A. R., Kerby, G., Naughton-Treves, L., Treves, A., Chapman, C.

and Wrangham, R. (1998). Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology* 35:596–606.

Porter, L.L., Sterr, S.M. and Garber, P.A. (2007). Habitat Use and Ranging Behavior of Callimico goeldii. *International Journal of Primatology* 28:1035–1058.

Purvis, A., Gittleman, J.L., Cowlishaw, G. and Mace, G.M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society of London B: Biological Sciences* 267: 1947-1952.

Raubenheimer, D., Machovsky-Capuska, G.E., Chapman, C.A. and Rothman, J.M. (2015). Geometry of nutrition in field studies: an illustration using wild primates. *Oecologia* 177:223–234.

Reynolds, V. (2005). *The chimpanzees of the Budongo forest: Ecology, behaviour and conservation.* Oxford University Press.

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

Righini, N. (2017). Recent advances in primate nutritional ecology. *American Journal of Primatology*: *doi:* 10.1002/ajp.22634.

Riley, E.P. (2007). The human-macaque interface: Conservation implications of current and future overlap and conflict in Lore Lindu National Park, Sulawesi, Indonesia. *American Anthropologist* 109: 473–484.

Riley, E. (2008). Ranging patterns and habitat use of Sulawesi Tonkean macaques (*Macaca tonkeana*) in a human-modified habitat. *American Journal of Primatology* 70: 670-679.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A. and Leemans, R. (2000). Global biodiversity scenarios for the year 2100. *science* 287: 1770-1774.

Santos, J., Benjamin, M., Yang, P.C., Prior, T. and Perdue, M.H. (2000). Chronic stress impairs rat growth and jejunal epithelial barrier function: role of mast cells. *American Journal of Physiology-Gastrointestinal and Liver Physiology* 278: G847-G854.

Sapolsky, R.M., Romero, L.M. and Munck, A.U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions 1. *Endocrine reviews* 21: 55–89.

Schwitzer, C., Glatt, L., Nekaris, K.A.I. and Ganzhorn, J.U. (2011). Responses of animals to habitat alteration: an overview focussing on primates. *Endangered Species Research* 14: 31-38.

Steffen, W., Grinevald, J., Crutzen, P. and McNeill, J. (2011). The Anthropocene: conceptual and historical perspectives. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences* 369: 842-867.

Sternberg, E.M., Chrousos, G.P., Wilder, R.L. and Gold, P.W. (1992). The stress response and the regulation of inflammatory disease. *Annals of Internal Medicine* 117: 854-866.

Sugiyama, Y. and Koman, J. (1992). The Flora of Bossou: its Utilization by Chimpanzees and Humans. *African Study Monographs* 13:127–169.

Takemoto, H. (2002). Feeding ecology of chimpanzees in Bossou, Guinea: coping with the seasonal fluctuation of food supply and micrometeorology in the tropical forest. *Unpublished PhD thesis, Kyoto University, Kyoto, Japan*.

Takemoto, H. (2003). Phytochemical determination for leaf food choice by wild chimpanzees in Guinea, Bossou. *Journal of chemical ecology* 29: 2551-2573.

The IUCN Red List of Threatened Species. Version 2016-3. <www.iucnredlist.org>. Downloaded on 19 February 2017.

Thirgood, S. and Redpath, S. (2008). Hen harriers and red grouse: science, politics and human–wildlife conflict. *Journal of Applied Ecology* 45: 1550-1554.

Trimble, M.J. and van Aarde, R.J. (2014). Supporting conservation with biodiversity research in sub-Saharan Africa’s human-modified landscapes. *Biodiversity and Conservation 23*: 2345-2369.

Tweheyo, M., Hill, C.M. and Obua, J. (2005). Patterns of crop raiding by primates around the Budongo Forest Reserve, Uganda. *Wildlife Biology* 11: 237–247.

Wich, S.A., Garcia-Ulloa, J., Kuhl, H.S., Humle, T. and Lee, J.S.H. . (2014). Will oil palm’s homecoming spell doom for Africa’s great apes? *Current Biology* 24:1659–1663.

Wilson, M.L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I.C., Hashimoto, C., Hobaiter, C.L., Hohmann, G., Itoh, N., Koops, K. and Lloyd, J.N. (2014). Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature* 513: 414-417.

Wilson, M.L., Hauser, M.D. and Wrangham, R.W. (2007). Chimpanzees (*Pan troglodytes*) modify grouping and vocal behaviour in response to location-specific risk. *Behaviour* 144: 1621–1653.

Wrangham, R., Wilson, M., Hare, B. and Wolfe, N.D. (2000). Chimpanzee predation and the ecology of microbial exchange. *Microbial Ecology in Health and Disease* 12: 186-188.

Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *American Journal of Physical Anthropology* 106: 283–295.

Yamakoshi, G. (2005). What is happening on the border between humans and chimpanzees. *Wildlife conservation in West African rural landscapes. Coexistence with nature in a 'globalising' world: field science perspectives. In: 7th Kyoto University international symposium.* Kyoto: Kyoto University: 91-97.

Yamakoshi, G. (2011). The ‘prehistory’ before 1976: looking back on three decades of research on Bossou chimpanzees. In: Matsuzawa, T., Humle, T. and Sugiyama, Y. eds *The Chimpanzees of Bossou and Nimba*. London, Springer, 35–44.

Chapter 2 CHIMPANZEES IN AN ANTHROPOGENIC LANDSCAPE: EXAMINING FOOD RESOURCES ACROSS HABITAT TYPES AT BOSSOU

2.1 ABSTRACT

Many primate populations occur outside protected areas in fragmented anthropogenic landscapes. Empirical data on the ecological characteristics that define an anthropogenic landscape are urgently required if conservation initiatives in such environments are to succeed. The main objective of our study was to determine the composition and availability of chimpanzee (*Pan troglodytes verus*) food resources across fine spatial scales in the anthropogenic landscape of Bossou, Guinea, West Africa. We examined food resources in all habitat types available in the chimpanzees' core area. We surveyed resource composition, structure and heterogeneity (20m x 20m quadrats, N=54) and assessed temporal availability of food from phenology trails (total distance 5951 m; 1073 individual trees) over 1 year (2012-2013). Over half of Bossou consists of regenerating forest and is highly diverse in terms of chimpanzee food species; large fruit bearing trees are rare and confined to primary and riverine forest. Moraceae (mulberries and figs) was the dominant family, trees of which produce drupaceous fruits favored by chimpanzees. The oil palm occurs at high densities throughout and is the only species found in all habitat types except primary forest. Our data suggest that the high densities of oil palm and fig trees, along with abundant terrestrial herbaceous vegetation and cultivars, are able to provide the chimpanzees with widely available resources, compensating for the scarcity of large fruit trees. A significant difference was found between habitat types in stem density/ha and basal area m^2 /ha of chimpanzee food species. Secondary, young secondary and primary forest emerged as the most important habitat types for availability of food tree species. Our study emphasizes the importance of examining ecological characteristics of an anthropogenic landscape as each available habitat type is unlikely to be equally important in terms of spatial and temporal availability of resources.

Keywords: *Human-dominated landscape; ecological characteristics; resource composition; food availability; primate conservation*

2.2 INTRODUCTION

Deforestation is one of the biggest threats facing non-human primates (hereafter primates) today (Chapman & Peres, 2001). Exploitation of forest and other land resources through large scale logging and mining, slash and burn agriculture, and cash crop plantations are causing considerable degradation and fragmentation of primate habitats. This continued decline in forested areas coupled with an ever expanding human population means that many primates are increasingly found in highly disturbed environments in close proximity to humans and human activity.

Such environments, often termed as human dominated, or anthropogenic, are typically fragmented mosaic landscapes with past and continuing direct human alteration of ecological processes, often reflecting human land use activities and natural resource exploitation (Ellis et al, 2006). Anthropogenic landscapes are characterized by a matrix of managed and unmanaged land use types including fragments of forested areas, varying stages of successional habitat, agricultural fields and plantations, human-made roads, and clusters of buildings for human settlement. Human activities in these landscapes have long term effects on vegetation composition and structure, as well as abiotic and biotic environmental processes (Daily et al, 2003; Elmore et al, 2006; Ferguson et al, 2003; Lunt & Spooner, 2005; Morris et al, 2011). Likewise, human induced changes on the distribution and abundance of available vegetation can have profound effects on the ecology, behavior, health and reproduction of primates and other wildlife (Campbell-Smith et al, 2011; Pozo-Montuy et al, 2013). The active management of wild and cultivated plant species can alter the density and spatial distribution of edible resources across the matrix of habitat types. Human-modified habitats may in some cases actually attract primates or help support their persistence in the landscape (Anderson et al, 2007; Fimbel, 1994; Naughton-Treves, 2002), affecting their spatial and temporal use of different habitat types (Campbell-Smith et al, 2011; Duvall, 2008). Changes in the availability of forested areas and/or natural resources can result in a shift in primate ranging patterns and the incorporation of human grown foods in their diets (Hockings et al, 2009; McKinney, 2011; McLennan & Hockings, 2014; Naughton-Treves et al, 1998). However, hunting of primates is common in recently abandoned fields and settlements (Naughton-Treves et al, 2003; Schulte-Herbrüggen et al, 2013; Smith, 2005) and negative interactions between people and primates due to crop foraging is well documented (e.g. Brncic et al, 2010; Hill, 2000; Hockings & Sousa, 2013; McLennan, 2013; Tweheyo et al, 2005). Determining the ecological patterns of specific primate resources across habitat types can help reduce assumptions on the suitability of anthropogenic landscapes for resident primate populations. Furthermore, studies that examine resource distribution and availability at habitat level are better placed to assess the ability of species to adapt to their environment when faced with anthropogenic induced environmental changes (Wiens, 1989).

The need for examining anthropogenic landscapes for conserving primate populations has become apparent in recent years (Chapman & Peres, 2001; Schwitzer et al, 2011) and an increasing number of primate studies and conservation activities are now focusing on these human dominated environments (e.g. Benchimol & Peres, 2013; Chapman et al, 2005; Cowlishaw & Dunbar, 2000; Halloran et al, 2014; Irwin et al, 2010). However, empirical data on biodiversity in agricultural-forest mosaics in primate range countries, particularly across Africa is lacking (Blanco & Waltert, 2013; Norris et al, 2010; Trimble & van Aarde, 2014). Quantifying the ecological parameters that define an anthropogenic landscape, particularly from the perspective of the primate population under investigation is challenging as each anthropogenic landscape will have dynamic spatial and temporal patterns influenced by sociocultural and ecosystem processes (Duvall, 2011). The response of a primate population to an anthropogenic landscape will be affected by these patterns, as well as the behavioral and ecological flexibility the given species has to environmental change. However, characterizing quantitatively the ecology of an anthropogenic landscape at fine spatial scales will allow comparisons to be made between studies, building on existing knowledge of what defines such environments, as well as their suitability as viable long term habitats for primate populations. Such information is imperative if conservation initiatives for primates living in these landscapes are to be successful.

Within this context, our paper focuses on quantifying the ecological parameters of the core area of a community of West African chimpanzees (*Pan troglodytes verus*) that inhabit the anthropogenic landscape of Bossou, the Republic of Guinea. *P.t. verus* is one of the most endangered of the four subspecies of chimpanzee, and is predominantly threatened by human population growth causing the expansion of agricultural practices into forested areas and increased proximity between chimpanzees and people (Humle et al, 2008). The majority of the forested landscapes across West Africa, including Guinea, are now dominated by forest-agricultural mosaics (Norris et al, 2010). Although Guinea is believed to have the largest population of *P.t. verus* (8,113-29,011 individuals) as much as 80-95% of the population is located outside of protected areas (Kormos et al, 2003). Understanding the suitability of these unprotected anthropogenic landscapes for chimpanzees, as well as chimpanzees responses to habitat changes, is of paramount importance for conservation efforts outside protected areas.

The chimpanzee population inhabiting the anthropogenic landscape of Bossou is ideal for addressing our current study. Many aspects of chimpanzee behavior along with the cultural beliefs and past and present land use practices of the local people are well understood (Matsuzawa et al, 2011; Sugiyama & Koman, 1992; Yamakoshi, 2005). Slash and burn agriculture has been practiced in this region at least since the early sixties (Kortlandt, 1986). Shifting cultivation and the natural regeneration of fallow land have created a highly heterogeneous mosaic landscape.

Accordingly, our study aimed to describe the structure, composition and diversity of known chimpanzee food species across the core area and for all habitat types found at Bossou, and to compare the suitability of the different habitat types for foraging by examining food availability. The density and availability of *Ficu*s species and terrestrial herbaceous vegetation (THV) at Bossou will be compared and discussed in relation to other chimpanzee populations as these food sources are known to be consumed by chimpanzees, to varying degrees across seasons at most sites (e.g. Basabose, 2002; Boesch, 1996; Malenky &

Wrangham, 1994; Matsumoto-Oda, 2002; Newton-Fisher, 1999; Wrangham et al, 1993; Yamakoshi, 1998).

2.3 METHODS

2.3.1 Study site

Our study was conducted in the south-eastern forest region of the Republic of Guinea, West Africa near the border with Liberia and Cote d'Ivoire. The study site is located in the anthropogenic landscape that surrounds the village of Bossou (7°38'71.7'N, 8°29'38.9'W) and is isolated from the nearest stretch of continuous mature forest in the Nimba Mountains by approximately 6 km of savanna. The climate in this region is classified as tropical wet seasonal with a long rainy season from March to October and a short dry season from November to February (Humle, 2011). The village of Bossou is surrounded by four small hills (70-150 m high) and the landscape is a patchy mosaic of primary, secondary and riverine forest, coffee plantations, cultivated fields, and fallow areas of varying successional stages (Hockings et al, 2009; Sugiyama & Koman, 1992). During our 12 month study (April 2012-March 2013), the chimpanzee community size ranged between 12-13 individuals, with 4 adult males and 6 adult females throughout.

2.3.2 Spatial composition, distribution and availability of chimpanzee resources

We conducted vegetation surveys in all available habitat types across the chimpanzees' core area to determine the floristic heterogeneity and diversity of chimpanzee food species, based on a comprehensive published list of over 200 wild, feral and cultivated plant species consumed by this chimpanzee community (Humle et al, 2011). Four forested habitat types (primary, secondary, young secondary and riverine forest) and five highly disturbed habitat types (fallow stage 1, 2, and 3, coffee plantations, and cultivated fields) were sampled (Table 2.1).

We investigated chimpanzee food species distribution across habitat types by conducting quadrat sampling. We sampled over 70% (4.3 km^2) of the Bossou chimpanzee core area (6 km^2) (Matsuzawa et al, 2011), excluding village areas, roads and paths, and inaccessible parts, such as rivers. As such, our sampling design was deemed adequate for capturing and representing all habitat types found in the Bossou landscape. We created a 250m cell grid using ArcGIS which was then overlaid onto a digitalized satellite map of the chimpanzee's core area. The midpoint within each cell represented the start point for each quadrat and each midpoint was 250m apart. GPS Expert was then used to enter these midpoints into a handheld GPS. We established a 20m x 20m ($400m^2$=0.04ha) quadrat at each midpoint and sampled a total of 54 quadrats (2.24 ha). The habitat type within each quadrat was determined directly in the field. We selected this quadrat size to ensure sampling of only one habitat type within each quadrat as larger quadrats would have risked extending across habitat types due to the highly heterogeneous nature of the study site. Furthermore, the selected quadrat size allowed a fairly rapid assessment of the survey area whilst being large enough to capture a significant proportion of chimpanzee food trees. All chimpanzee food tree species and lianas ≥ 10cm diameter at breast height (DBH, measured 1.3 m above the ground) and banana plants were identified, counted, and measured by NBM and experienced local field assistants. We measured the DBH above the buttresses for all buttressed trees.

Table 2.1 Sampled habitat types with descriptions, codes and percentage of sampled quadrats in the chimpanzee core area of Bossou, Guinea

	Habitat types and codes	**Description**	**Percentage of sampled quadrats**
Forested	Primary Forest (PF)	Old growth, mature forest > 70 years old. Concentrated on the summit of one of the small hills. Dense forest with little to no signs of human disturbance.	4
	Riverine Forest (RVF)	Seasonally flooded forest, located along waterways to a depth of approximately 20 meters.	8
	Secondary Forest (SF)	Mature secondary regrowth of vegetation. 30+ years old with a closed canopy. Dominant habitat type in core area.	25
	Young Secondary Forest (YSF)	Young secondary regrowth of vegetation. > 15 years old <30 years old with an open canopy. Dominated by stands of small, young regenerating tree species.	15
Highly disturbed	Fallow Stage 1 (F1)	Previously cultivated areas that have been recently abandoned and are < 1 year old. Cultivars still present. Dominated by the invasive species, *Chromolaena odorata.*	8
	Fallow Stage 2 (F2)	*Chromolaena odorata* still present but no longer dominant. Tree saplings, lianas and terrestrial herbaceous vegetation (THV) emerging.	8
	Fallow Stage 3 (F3)	*Chromolaena odorata* no longer present. < 15 years old. Characterized by dense tree saplings, lianas and THV.	15
	Coffee Plantation (Café)	Maintained areas dominated by cultivated coffee trees. Banana plants, oil palm (*Elaeis guineensis*) and other cultivated fruit trees such as *Citrus* species and mango (*Mangifera indica*) often present.	9
	Cultivated Field (CF)	Characterized by active cultivation. Usually contain a mix of cultivars such as cassava (*Manihot esculenta*), maize (*Zea mays*), okra (*Hibiscus esculentus*) and rice (*Oryza* sp.)	9

Note: Percentage does not sum 100 due to rounding. Forested habitats age categories adapted from Schroeder et al, 2010; Sugiyama & Koman, 1979; and Sugiyama & Koman, 1992.

Non-feeding trees were also counted to aid in characterizing habitat types within the quadrats and to establish overall tree density. However, we did not identify or measure non-feeding trees as our main aim was to establish the availability of chimpanzee feeding trees across habitat types. We further established a 1m x 1m quadrat at each midpoint within the 20m x 20m quadrat to sample the availability of THV.

2.3.3 Temporal availability of food resources

To monitor temporal chimpanzee food availability, we set up phenology surveys along existing chimpanzee trails that covered all of the four hills (total distance 5951 m). We calibrated our results using the density measures for each species as determined by the quadrat surveys, thus accounting for differences in species abundance (Chapman et al, 1994). We tagged and measured all chimpanzee food tree species and lianas ≥10 cm DBH, located within 5m either side of the trails (Chapman et al, 1992, 1994). We sampled each food tree whose trunk mid-point was within the 5m (Ganzhorn, 2003). A total of 67 species and 1073 individual trees (from 1 to 49 individuals sampled per species) were tagged and monitored. We conducted a phenology survey in the second and fourth week of each month for a total of 12 months (April 2012 – March 2013). We estimated a visual abundance score for each tree and liana on a scale of 0-4 (0: absent; 1: 1-25% canopy cover; 2: 26 -50% cover; 3: 51-75% cover; 4: 76 -100% cover) (Sun et al, 1996) for the plant part known to be eaten by the chimpanzees for that particular species. Plant parts reported here included young leaves, unripe fruit and ripe fruit as these make up the bulk of the chimpanzee diet (Hockings, 2007; Takemoto, 2002; Yamakoshi, 1998).

2.3.4 Data analyses

We carried out all statistical analyses using SPSS version 21. We tested all data for normality using a Kolmogorov-Smirnov test and used non-parametric tests throughout as our data were not normally distributed. We used two-tailed tests and set the significance level at $P \leq 0.05$.

2.3.5 Spatial resource composition, distribution and availability

We calculated the stem density per hectare and basal area (BA) m^2 per hectare of food tree species for each habitat type and for the survey area overall. Basal area gives a good indication of total fruit production and is often used as an index of primate food availability (Chapman et al, 1994; Ganzhorn, 1995; Rode et al, 2006). We assessed differences in the stem density/ha and BA m^2/ha of sampled chimpanzee food species between habitat types (N=9) using non-parametric Kruskal-Wallis one-way ANOVA test. We carried out post-hoc Mann-Whitney *U* tests with a Bonferroni correction to determine which habitat types significantly differed from one another. To evaluate THV availability, we determined stem density (m^2) at the family and species level per habitat type and overall for the area. We quantified the ecological importance of all counted food trees and lianas by calculating an importance value index at the family and species level (Mori & Boom, 1987). We calculated importance values for family and species as these combine the three most commonly reported vegetation measurements of density, frequency (or diversity), and dominance into a single index (Mori & Boom, 1987). As the importance value index is calculated as relative values, they can be used to compare between different forest communities in spite of differences in sampling intensity and area size.

Family Importance Values (FIVs) were calculated using the following equation:

FIVs = *relative density* + *relative diversity* + *relative dominance*

Where *relative density* is the percentage of stems per family of the total number of stem counts of all species/ha, *relative diversity* is the percentage species per family of the total occurrence of species in quadrats, and *relative dominance* is the percentage BA per family of the total BA m^2/ha. *Species Importance Values* (SIVs) were calculated using a similar equation:

SIVs=*relative density* + *relative frequency* + *relative dominance*

Where *relative density* is the percentage stem counts per species of the total number of stem counts of all species/ha, *relative frequency* is the percentage occurrence of each species in quadrats of the total occurrence of all species in quadrats, and *relative dominance* is the percentage BA per species of the total BA m^2/ha. Both the FIVs and SIVs total 300 and are unitless. To quantify the level of heterogeneity of chimpanzee food species, we used the Shannon-Wiener diversity index (*H'*):

$H' = - \sum_{i=1}^{S} pi \ln(pi)$

Where *pi* is the proportion of individuals belonging to the *i* th species, ln is the natural logarithm, and *S* is the total number of species in the sample (Magurran, 2004). Values for *H'* generally lie between 1.5 and 3.5; large values reflect high levels of diversity. We examined the relative abundance of each of the food species sampled by calculating the evenness using the following formula:

$J'=H'/\ln S$

Where *H'* is the Shannon-Weiner Index, ln is the natural logarithm, and *S* is the total number of species sampled (Magurran, 2004). The value of *J'* ranges from 0-1, with maximum values reached when all species sampled are of equal abundance. We also estimated the spatial distribution for each of the food species sampled using the Index of Dispersion (*ID*) and Green's Index (*GI*) (Ludwig & Reynolds, 1988) as follows:

ID = variance/mean number of individual trees of each species per quadrat

GI = (*ID*-1/*N*-1)

Where *N* is the number of individuals of a particular species. *ID* values of less than one indicate an even distribution, greater than one indicate a clumped distribution, and equal to one a random distribution. For *GI*, values less than zero indicate an even distribution, greater than zero a clumped distribution, and equal to zero a random distribution (Ludwig & Reynolds, 1988).

2.3.6 Temporal food resource availability

We calculated an index of food availability (*FAI*) for unripe fruit, ripe fruit, and young leaves using the following equation:

$FAI=\sum_{k=1}^{n} Fkm \text{ X } Dk \text{ X } Sk$

Where *Fkm* is the mean phenology score of unripe fruit, ripe fruit or young leaves of all sampled individuals in species *k* during month *m*, *Dk* is the density of species *k* from quadrat samples, and *Sk* is the mean size DBH of species *K* from quadrat samples (Fawcett, 2000; McLennan, 2013; Sun et al, 1996). We calculated monthly food availability by averaging the phenology scores of the biweekly surveys taken each month. We used this FAI index to allow comparisons between studies. However, in highly anthropogenic landscapes such as Bossou, the *Dk* density values obtained from the quadrat samples may not fully capture habitat–wide food availability due to the sparse distribution of large feeding trees.

2.4 RESULTS

2.4.1 Community wide structure, density and basal area of chimpanzee food species

Pooling the data from all of the quadrat surveys, we recorded a total of 332 chimpanzee food trees and lianas (≥ 10cm DBH) and banana stems, comprising 47 species representing 37 genera and 21 families. Overall density of chimpanzee food species was 153.7 stems/ha and community wide density for both food and non-food species (≥10cm DBH) was 253.7 stems/ha. Total BA of chimpanzee food tree and liana species was 13.0 m^2/ha. The mean ± SD DBH for all counted food tree and liana stems was 21 ± 14.2 cm. Over 60% of stems had a DBH of 10-19cm and less than 5% of stems were over 50cm DBH. Very large feeding trees are rare at Bossou with only one individual each of the species *Aningeria altissima* and *Parkia bicolor* measuring over 90cm DBH in our sample, both of which were found in primary forest.

2.4.2 Habitat composition, distribution and availability of chimpanzee food resources

Secondary forest was the most frequently encountered habitat type accounting for 25% of sampled quadrats. Both young secondary forest and old fallow (stage 3) accounted for 15% each of sampled quadrats, suggesting that a high percentage of the chimpanzees' core area is regenerating forest. All of the other highly disturbed habitat types and riverine forest were encountered in 8-9% of quadrats respectively, whilst primary forest was the rarest habitat accounting for only 4% of sampled quadrats. There was a significant difference in the stem density/ha and BA m^2/ha of food species between habitat types (Kruskal- Wallis test; stem density: X^2 (8) =80.732, P< 0.001; BA: X^2 (8) =97.897, P<0.001). Table 2.2 details the significant results of the post-hoc Mann- Whitney *U* Tests for stem density and BA of food species between habitat types. Overall young secondary forest had the highest stem density/ha followed by primary and secondary forest respectively (young secondary forest: 306 stems/ha; primary forest: 250 stems/ha; secondary forest: 248 stems/ha) (Fig. 2.1a). Secondary forest had the highest BA m^2/ha followed by young secondary and primary forest (secondary forest: 5.18 m^2/ha; young secondary forest: 4.01 m^2/ha; primary forest: 2.76 m^2/ha) (Fig. 2.1b). Stem density and BA was comparatively low for all of the highly disturbed habitat types (Fig. 2.1a, b).

Table 2.2 Significant results from the post-hoc Mann-Whitney U Test with Bonferroni correction applied for between habitat types differences in chimpanzee food species stem density/ha and basal area m^2/ha in Bossou, Guinea

Stem density/ha			**Basal area m^2/ha**		
RVF-F1	$U = 804$	$P = 0.001$	PF-F1	$U = 824$	$P = 0.001$
SF-F3	$U = 559$	$P < 0.001$	RVF-F1	$U = 802.5$	$P < 0.001$
SF-F2	$U = 417$	$P < 0.001$	SF-PF	$U = 610$	$P < 0.001$
SF-F1	$U = 399$	$P < 0.001$	SF-RVF	$U = 632$	$P < 0.001$
SF-Cafe	$U = 443$	$P < 0.001$	SF-F3	$U = 462$	$P < 0.001$
SF-CF	$U = 514$	$P < 0.001$	SF-F2	$U = 401.5$	$P < 0.001$
YSF-F2	$U = 698.5$	$P < 0.001$	SF-F1	$U = 357$	$P < 0.001$
YSF-F1	$U = 686$	$P < 0.001$	SF-Cafe	$U = 442.5$	$P < 0.001$
YSF-Cafe	$U = 721.5$	$P < 0.001$	SF-CF	$U = 463.5$	$P < 0.001$
			YSF-F3	$U = 764$	$P = 0.001$
			YSF-F2	$U = 702.5$	$P < 0.001$
			YSF-F1	$U = 659.5$	$P < 0.001$
			YSF-Cafe	$U = 735.5$	$P < 0.001$
			YSF-CF	$U = 756.5$	$P < 0.001$

PF: Primary Forest; RVF: Riverine Forest; SF: Secondary Forest; YSF: Young Secondary Forest; F3: Fallow Stage 3; F2: Fallow Stage 2; F1: Fallow Stage 1; Café: Coffee Plantation; CF: Cultivated Field. For habitat type definitions see Table 2.1

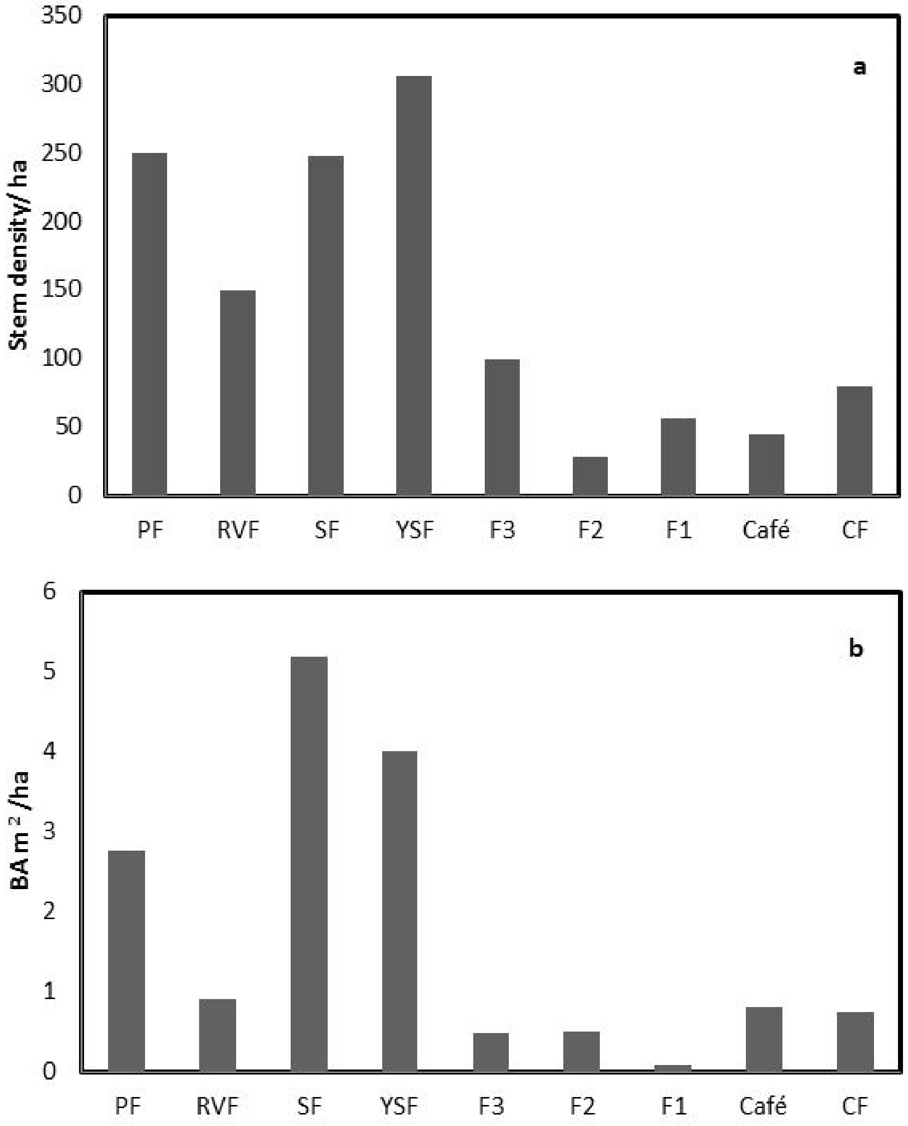

Figure 2.1 a) Total stem density/ha and b) Total basal area (BA) m^2 /ha of all sampled chimpanzee food tree species in each habitat type found in the chimpanzee core area at Bossou, Guinea. PF: Primary Forest; RVF: Riverine Forest; SF: Secondary Forest; YSF: Young Secondary Forest; F3: Fallow Stage 3; F2: Fallow Stage 2; F1: Fallow Stage 1; Café: Coffee Plantation; CF: Cultivated Field. For habitat type definitions see Table 2.1. See Supplementary Table 2.S2 for summary of results of chimpanzee food species sampling in all habitat types

The overall stem density/m^2 of THV species consumed by chimpanzees was 1.00 stems/m^2. THV of the Marantaceae family were the most frequently encountered with an overall density of 0.53 stems/m^2. Within this family, the species *Thaumatococus daniellii* had the highest overall density at 0.49 stems/m^2. The majority of *T. daniellii* stems were found in riverine forest (3.25 stems/m^2), followed by primary forest (3.00 stems/m^2). Zingiberaceae species were the only other THV family repeatedly encountered (overall density 0.36 stems/m^2) with the majority of stems belonging to the species *Aframomum latifolium* (overall density 0.21 stems/m^2). Most *A. latifolium* stems were found in secondary forest (0.62 stems/m^2). Stems of the cultivated cassava plant, *Manihot esculenta*, were the most frequently encountered herb in the highly disturbed habitat types (0.08 stems/m^2).

Moraceae (mulberries and figs) was the dominant tree family in Bossou with the most species (13 species representing 28% of the 46 tree species counted) and the highest density (32.40 stems/ha representing 23% of all counted stems). The Moraceae family also accounted for 19% of the total BA (2.50 m^2 /ha) of food trees. In contrast, all other families were characterized by 4 or less species with 55% represented by only 1 species. The second highest ranked family by FIVs, Mimosaceae, contained only 3 species with *Albizia zygia* accounting for 83% of the family total BA m^2/ha, whilst the third ranked family, Sterculiaceae was dominated by the species *Sterculia tragacantha* which accounted for 94% of the family density.

Table 2.S1 lists all sampled chimpanzee food tree species in order of highest ranked Species Importance Value (SIVs). The highest ranked species, *Albizia zygia*, occurred in 31% of quadrats and had the largest overall BA (2.39 m^2/ha). *Sterculia tragacantha* was the second highest ranked species and had the most counted stems in the sample (49 stems) and the largest overall density at 22.69 stems/ha. The oil palm tree, *Elaeis guineensis* (ranked fourth) was found in 37% of quadrats and had the second highest density of any recorded food species (17.59 stems/ha). Four *Ficus* species were identified to species level and all were

found at relatively low densities with *F. sur* and *F. exasperata* the highest with 2.78 and 2.31 stems/ha respectively. The combined density of *Ficus* species was 6.48 stems/ha. The top 7 ranked species accounted for 55% of the pooled species importance value (165 of 300 SIVs). When SIVs are pooled for each habitat type (Table 2.SI), primary forest emerged as the most important habitat for encountered chimpanzee food species. This is closely followed by secondary and young secondary forest respectively. Early stage fallow (stage 1) showed the lowest SIVs for the highly disturbed habitat types. Mid to late stage fallow (stage 2 and 3), coffee plantations and cultivated fields all presented comparable SIVs likely due to the presence of oil palm trees and intermittent large wild trees of value to local villagers, such as *Chlorophora excelsa* (Sugiyama & Koman, 1992).

2.4.3 Heterogeneity and spatial distribution of chimpanzee food species

The Shannon-Wiener diversity index (*H′*) for the entire sample of chimpanzee food species was 3.22 and the associated evenness measure (*J′*) was 0.84. The average Index of Dispersion (ID) for all sampled food species where more than one stem was counted was 6.93, and the average Green's index (GI) was 0.97. These values signify that chimpanzee food species at Bossou are characterized by high species diversity (*H′*) and species evenness *(J′*), and have a highly clumped spatial distribution (ID and GI). When we examined individual habitat types, all of the forested habitats were characterized by a range of chimpanzee food species with only marginal differences in the number of encountered stems within habitats, whereas the highly disturbed habitat types were dominated by only one or two cultivated or feral species namely oil palm trees and banana plants. Consequently, diversity and evenness measures were higher in all of the forested habitat types compared to the highly disturbed habitats (Table 2.S2). Secondary forest was the most diverse (*H'* = 3.01) and young fallow (stage1) the least diverse (*H'*=0.35) of all habitat types (Table 2.S2). Old fallow (stage3) was the most diverse of the highly disturbed habitat types, illustrating the successional stages and increasing diversity that occurs when previously cultivated land is allowed to regenerate (Table 2.S2).

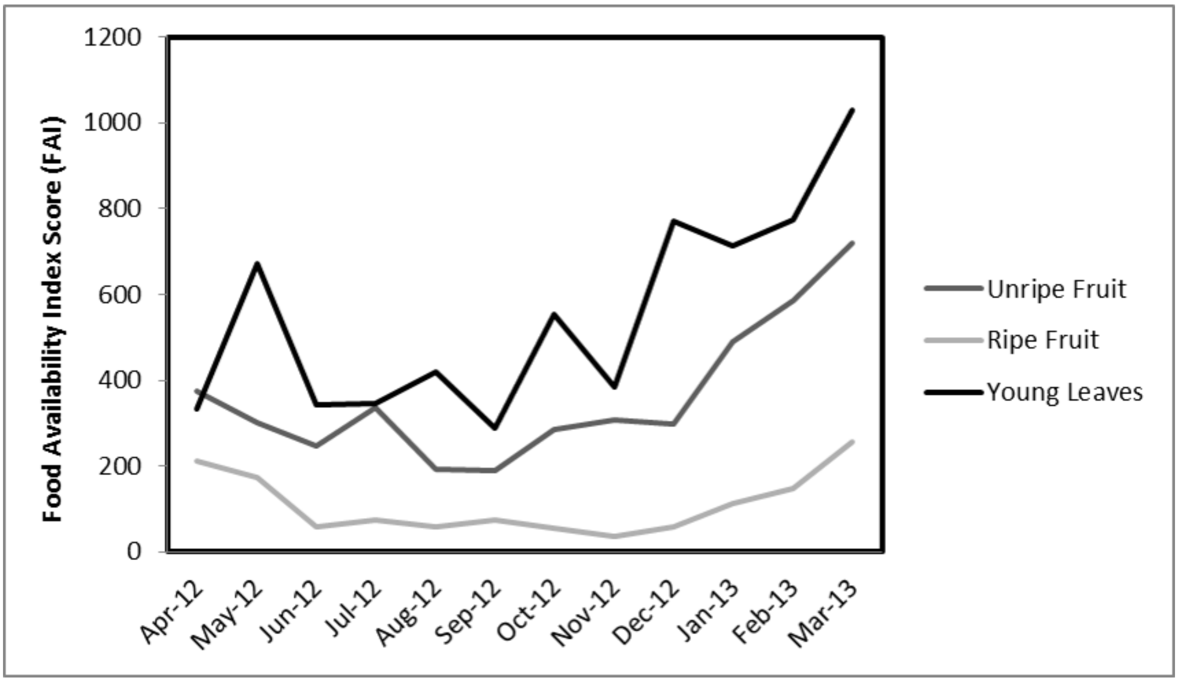

Figure 2.2 Chimpanzee food availability index score (FAI) for unripe fruit, ripe fruit, and young leaves each month for the 12 month study period (April 2012 - March 2013) in Bossou, Guinea. Wet season: April - November; Dry season: December - March

2.4.4 Temporal availability of fruit and young leaves

Ripe fruit availability was consistently low between June - December which coincides with the wet season (April - November) and the beginning of the dry season (December - March) (Fig. 2.2). Overall, ripe fruit availability was highest from January - May, with peaks in March and April, i.e. late dry season and the beginning of the rainy season (Fig. 2.2). Unripe fruit availability was considerably higher in all months compared with ripe fruit availability (Fig.

2.2). There was a peak in unripe fruit availability in July and a steady increase in availability from the month of October (Fig. 2.2). Unripe fruit availability was highest during the dry season. It is unclear whether this discrepancy between unripe and ripe fruit availability is due to fruit on some trees not reaching ripeness, increased fruit fall for ripe fruit, or if animals consumed them before they could be scored during phenology surveys. Young leaves were available throughout the 12 month period, although availability fluctuated with peaks during the dry months between December and March (Fig. 2.2).

We found that for monitored wild food trees, four species, i.e. *Canarium schweinfurthii*, *Diospyros heudolotti*, and *Ficus sur*, produced ripe fruit for extended periods (≥ 7 months), while *Pycnanthus angolensis* produced ripe fruit year round. *F. sur* was the only species of *Ficus* on the phenology trails to consistently bear ripe fruit. The cultivated orange tree, *Citrus sinensis*, produced ripe fruit in all but one month (July), while ripe fruit was available year round for the feral or wild oil palm (*E. guineensis*). The majority of other monitored chimpanzee fruit species showed seasonal fruiting patterns, except for *Musanga cercropiodes,* which produced ripe fruit intermittently throughout the 12 month period.

2.5 DISCUSSION

2.5.1 Community wide structure, density and basal area of chimpanzee food species

The majority of Bossou is regenerating forest (55% of sampled quadrats: secondary forest, young secondary forest and stage 3 fallow combined) with only very small patches of old growth primary and riverine forests (4% and 9% of quadrats, respectively). The rest of the landscape is composed of highly degraded anthropogenic habitats (32% of sampled quadrats) including cultivated and abandoned fields and coffee plantations. The scarcity of old growth forest and the prevalence of human altered land types likely explain why Bossou deviates from many other tropical forest areas (Richards, 1996). Indeed, the community wide (non-food and food species combined) density of 253.7 stems/ha falls below the reported range of 300-700 stems for tropical forests (Richards, 1996). The stem density for Bossou is also far below the density of 467 stems/ha for the forest fragments in Bulindi, Uganda (McLennan & Plumptre, 2012) and the stem density values reported for the highly disturbed forest fragments in Mpigi, Uganda (Private Forest: 383.5 stems/ha; Local forest: 360.6 stems/ ha; Central Forest: 360.2 stems/ha) (Turyahabwe et al, 2008). The overall BA (13.0 m^2/ha), and average DBH (21 ± 14.9 cm) for chimpanzee food species further reflects the fact that many of the areas in Bossou are young forest regenerating on past cultivated land. Large fruit bearing trees are very rare and only found in the small patches of primary and riverine forests.

2.5.2 Heterogeneity and spatial distribution of chimpanzee food species

Bossou is highly diverse for chimpanzee food species (H'=3.22) with stems fairly evenly distributed between species (J'= 0.84). The high percentage of species with only a few stems within the sample may be driving this heterogeneity and evenness. Additionally, ten stems or more were encountered for only 7 of the 47 sampled chimpanzee food species and these species also accounted for over 50% of total density (76.90 stems/ha), and nearly 70% of overall BA (8.90 m^2/ha). Again this suggests that whilst the chimpanzee food species available at Bossou is diverse, a small number of species numerically dominate. The relatively common species display a highly clumped distribution (ID and GI) and were frequently encountered across the survey area. The clumped distribution of more common food species means that the chimpanzees can maximize foraging efficiency by feeding on multiple stems in close proximity during periods when one or more of the common species produce food (Potts & Lwanga, 2013).

2.5.3 Habitat composition, distribution, and spatial and temporal availability of chimpanzee food resources

The dominance of the Moraceae family (mulberries and figs) at Bossou appears to be rare for more continuous stretches of tropical forests in Africa (Turner, 2001; White, 1983). However, Moraceae is also the most prevalent family in the forest fragments of Bulindi, Uganda (Mclennan & Plumptre, 2012). Bortolamiol et al (2014) examined three distinct sites within Kibale National Park, Uganda and found that fig trees had a higher density with a greater BA at the highly disturbed site (Sebitoli) than at the moderately disturbed (Kanyawara) or least disturbed forest (Ngogo) site. The combined BA of 0.30 m^2/ha for all encountered *Ficus* species at Bossou is lower than that recorded for all three sites in Kibale National Park (Sebitoli: 1.52 m^2/ha; Kanyawara: 0.82 m^2/ha; Ngogo: 0.54 m^2/ha) (Bortolamiol et al, 2014). However, the combined density for all encountered *Ficus* species at Bossou (6.5 stems/ha) is higher than published results for the more continuous forest site of Budongo, Uganda (5.9 stems/ha) (McLennan & Plumptre, 2012), although it is considerably lower than the 16.8 stems/ha recorded for the wet riverine forest fragments in Bulindi (McLennan & Plumptre, 2012). Increased light conditions caused by the formation of gaps and edges through anthropogenic activities may explain the dominance of certain species of the Moraceae family, including some *ficus* species, in forested areas with high levels of human disturbance (Gautier-Hion & Michaloud, 1989; Fashing, 2001). Many species of Moraceae produce drupaceous fruits that are favored by chimpanzees and other frugivores. *Ficus* fruits are noted as an important food source for chimpanzees particularly during times of low fruit availability, as *Ficus* species fruit asynchronously throughout the year (Wrangham et al, 1993). Fig fruits are a preferred food for the Bossou chimpanzees (Takemoto, 2002) with fruits from *Ficus* species making up 7% of overall chimpanzee feeding time (Bryson-Morrison, unpublished data). *Ficus sur* produced ripe fruit for extended periods during this study, while other *Ficus* species rarely bore fruits and for any length of time on the phenology trails. However due to the asynchronous fruiting patterns of *Ficus* species, it is unlikely that monitored stems reflect fruiting patterns of the community wide *Ficus* population.

The most abundant chimpanzee food tree species in Bossou, *Albizia zygia* and *Sterculia tragacantha*, are fast growing pioneer species that are characteristic of regenerating secondary forests (Burkill, 1985). The oil palm tree, *Elaeis guineensis*, also occurs at high densities and is the only species to be found in every habitat type at Bossou except primary forest. The oil palm is native to West Africa (Zeven, 1972; Hartley, 1988; Sowunmi, 1999) and is particularly common in forested areas that are subject to anthropogenic disturbances. The oil palm tree serves as an important resource for local people at Bossou, where it is predominantly used in the production of palm oil for domestic and commercial use. The chimpanzees also rely heavily on the oil palm tree for food with ripe fruit and other plant parts available year round (Humle & Matsuzawa, 2004). The high density of oil palm and fig trees may offset the rarity of large fruit bearing trees at Bossou, providing important year round resources for the chimpanzees. Similar results were found in Bulindi (McLennan

& Plumptre, 2012) where *Phoenix reclinata* palms, as well as *Ficus* species, were highly abundant.

THV is also abundant at Bossou, particularly species of the Marantaceae and Zingiberaceae families. The overall stem density of THV at Bossou (1.00 stems/m^2) is comparable with reported results for other chimpanzee habitats (0.90 stems/m^2 Kibale National Park, Uganda and 1.06 stems/m^2 Lomako Forest, Zaire: Malenky & Wrangham, 1994; 1.03 stems/m ^{2} Kahuzi Forest, DRC: Basabose, 2002), although it should be noted that our sample size was smaller than that of other sites. Chimpanzee consumption of THV differs between study sites (Boesch, 1996; Chapman et al, 1995; Matsumoto-Oda, 2002; Newton-Fisher, 1999; Wrangham et al, 1996; Yamakoshi, 1998). Chimpanzee THV consumption has been found to increase during fruit scarce periods at some sites (e.g. Kibale, Uganda: Wrangham et al, 1996), whilst others have shown THV consumption to be consistently low regardless of fruit availability (e.g. Budongo, Uganda: Newton-Fisher, 1999). Previous studies at Bossou found that the chimpanzees fed on THV evenly throughout the year with no relationship between fruit availability and THV consumption (Yamakoshi, 1998). Like oil palm and fig trees, THV also appears to provide a widely available year round resource for the chimpanzees.

The relatively low density and basal area of chimpanzee food resources in the highly disturbed habitats reflects the scarcity of large mature trees and the prevalence of cultivars and/or early stage successional vegetation and saplings in the chimpanzees' core area. We did not find a significant difference in stem density or basal area of chimpanzee food trees between any of the highly disturbed habitat types. This may reflect limitations in our sampling for these habitat types as time and resources did not allow us to survey saplings or stems measuring < 10cm DBH. However, future studies should endeavor to do so to fully determine the floristic characteristics and regenerating capacities of different types of disturbed habitat for chimpanzee resources. The SIVs for secondary and young secondary forest were comparatively large (Table SI) with both age classes of secondary forest producing an abundant and diverse source of chimpanzee food species, emphasizing the conservation value of disturbed areas that represent key habitat for chimpanzees. Despite its small size (<1km^2) (Humle, 2011), primary forest emerged as a critical habitat for chimpanzee food species as reflected by its high SIVs (Table 2.S1). The local cultural beliefs mean that a 'sacred' patch of primary forest has been left untouched providing an important source of old growth fruit trees, lianas and THV for the chimpanzees (Kortlandt, 1986). The land use patterns of the people that inhabit Bossou also act to create and maintain habitat that is attractive to the chimpanzees. The traditional use of shifting cultivation means that Bossou presents large areas of regenerating forest providing important sources of food from secondary forest specialists and disturbance adapted species, such as *Musanga cecropioides* and *Myrianthus* species. Research in the Budongo Forest Reserve, Uganda, has also revealed that logged forest and forest edges, which offer an abundance of disturbance adapted and pioneer species, represent important habitat for food for chimpanzees at this site (Tweheyo et al, 2004).

Compared to the other forested habitat types, riverine forest presented a small stem density/ha, BA m^2/ha and SIVs for encountered chimpanzee food tree species. Most of the riverine forest patches in Bossou are relatively small and surrounded by wet cultivated fields comprised of rice (*Oryza* sp.), groundnuts (*Arachis hypogaea*), and oil and raffia (*Raphia gracilis*) palm trees. The riverine forest areas in Bossou have an abundance of liana species, which is characteristic of wet forest habitat (Bongers et al, 2002). However, many of these lianas were not counted during our surveys as they measured < 10 cm DBH but are likely to be important sources of ripe fruits for the chimpanzees, particularly during fruit scarce periods as various liana species have been found to fruit asynchronously (Moscovice et al, 2007). Very large old growth trees are present in riverine forest areas, many of which are held as sacred by the local Manon people, but they are both numerically and spatially rare and as such were not captured during our surveys. Furthermore, riverine forest habitat has a large density of THV, particularly *Thaumatoccocus daniellii* of the Marantaceae family, and provides important sources of water for the chimpanzees during the dry season (Pers. Obs.). It is therefore likely that these riverine forest areas serve as temporally important habitat for resources for the Bossou chimpanzees but further research is required to verify this.

Although all of the highly disturbed habitat types had relatively low SIVs for chimpanzee food species compared to forested habitats (Table 2.S1), both cultivated and abandoned areas provide the chimpanzees with a significant source of cultivated foods. For example, the cultivated orange tree, *Citrus sinensis*, which is found in coffee plantations and cultivated fields, almost continually produced ripe fruit over the course of the 12 month study period providing the chimpanzees with an important source of ripe fruit during the wild fruit scarce season. A wide variety of cultivated foods are fully incorporated into the Bossou chimpanzee diet (Takemoto, 2002; Hockings et al, 2009) and appear to be a key alternative and/or preferred food source to wild fruits (Hockings et al, 2009). The chimpanzees at Bossou are totemic to the local Manon people which afford them a degree of tolerance and protection when crop foraging as it is culturally forbidden to kill a chimpanzee (Matsuzuwa et al, 2011). However, each area where chimpanzees and other primates co-exist alongside people face a unique set of cultural, economic, and ecological factors influencing the prevalence of crop consumption as well as people's tolerances of, and reactions to such incursions into their fields (Hill, 2015). Consequently, crop foraging by chimpanzees and other primates presents significant challenges to the co-existence between people and primates, complicating species conservation in anthropogenic landscapes.

2.5.4 Conclusions

Our study clearly shows that the anthropogenic landscape at Bossou is highly diverse for chimpanzee food species and that different habitat types vary significantly in food species availability. The combination of a small patch of old growth forest, abundant fig and oil palm trees, cultivars that produce ripe fruit nearly year round, and THV provide the chimpanzees with a diversity of food resources. Furthermore, this combination compensates for the scarcity of large fruit trees, providing the chimpanzees with a readily available supply of alternative foods during the fruit scarce season. However, many of the foods that the Bossou chimpanzees rely on are grown and/or maintained by people. Consequently, a fairly large proportion of the chimpanzee resources are susceptible to shifts in crop production which could cause significant and rapid changes in the amount of food available to the chimpanzees.

The oil palm tree occurs at high densities throughout Bossou and provides the chimpanzees with six different types of food (i.e. ripe fruit, nut kernel, leaf petiole, leaf pith, flower, and heart) year round (Humle & Matsuzawa, 2004). Although the oil palm is a shared resource between local people and chimpanzees at Bossou there is little competition over its use (Humle et al, 2014). The oil palm evidently plays an important role in aiding chimpanzee survival in this particular anthropogenic landscape. However, Humle et al (2014) found that people across West Africa vary greatly in their perceptions of chimpanzees as competitors for the oil palm in landscapes where this resource is shared between people and chimpanzees. Furthermore, the extent to which chimpanzee communities rely on oil palm also differs greatly (Humle et al, 2014). Orangutan reliance on oil palm, and conflict between orangutans and oil palm growers, has also been found to vary across sites in Sumatra and Malaysia (Marchal & Hill, 2009). These differences highlight the need to understand the ecological reliance of shared resources from the perspective of primates and people, as well as the dynamics surrounding the relationships between people and primates in anthropogenic landscapes (Fuentes & Hockings, 2010). What applies to one area may be very different in another requiring a unique approach to conservation and education initiatives.

Our study also critically highlights the importance of defining ecological characteristics across available habitat types within an anthropogenic landscape and the need to monitor these as landscape characteristics change over time with shifts in climate and land use patterns (Chapman et al, 2011). Evidently each available habitat type is not equally important in terms of resource availability for the chimpanzees. It is necessary to understand which habitat types provide different resources to enable important species and/or habitats to be prioritized in conservation management plans. Additional research is required for chimpanzees and other primates to assess how such landscapes affect ranging patterns, feeding and social behaviors, nutritional requirements, and overall demographic rates. Indeed, further in-depth studies are vital to increase our understanding of the suitability of anthropogenic landscapes for the long term survival of chimpanzees and other wildlife species.

2.6 REFERENCES

Anderson J, Rowcliffe JM, Cowlishaw G. (2007). Does the matrix matter? A forest primate in a complex agricultural landscape. *Biological Conservation* 135:212-222.

Basabose AK. (2002). Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. *American Journal of Primatology* 58: 1-21.

Benchimol M, Peres CA. (2013). Anthropogenic modulators of species–area relationships in Neotropical primates: a continental-scale analysis of fragmented forest landscapes. *Diversity and Distributions* 19: 1339-1352.

Blanco V, Waltert M. (2013). Does the tropical agricultural matrix bear potential for primate conservation? A baseline study from Western Uganda. *Journal for Nature Conservation* 21: 383-393.

Boesch C. (1996). Social grouping in Tai'chimpanzees. In: McGrew WC, Marchant LF, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 101-113.

Bongers F, Schnitzer S, Traore D. (2002). The importance of lianas and consequences for forest management in West Africa. *BioTerre Special edition*: 59-70.

Bortolamiol S, Cohen M, Potts K, et al. (2014). Suitable habitats for endangered frugivorous mammals: small-scale comparison, regeneration forest and chimpanzee density in Kibale National Park, Uganda. *PloS one* 9: 1-12.

Brncic T, Amarasekaran B, McKenna A. (2010). Sierra Leone national chimpanzee census 2010. *Tacugama Chimpanzee Sanctuary, Freetown, Sierra Leone*.

Burkill HM. (1985). *The useful plants of west tropical Africa, second edition*. Kew: Royal Botanical Gardens.

Campbell-Smith G, Campbell-Smith M, Singleton I, Linkie M. (2011). Raiders of the lost bark: Orangutan foraging strategies in a degraded landscape. *PloS one* 6: 1-8.

Chapman CA, Chapman LJ, Ghai RR, et al. (2011). Complex responses to climate and anthropogenic changes: An evaluation based on data from Kibale National Park, Uganda. In Plumptre AJ, editor. *Long term changes in Africa's Rift Valley: impacts on Biodiversity and Ecosystems.* Hauppauge, New York: Nova Science Publishers: 70-87.

Chapman CA, Chapman LJ, Wrangham R. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*: 36: 59-70.

Chapman CA, Chapman LJ, Wrangham R, et al. (1992). Estimators of fruit abundance of tropical trees. *Biotropica* 24: 527-531.

Chapman CA, Gillespie TR, Goldberg TL. (2005). Primates and the ecology of their infectious diseases: How will anthropogenic change affect host-parasite Interactions? *Evolutionary Anthropology: Issues, News, and Reviews* 14: 134-144.

Chapman CA, Peres CA. (2001). Primate conservation in the new millennium: the role of scientists. *Evolutionary Anthropology* 10: 16-33.

Chapman CA, Wrangham R, Chapman LJ. (1994). Indices of habitat-wide fruit abundance in tropical forest. *Biotropica* 26: 160-171.

Cowlishaw G, Dunbar RI. (2000). *Primate conservation biology*. Chicago: University of Chicago Press.

Daily GC, Ceballos G, Pacheco J, Suzán G, Sánchez-Azofeifa A. (2003). Countryside biogeography of Neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology* 17: 1814-1826.

Duvall CS. (2008). Human settlement ecology and chimpanzee habitat selection in Mali. *Landscape Ecology* 23: 699-716.

Duvall CS. (2011). Biocomplexity from the ground up: Vegetation patterns in a West African savanna landscape. *Annals of the Association of American Geographers* 101: 497-522.

Ellis EC, Wang H, Xiao K, et al. (2006). Measuring long-term ecological changes in densely populated landscapes using current and historical high resolution imagery. *Remote Sensing of Environment* 100: 457-473.

Elmore AJ, Mustard JF, Hamburg SP, Manning SJ. (2006). Agricultural legacies in the Great Basin alter vegetation cover, composition, and response to precipitation. *Ecosystems* 9: 1231-1241.

Fashing PJ. (2001). Feeding ecology of Guerezas in the Kakamega Forest, Kenya: The importance of Moraceae fruit in their diet. *International Journal of Primatology* 22: 579-609.

Fawcett KA. (2000). *Female relationships and food availability in a forest community of chimpanzees* (PhD thesis). Edinburgh: University of Edinburgh. Available from: EThOS (uk.bl.ethos.531608).

Ferguson BG, Vandermeer J, Morales H, Griffith DM. (2003). Post-agricultural succession in El Petén, Guatemala. *Conservation Biology* 17: 818-828.

Fimbel C. (1994). The relative use of abandoned farm clearings and old forest habitats by primates and a forest antelope at Tiwai, Sierra Leone, West Africa. *Biological Conservation* 70: 277-286.

Fuentes A, Hockings KJ. (2010). The ethnoprimatological approach in primatology. *American Journal of Primatology* 72: 841-847.

Ganzhorn JU. (1995). Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology* 76: 2084-2096.

Ganzhorn JU. (2003). Habitat description and phenology. In Setchell JM, Curtis DJ, editors. *Field and laboratory methods in primatology*. Cambridge: Cambridge University Press. p 40-56.

Gautier-Hion A, Michaloud G. (1989). Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology* 70: 1826-1833.

Halloran AR, Cloutier CT, Monde S, Sesay PB. (2014). The Tonkolili Chimpanzee Project in Sierra Leone: Implications for chimpanzee conservation strategies in anthropogenic landscapes. *African Primates* 9: 15-22.

Hartley C. (1988). *The oil palm. Tropical Agriculture Series*. London: Longman.

Hill CM. (2000). Conflict of interest between people and baboons: crop raiding in Uganda. *International Journal of Primatology* 21: 299-315.

Hill CM. (2015). Perspectives of “conflict” at the wildlife-agriculture boundary: 10 Years on. *Human Dimensions of Wildlife* 20: 296-301.

Hockings KJ (2007). *Human-chimpanzee coexistence at Bossou, the Republic of Guinea: A chimpanzee perspective* (PhD Thesis). Stirling: University of Stirling. Available from: EthOS (uk.bl.ethos.513696).

Hockings KJ, Anderson, JR, 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: 636-646.

Hockings KJ, Sousa C. (2013). Human-chimpanzee sympatry and interactions in Cantanhez National Park, Guinea-Bissau: current research and future directions. *Primate Conservation* 26: 57-65.

Humle T. (2011). Location and ecology. In Matsuzawa T, Humle T, Sugiyama Y, editors. *The chimpanzees of Bossou and Nimba.* London: Springer. p 13-21.

Humle T, Boesch C, Duvall C, et al. (2008). *Pan troglodytes* ssp. *verus*. *The IUCN Red List of Threatened Species.* Version 2014.3. Available from: www.iucnredlist.org (Downloaded on 08 June 2016).

Humle T, Garriga R, McKenna A, Amarasekaran B. (2014). *The interface between wild chimpanzee culture, land use management and agricultural development: the case of the oil palm*. Paper presented at the International Primatological Society. Vietnam: 11-16 August.

Humle T, Koops K, Cherif P. (2011). Appendix B: Plant food list of Bossou chimpanzees. In Matsuzawa T, Humle T, Sugiyama Y, editors. *The chimpanzees of Bossou and Nimba*. London: Springer:406-411.

Humle T, Matsuzawa T. (2004). Oil palm use by adjacent communities of chimpanzees at Bossou and Nimba Mountains, West Africa. *International Journal of Primatology* 25: 551-581.

Irwin MT, Wright PC, Birkinshaw C, et al. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation* 143: 2351-2362.

Kormos R, Boesch C, Bakarr M, Butynski T. (2003). *West African chimpanzees, status survey and conservation action plan.* IUCN/SSC Primate Specialist Group. Gland, Switzerland and Cambridge, UK: IUCN.

Kortlandt A. (1986). The use of stone tools by wild-living chimpanzees and earliest hominids. *Journal of human evolution* 15: 77-132.

Ludwig J, Reynolds J. (1988). *Statistical ecology*. New York: Wiley-Liss.

Lunt ID, Spooner PG. (2005). Using historical ecology to understand patterns of biodiversity in fragmented agricultural landscapes. *Journal of Biogeography* 32: 1859-1873.

Magurran A E. (2004). *Measuring biological diversity*. Oxford: Blackwell.

Malenky RK, Wrangham RW. (1994). A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. *American Journal of Primatology* 32: 1-12.

Marchal V, Hill C. (2009). Primate crop-raiding: a study of local perceptions in four villages in North Sumatra, Indonesia. *Primate conservation* 24: 107-116

Matsumoto-Oda A. (2002). Behavioral seasonality in Mahale chimpanzees. *Primates* 43: 103-117.

Matsuzawa T, Humle T, Sugiyama Y, editors. (2011). *The chimpanzees of Bossou and Nimba.* London: Springer.

Mckinney T. (2011). The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced Capuchins (*Cebus capucinus*). *American Journal of Primatology* 73: 439-448.

McLennan MR. (2013). Diet and feeding ecology of chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: Foraging strategies at the forest–farm interface. *International Journal of Primatology* 34: 1-30.

McLennan MR, Hockings KJ. (2014). Wild chimpanzees show group differences in selection of agricultural crops. *Scientific reports* 4: 1-7.

McLennan MR, Plumptre AJ. (2012). Protected apes, unprotected forest: composition, structure and diversity of riverine forest fragments and their conservation value in Uganda. *Tropical Conservation Science* 5: 79-103.

Mori S A, Boom B M. (1987). Chapter II, The forest. In: Mori SA, editor. *The Lecythidaceae of a lowland Neotropical forest: La Fumée Mountain, French Guiana*. New York: Memoires of the New York Botanical Garden 44. P 9-29.

Morris L, Monaco T, Sheley R. (2011). Land-use legacies and vegetation recovery 90 years after cultivation in Great Basin sagebrush ecosystems. *Rangeland Ecology & Management* 64: 488-497.

Moscovice L, Issa M, Petrzelkova K, et al. (2007). Fruit availability, chimpanzee diet, and grouping patterns on Rubondo Island, Tanzania. *American Journal of Primatology* 69: 487-502.

Naughton-Treves L. (2002). Wild animals in the garden: Conserving wildlife in Amazonian agroecosystems. *Annals of the Association of American Geographers* 92: 488-506.

Naughton-Treves L, Mena JL, Treves A, Alvarez N, Radeloff VC. (2003). Wildlife survival beyond park boundaries: The impact of slash-and-burn agriculture and hunting on mammals in Tambopata, Peru. *Conservation Biology* 17: 1106-1117.

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: 596-606.

Newton-Fisher NE. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *African Journal of Ecology* 37: 344-354.

Norris K, Asase A, Collen B, et al. (2010). Biodiversity in a forest-agriculture mosaic–The changing face of West African rainforests. *Biological Conservation* 143: 2341-2350.

Potts KB, Lwanga JS. (2013). Floristic heterogeneity at Ngogo, Kibale National Park, Uganda and possible implications for habitat use by chimpanzees (*Pan troglodytes*). *African Journal of Ecology* 52: 1-11.

Pozo-Montuy G, Serio-Silva JC, Chapman CA, Bonilla-Sánchez YM. (2013). Resource use in a landscape matrix by an arboreal primate: evidence of supplementation in black howlers (*Alouatta pigra*). *International Journal of Primatology* 34: 714-731.

Richards P. (1996). *The tropical rain forest*. Cambridge: Cambridge University Press.

Rode KD, Chapman CA, McDowell LR, Stickler C. (2006). Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*). *Biotropica* 38: 625-634.

Schulte-Herbrüggen B, Rowcliffe JM, Homewood K, et al. (2013). Wildlife depletion in a West African farm-forest mosaic and the implications for hunting across the landscape. *Human Ecology* 41: 795-806.

Schroeder J, Oke D, Onyekwelu J, Yirdaw E. (2010). Secondary forests in West Africa: A challenge and opportunity for management. In Mery G, Katila P, Galloway G, Alfaro R, Kanninen M, editors. *Forests and society – responding to global drivers of Change 25.* Vienna: IUFRO World Series. p 335-353.

Schwitzer C, Glatt L, Nekaris KAI, Ganzhorn JU. (2011). Responses of animals to habitat alteration: an overview focusing on primate. *Endangered Species Research* 14: 31-38.

Smith DA. (2005). Garden game: shifting cultivation, indigenous hunting and wildlife ecology in Western Panama. *Human Ecology* 33: 505-537.

Sowunmi MA. (1999). The significance of the oil palm (*Elaeis guineensis* Jacq.) in the late Holocene environments of west and west central Africa: a further consideration. *Vegetation History and Archaeobotany* 8: 199-210.

Sugiyama Y, Koman J. (1979). Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* 20: 323-339.

Sugiyama Y, Koman J. (1992). The flora of Bossou: Its utilization by chimpanzees and humans. *African Study Monographs* 13: 127-169.

Sun C, Kaplin BA, Kristensen KA, et al. (1996). Tree phenology in a tropical montane forest in Rwanda. *Biotropica* 28: 668-681.

Takemoto H. (2002). *Feeding ecology of chimpanzees in Bossou, Guinea: Coping with the seasonal fluctuation of food supply and micrometeorology in the tropical forest*. (Unpublished PhD thesis). Kyoto: Kyoto University.

Trimble MJ, van Aarde RJ. (2014). Supporting conservation with biodiversity research in sub-Saharan Africa's human-modified landscapes. *Biodiversity and Conservation* 23: 2345-2369.

Turner IM. (2001). Rainforest ecosystems: Plant diversity. In Levin SA, editor. *Encyclopedia of biodiversity volume 5*. San Diego: Academic Press. p 13-23.

Turyahabwe N, Geldenhuys C, Watts S, Tweheyo M. (2008). Linking forest tenure and anthropogenic factors with institutions and the effectiveness of management in Mpigi forests, central Uganda. *Southern Forests: a Journal of Forest Science* 70: 255-267.

Tweheyo M, Hill CM, Obua J. (2005). Patterns of crop raiding by primates around the Budongo Forest Reserve, Uganda. *Wildlife Biology* 11: 237-247.

Tweheyo M, Lye KA, Weladji RB. (2004). Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management* 188: 267-278.

White F. (1983). *The vegetation of Africa*. Paris: UNESCO.

Wiens JA. (1989). Spatial scaling in ecology. *Functional Ecology* 3: 385-397.

Wrangham RW, Chapman CA, Clark-Arcadi AP, Isabirye-Basuta G. (1996). Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups.

In McGrew WC, Marchant LF, Nishida, T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 45-57.

Wrangham R, Conklin N, Etot G, et al. (1993). The value of figs to chimpanzees. *International Journal of Primatology* 14: 243-256.

Yamakoshi G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *American Journal of Physical Anthropology* 106: 283-295.

Yamakoshi G. (2005). What is happening on the border between humans and chimpanzees? Wildlife conservation in West African rural landscapes. In Hiramatsu K, editor. *Coexistence with nature in a 'globalising' world: field science perspectives. Proceedings of the 7th Kyoto University International Symposium*. Kyoto: Kyoto University: 91-97.

Zeven A. (1972). The partial and complete domestication of the oil palm (*Elaeis guineensis*). *Economic Botany* 26: 274-279.

2.7 SUPPORTING INFORMATION

2.7.1 Appendix 2.S1: Table 2.S1

Table 2.S1 Species Importance Values (SIVs) of chimpanzee food tree species recorded in quadrats for each habitat type in the chimpanzee core area in Bossou, Guinea. PF: Primary Forest; RVF: Riverine Forest; SF: Secondary Forest; YSF: Young Secondary Forest; F3: Fallow Stage 3; F2: Fallow Stage 2; F1: Fallow Stage 1; Café: Coffee Plantation; CF: Cultivated Field. For habitat type definitions see Table 2.1

Species	Family	PF	RVF	SF	YSF	F3	F2	F1	Café	CF
Albizia adiantifolia	Mimosaceae			0.1	0.4	0.3	0.3			
Albizia ferruginea	Mimosaceae		0.3	0.5						
Albizia zygia	Mimosaceae		0.3	1.2	1.0		0.4			
Alchornea cordifolia	Euphorbiaceae			0.2						
Aningueria altisima	Sapotaceae	0.9		0.2						
Antiaris africana	Moraceae			0.3						0.5
Blighia welwitschii	Sapindaceae	0.6		0.3	0.1					
Bosquiea angolensis	Moraceae	0.6		0.2						
Brideria micratha	Euphorbiaceae			0.1						
Canarium schweinfurthii	Burseraceae		0.3	0.2						
Ceiba pentandra	Bombacaceae	0.6	0.3	0.1	0.3					
Chlorophora excelsa	Moraceae		0.3	0.9	0.6	0.4			0.6	0.4
Citrus sinensis	Rutaceae								0.4	
Cola cordifolia	Sterculiaceae	0.6								
Craterispermum laurinum	Rubiaceae			0.4						
Elaeis guineensis	Palmae		0.5	0.4	0.8	0.4	2.1	1.3	1.6	1.1
Ficus bignonifolia	Moraceae					0.5				
Ficus exasperata	Moraceae			0.3	0.3					
Ficus ovata	Moraceae			0.1						
Ficus sur	Moraceae			0.1	0.3					
Funtumia elastica	Apocynaceae		0.3	0.4	0.1					
Hannoa klaineana	Siimaroubaceae			0.1						
Macaranga barteri	Euphorbiaceae		0.6	0.2						
Mangufera indica	Anacardiaceae									0.3
Monodora tenuifolia	Annonacea			0.2						
Morus mesozygia	Moraceae		0.3	0.1						

Musanga cecropioides	Moraceae				0.2	0.3				
Myrianthus arboreus	Moraceae			0.2	0.6					
Myrianthus libericus	Moraceae	0.6	0.4	0.3	0.4					
Myrianthus serratus	Moraceae			0.3						
Nauclea latifolia	Rubiaceae								0.3	
Newbouldia laevis	Bignoniaceae	0.6								
Parinari exselsa	Rosaceae			0.2						
Parkia bicolor	Rosaceae	1.6	0.4		0.1					0.8
Pseudospondias microcarpa	Anacardiaceae	1.3	0.3	0.2	0.6					
Pycnathus angolensis	Myristicaceae	0.6	1.0	0.2		0.6				
Spondias cythera	Anacardiaceae		0.4	0.1	0.3					
Spondias mombin	Anacardiaceae				0.2					
Sterculia tragacantha	Sterculiaceae	1.1		0.7	1.3					
Tetrorchidium didymostemon	Euphorbiaceae			0.3	0.3					
Trichilia amerta	Meliaceae			0.1						
Trichilia heudelotii	Meliaceae	0.6		0.1	0.3					
Triplochiton scleroxylon	Sterculiaceae	0.6								
Vitex doniana	Verbenaceae				0.1					
Total per habitat type		**10**	**5.7**	**8.7**	**8.3**	**2.5**	**2.8**	**1.3**	**3.0**	**3.1**

.

2.7.2 Appendix 2.S2: Table 2.S2

Table 2.S2 Summary of results for chimpanzee food species sampling for all habitat types in the chimpanzee core area in Bossou, Guinea. Overall values are community wide. PF: Primary Forest; RVF: Riverine Forest; SF: Secondary Forest; YSF: Young Secondary Forest; F3: Fallow Stage 3; F2: Fallow Stage 2; F1: Fallow Stage 1; Café: Coffee Plantation; CF: Cultivated Field. For habitat type definitions see Table 2.1

Habitat type	Stem density/ha	Basal Area (m^2/ha)	Heterogeneity (*H'*)	Evenness (*J'*)
PF	250.00	2.76	2.42	0.94
RVF	150.00	0.76	2.56	0.95
SF	248.08	5.45	3.01	0.85
YSF	306.25	3.33	2.81	0.94
F3	100.00	0.40	1.56	0.80
F2	28.13	0.06	0.85	0.77
F1	56.25	0.08	0.35	0.50
Café	45.00	0.34	1.00	0.72
CF	80.00	0.66	1.51	0.84
Overall	**153.70**	**12.99**	**3.22**	**0.84**

Chapter 3 CHIMPANZEE ACTIVITY AND HABITAT USE

3.1 ABSTRACT

Many primate populations inhabit anthropogenic landscapes. Understanding their long-term ability to persist in such environments and associated real and perceived risks for both primates and people is essential for effective conservation planning. Primates in forest-agricultural mosaics often consume cultivars to supplement their diet, leading to potentially negative encounters with farmers. When crossing roads, primates also face the risk of encounters with people and collision with vehicles. Chimpanzees (*Pan troglodytes verus*) in Bossou, Guinea, West Africa, face such risks regularly. In this study, we aimed to examine their activity budget across habitat types and the influence of anthropogenic risks associated with cultivated fields, roads and paths on their foraging behaviour in non-cultivated habitat. We conducted six hour morning or afternoon follows daily from April 2012-March 2013. Chimpanzees preferentially used forest habitat types for travelling and resting and highly disturbed habitat types for socialising. Wild fruit and crop availability influenced seasonal habitat use for foraging. Overall, chimpanzees preferred mature forest for all activities. They showed a significant preference for foraging at > 200m from cultivated fields compared to 0-100m and 101-200m, with no effect of habitat type or season, suggesting an influence of associated risk. Nevertheless, the chimpanzees did not actively avoid foraging close to roads and paths. Our study reveals chimpanzee reliance on different habitat types and the influence of human-induced pressures on their activities. Such information is critical for the establishment of effective land use management strategies in anthropogenic landscapes.

Keywords: *Forest-agricultural mosaic; Habitat selection; Risk perception; Human-wildlife coexistence*

3.2 INTRODUCTION

Habitat loss due to deforestation and land conversion are major causes of the decline of non-human primate (hereafter primate) species (Chapman & Peres, 2001; Estrada, 2013). The continued degradation of forested areas, together with ongoing human population growth across most primate range countries, means that many primate populations now occur in forest-agricultural mosaics (Estrada, 2013). Primates inhabiting these landscapes face multiple challenges including habitat degradation and fragmentation, human infrastructures such as roads or settlements, and increased encounters with people (Hockings et al, 2015). Their long-term survival critically depends on their ability to adapt to these human-dominated environments (Isabirye-Basuta & Lwanga, 2008), as well as people's tolerance of and behaviour towards primates within these landscapes (Hill & Webber, 2010).

Recent studies have revealed that many primates prefer areas with lower disturbance levels (chimpanzees (*Pan troglodytes*) and sooty mangabeys (*Cercocebus atys*): Brncic et al, 2015; bonobos (*Pan paniscus*): Hickey *et al*, 2013; chimpanzees, bonobos and gorillas (*Gorilla* spp.): Junker *et al,* 2012; chimpanzees: Plumptre *et al,* 2010; mountain gorillas (*G. beringei beringei*): Van Gils et al*,* 2009; orangutans (*Pongo pygmaeus*): Wich et al*,* 2012). These broad-scale studies have yielded important insights into the factors that influence the spatial distribution of a species on a national or regional scale. However, species persistence across landscapes can be scale-dependent (Sawyer & Brashares, 2013), and a finer-scale approach is required for understanding the effects of anthropogenic influences and disturbances on primate habitat use and behavioural flexibility (Bortolamiol et al*,* 2016). Such studies can help to inform land use planning aimed at balancing species conservation and development at a local scale in human-dominated environments.

Primate species show variable and multiple responses to environmental disturbances. Human-induced modifications in habitat quality can cause changes in primate feeding behaviour, dietary diversity and resource use (e.g. Guzman et al*,* 2016; Lee, 1997; Menard et al*,* 2014; Riley, 2007; Singh et al, 2001; Tutin, 1999; Wong et al, 2006). Primate responses to the availability of wild and anthropogenic food sources are often species and/or context specific (McLennan & Hockings, 2014). Some primates predominantly use areas of their home range in locations where important wild resources still remain (e.g. Heiduck, 2002; Leighton, 1993; Li, 2004; O'Brien & Kinnaird, 1997; Raboy & Dietz, 2004; Riley, 2008; Terada et al*,* 2015; Tweheyo et al, 2004). However, highly clumped and predictable food resources, such as exotic vegetation, cultivars, and human food waste, can also attract primates (Bortolamiol et al, 2016; Duvall, 2008; Hill, 2005; Hockings et al, 2009; Hoffman & O'Riain, 2011; McKinney, 2011).

Changes in primate habitat use, ranging, and activity budgets are often associated with anthropogenically disturbed environments. In locations where habitat quality and food resource availability are diminished, primates tend to exhibit larger home ranges and daily path lengths, spend more time travelling, and less time resting and feeding (e.g. white-faced capuchins (*Cebus capucinus*)*:* McKinney, 2011; long-tailed macaques (*Macaca fascicularis*)*:* Sha & Hanya, 2013). Conversely, primates that have access to, and use, spatially and temporally abundant human food sources tend to have smaller home ranges, spend less time travelling and foraging, and more time resting (e.g. yellow baboons (*Papio cynocephalus*)*:* Altmann & Muruthi, 1988; ring-tailed lemurs (*Lemur catta*): Gabriel, 2013; vervets (*Chlorocebus pygerythrus*): Saj et al, 1999). Most studies to date have focused on how habitat quality affects general patterns of primate activity budget allocation (e.g. Gabriel, 2013; Guzman et al, 2016; McKinney, 2011; Riley, 2007, 2008), while only a few have examined non-foraging activities across available habitat types within a landscape and within a single group (Terada et al, 2015). The preferences primates show for allocating activities to different habitats can provide insights into the relative value of these habitats, as well as species' ability to adapt to habitat change (Palminteri & Peres, 2012; Porter et al, 2007).

Risk and risk perception can also influence primate activity and range use. For example, predation risk influenced the use of different habitat types by chacma baboons (*Papio ursinus*) for resting and grooming (Cowlishaw, 1997). Many primate species use their ranges strategically in order to offset the risk of predation with food acquisition (Hill, 2016). Feeding is a risky behaviour, and where individuals choose to feed can impact fitness and survival as much as what they choose to feed on (Lambert & Rothman, 2015). It is likely that primates inhabiting anthropogenic landscapes aim to use habitats in such a way as to balance nutritional requirements with avoiding potential risks associated with human-induced pressures. Such risks can include negative interactions between farmers and primates due to cultivar-foraging (e.g. Brncic et al, 2010; Hill, 2000; Hockings et al, 2009; Hockings & Sousa, 2013; McLennan, 2013; Tweheyo et al, 2005), hunting pressure (Blake et al, 2007; Poulsen et al, 2009; Robinson et al, 1999) and risks from collisions with vehicles during road-crossing (Cibot et al, 2015; McLennan & Asiimwe 2016). Chimpanzees, in particular, show a variety of adaptive behaviours in response to perceived risks associated with anthropogenic environments (Hockings et al, 2015), many of which have been likened to predator avoidance strategies (Hockings et al, 2006; Sakura, 1994; Takemoto, 2002). When foraging on cultivars, chimpanzees may increase group cohesiveness and vigilance behaviours (Hockings et al, 2007; Hockings et al, 2012), vocalise less (Wilson et al, 2007), and forage at night to reduce the risk of detection by farmers (Krief et al, 2014). Chimpanzees also adapt their grouping patterns and behaviour before and during road-crossings (Cibot et al, 2015; Hockings, 2011). Recent studies have demonstrated that primates display signs of anxiety and stress when faced with anthropogenic pressures (chimpanzees: Hicks et al, 2012; Hockings, 2011; Hockings et al, 2006; mountain gorillas: Muyambi, 2005); some populations also show an increase in cortisol (a hormone which is released to buffer individuals in the short-term from the effects of acute stress (Cyr & Romero, 2008; Wingfield & Romero, 2010)) concentration levels (vervets: Fourie et al, 2015; spider monkeys (*Ateles geoffroyi yucatanensis*): Rangel-Negrin et al, 2009). Prolonged exposure to increased levels of anxiety and stress has negative impacts on fitness (Sapolsky et al, 2000). However, besides cultivar-foraging and road-crossing, we have a limited understanding of how human-induced pressures and risks impact primate habitat use and activity in anthropogenic landscapes.

The chimpanzee (*Pan troglodytes verus*) community at Bossou in Guinea, West Africa, is particularly well-suited for examining responses to human disturbances and pressures. It has been rated as the most heavily impacted long-term chimpanzee research site (Wilson et al, 2014) and many aspects of chimpanzee ecology and behaviour, as well as the practises and cultural beliefs of the local people, are well understood (Matsuzawa et al, 2011). Local people practise slash and burn agriculture, which has resulted in a highly heterogeneous anthropogenic landscape (Hockings et al, 2009; Sugiyama & Koman, 1992). The density and availability of chimpanzee wild foods varies across forest and anthropogenic habitat types (Bryson-Morrison et al, 2016), and wild fruit availability is highly seasonal (Bryson-Morrison et al, 2016; Hockings et al, 2009; Takemoto, 2002; Yamakoshi, 1998). The chimpanzees regularly visit cultivated areas to forage on crops and cultivated fruit trees, particularly during seasonal wild fruit scarcity, although they consume some crops regardless of wild fruit availability (Hockings et al, 2009). The chimpanzees crop forage at any time of day, including on occasions when local people are present (Hockings, 2007). The chimpanzees at this site are traditionally not hunted or killed due to the totemic beliefs of the local Manon people (Kortlandt, 1986; Yamakoshi, 2011). However, chimpanzee incursions into cultivated fields are rarely tolerated, and farmers frequently chase them away using noise and/or by throwing stones (Hockings et al, 2009). Two roads dissect the chimpanzees' home range and crossing both these roads is necessary, but risky for them due to the high presence of vehicles and pedestrians (Hockings, 2011). In response to these human-induced risks, Bossou chimpanzees display adaptive behaviours and increased frequencies of external signs of anxiety (i.e. rough-self scratching) when foraging in cultivated fields and crossing roads (Hockings, 2011; Hockings et al, 2006, 2012).

We aimed to: 1) determine Bossou chimpanzees' overall and seasonal patterns of habitat use within their core area with respect to foraging, traveling, resting and socialising and 2) examine the influences of risky areas, i.e. cultivated fields and human-made roads and paths, on foraging in non-cultivated habitat. Given the highly seasonal availability of wild fruits coupled with the chimpanzees' reliance on terrestrial herbaceous vegetation (THV) and cultivars, we predicted that chimpanzee use of forest and highly disturbed habitat types for foraging would reflect the spatial and temporal availability of food resources (Bryson-Morrison et al, 2016; Hockings et al, 2009; Takemoto, 2002; Yamakoshi, 1998). However, due to the potential risks associated with encountering local people (Hockings, 2011; Hockings et al, 2006, 2012), we also predicted that the chimpanzees would prefer habitat types with fewer human-induced pressures and, when foraging in non-cultivated habitats, would avoid foraging close to cultivated fields and roads and paths (Cibot et al, 2015; Hockings, 2011; Hockings et al, 2006, 2012).

3.3 METHODS

3.3.1 Study site and population

We conducted our study in the anthropogenic landscape that surrounds the village of Bossou in the south-eastern forest region of the Republic of Guinea, West Africa (latitude 7°38'71.7'N and longitude 8°29'38.9'W). Bossou is isolated from the nearest stretch of continuous mature forest in the Nimba Mountain range by approximately 6 km of savannah. The climate in this region is classified as tropical wet seasonal (Richards, 1996), with a short dry season from November to February, when wild fruit availability is highest, and a distinct rainy season from March to October, when wild fruit availability is lower (Bryson-Morrison et al, 2016; Hockings et al, 2009; Humle, 2011; Takemoto, 2002; Yamakoshi, 1998). Four small hills (70-150 m high) surround the village of Bossou and form the core area (approximately 6 km^2) of the resident chimpanzee community which ranges in this landscape (15 km^2 home range) (Humle, 2011). During our study (April 2012-March 2013), the chimpanzee community size ranged between 12-13 individuals, with 4 adult males and 6 adult females. The Bossou chimpanzees exhibit less fission-fusion than other known communities (Hockings et al*,* 2012), often traveling and foraging in larger parties than expected relative to community size (Matsuzawa et al, 2011).

3.3.2 Habitat composition and food availability

We determined habitat composition using quadrat sampling that covered over 70% (4.3 km^2) of the chimpanzees' core area, excluding village areas, roads and paths, and rivers (Bryson-Morrison et al, 2016). Regenerating forest (i.e., young and older growth secondary forest) dominates the landscape, although areas of riverine forest and one small patch of mature forest remain (Bryson-Morrison et al, 2016; Humle, 2011). Cultivated fields, coffee plantations and fallow areas, of various successional stages, occur throughout (Bryson-Morrison et al, 2016; Humle, 2011). We included all forest (i.e., mature, riverine, secondary, and young secondary forest) and highly disturbed (i.e., fallow stage 1, 2, and 3, coffee plantations, and cultivated fields) habitat types in our study (Table 3.1) (Bryson-Morrison et al, 2016).

Regenerating and mature forest contain the highest densities of chimpanzee food tree species, while highly disturbed habitat types show relatively low densities (Table 3.1) (Bryson-Morrison et al, 2016). THV occurs in high densities in most forest habitat types, and in fallow stage 3 areas (Table 3.1) (Bryson-Morrison et al, 2016; Humle, 2011) and is found at relatively low densities in all other highly disturbed habitat types (Table 3.1) (Bryson-Morrison et al, 2016). The majority of cultivated fields in Bossou contain a mix of crops including maize (*Zea mays*), cassava (*Manihot esculenta*), okra (*Hibiscus esculentus*), rice (*Oryza* sp.), banana (*Musa sinensis*) and pineapple (*Ananasa comosus*), all of which provide food parts that are consumed by the chimpanzees (Hockings et al, 2009). In addition to coffee trees (*Coffea* sp.), most coffee plantations in Bossou contain cultivated fruit tree orchards that provide fruits consumed by the chimpanzees such as orange (*Citrus sinensis*), mandarin (*Citrus reticulata*), mango (*Mangifera indica*), and cacao (*Theobroma cacao*), as well as banana plants. Unlike cultivated fields, coffee plantations are seldom guarded and the chimpanzees are rarely chased away even when local people are present (Bryson-Morrison, pers. obs.). Human-made roads and paths (routes) are found throughout the chimpanzees' home range (Fig. 3.1).

Table 3.1 Description of the habitat types available at Bossou, Guinea, including percentage availability in the chimpanzees' core area, stem density/ha of food tree species (≥10cm DBH), terrestrial herbaceous vegetation (THV) density/m^2, and percentage chimpanzee foraging time. Forest habitats age categories were adapted from Schroeder et al, (2010) and Sugiyama & Koman (1979, 1992). The ecological characteristics of these habitat types are provided in further detail in Bryson-Morrison et al, (2016)

Habitat types	**Description**	**% availability**	**Stem density/ ha**	**THV density/ m^2**	**% foraging time**
Forest					
Mature Forest	Old growth forest > 70 years old. Concentrated on the summit of one of the small hills, known as Gban. Dense forest with little to no signs of human disturbance.	4	250	3.0	15
Riverine Forest	Seasonally flooded forest, located along waterways with an approximate width of 20 m on either side	8	150	3.3	4
Secondary Forest	Mature secondary regrowth of vegetation. 30+ years old with a closed canopy.	25	248	1.3	23
Young Secondary Forest	Young secondary regrowth of vegetation. > 15 years old with an open canopy. Dominated by small, young regenerating tree species.	15	306	0.4	6
Highly disturbed					
Fallow Stage 1	Cultivated areas abandoned < 1 year ago. Cultivars still present. Dominated by an invasive species, *Chromolaena odorata.*	8	56	0.3	2
Fallow Stage 2	*Chromolaena odorata* still present but no longer dominant. Tree saplings, lianas and THV emerging.	8	28	0.4	8
Fallow Stage 3	*Chromolaena odorata* no longer present, <15 years old. Characterized by dense tree saplings, lianas and THV.	15	100	2.3	11
Coffee Plantation	Maintained areas dominated by cultivated coffee trees. Banana plants, oil palm and cultivated fruit tree orchards often present.	9	45	0.2	17
Cultivated Field	Characterised by active cultivation. Usually contains a mix of cultivars such as cassava, maize, okra and rice.	9	80	0	14

The larger of the two dirt roads (approximately 12 m wide) serves as a main thoroughfare from Liberia to the forest region of Guinea and is frequently used by vehicles and pedestrians (Hockings, 2011). The smaller road (approximately 3 m wide) runs to nearby villages and is used by pedestrians and motorcycles (Hockings, 2011). Small paths dissect all four hills and are used by local people for access to forest and agricultural areas.

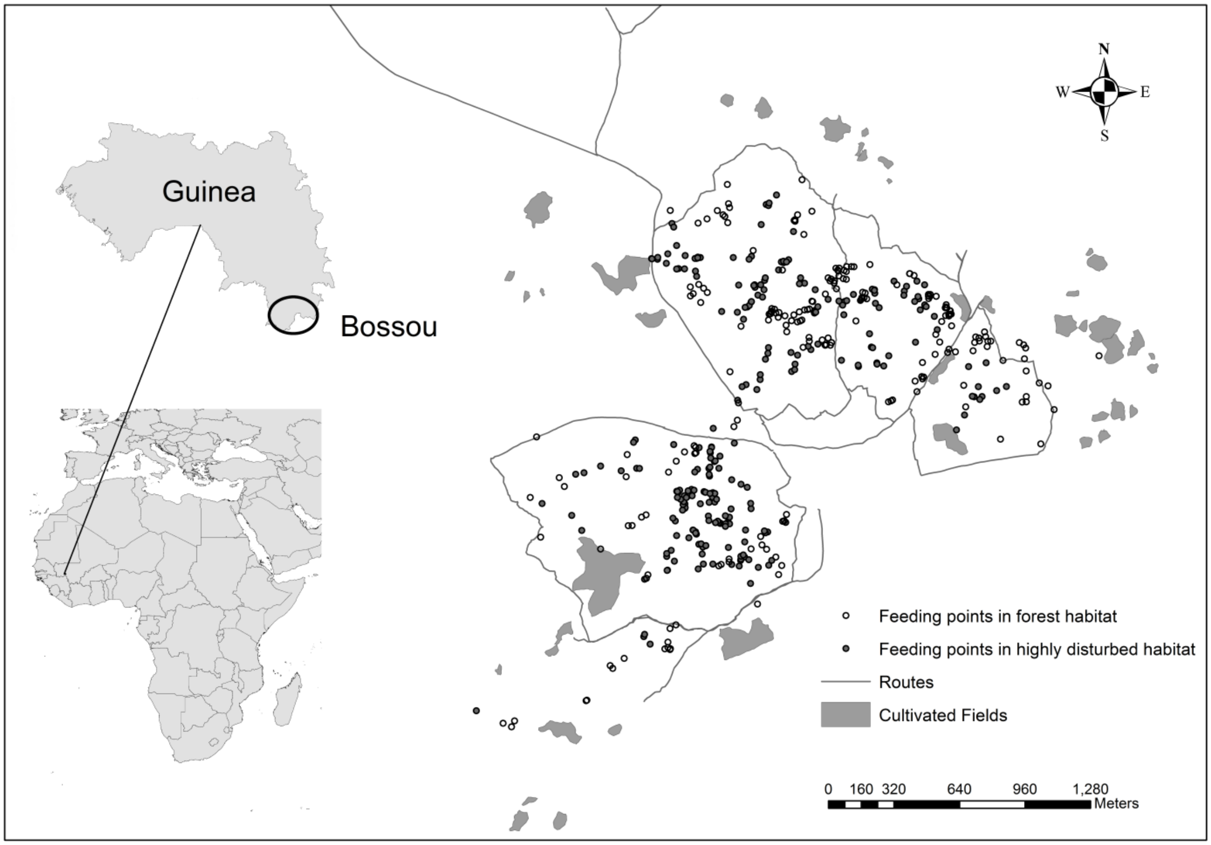

Figure 3.1 Map showing the location of all chimpanzee feeding event points (N = 474) in forest habitat (mature, riverine, secondary, and young secondary forest) (open circles) and highly disturbed habitat (fallow stage 1, 2, and 3, and coffee plantations) (closed circles) in relation to cultivated fields and routes (roads and footpaths) in Bossou, Guinea.

3.3.3 Mapping of anthropogenic features

We mapped routes (2 roads, 7 paths) and cultivated fields (43 fields) in the Bossou chimpanzees' core area using a handheld Garmin 62S GPS set to record a point every 10 m (open canopy accuracy of ± 3 m for GPS points) (Fig. 3.1).

3.3.4 Behavioural observations and feeding event locations

We collected data over a 12 month period from April 2012 to March 2013. We conducted behavioural follows for a maximum of 6 hours per day to comply with site regulations aimed at limiting the time spent observing the chimpanzees. We conducted behavioural follows in the morning between 06:30-12:30 (N = 331 hours) or afternoon between 12:30-18:30 (N = 237 hours) (total observations: 568 hours; Wet season (March-October): 440 hours; Dry season (November-February): 128 hours). We began daily follows when we first encountered the chimpanzees. Before each daily follow, we randomly selected an adult focal individual from a predetermined list to record all feeding events using a handheld Garmin 62S GPS. We sampled all adult individuals (N = 10) at least once per month. We defined a feeding event as foraging on a single food type and plant part from the same individual tree or food patch. We also recorded habitat type for all feeding events (Table 3.1). Feeding events excluded foraging on crops in cultivated fields, since we avoided following the chimpanzees into these areas during cultivar-foraging during our study to minimise the risk that our presence be viewed negatively by farmers. We observed the chimpanzees from a distance whenever possible to determine their activities within fields; however, this means that we may have underestimated chimpanzee use of cultivated fields. We used focal feeding event points (Forest habitat: N = 269; Highly disturbed habitat: N = 205) in spatial analyses to examine the distance from feeding events in non-cultivated habitat to cultivated fields and routes. We also conducted 15 minute instantaneous scan sampling (Altmann, 1974) to record habitat type and activity, i.e. traveling, resting, socialising and foraging (including actively searching, consuming and handling food items), for all individuals present in the focal individual's party (mean party size: 6.8 ± 0.6) (Lehmann et al, 2007). We performed all analyses at the community level due to the small size of the Bossou chimpanzee community at the time of this study.

3.3.5 Data Analyses

3.3.5.1 Habitat use and preferences

To examine chimpanzee habitat selection, we summed the number of 15 minute scans in forest habitat (i.e. mature, riverine, secondary, and young secondary forest combined) and highly disturbed habitat (i.e. fallow stage 1, 2, and 3, coffee plantations, and cultivated fields combined) for the entire research period (12 months) and for the wet and dry seasons. We also quantified habitat selection for each of the four mutually exclusive activities (foraging, traveling, resting, and socialising). We then examined habitat selection for each individual habitat type for all activities. Following Manly et al, (2002), we used a Pearson chi-square test to examine the null hypothesis that chimpanzee habitat selection was proportional to habitat availability. Similarly, we used a chi-square test to examine the null hypothesis that chimpanzee activities in each habitat type were proportional to the total number of observations. The results of both the chi-square tests allowed us to examine whether the chimpanzees were selectively using or avoiding a particular habitat type by calculating selection ratios using the following equation:

$$Wi = \frac{Oi}{\pi i}$$

Where Oi is the proportion of observations in habitat type *i* to the total number of recorded observations and πi is the proportion of area comprising habitat type *i* to the entire area available (Manly et al, 2002). Wi values > 1 indicate a positive selection for habitat type *i,* <1 indicate a negative selection for habitat type *i*, and values around 1 indicate that habitat type *i* was used proportionally to its availability. We standardised selection ratios to allow comparisons between studies using Manly's standardised selection ratio (Manly et al, 2002):

$$Bi = \frac{Wi}{\sum_{j=1} Wj}$$

Manly's standardised selection ratio ranges from 0 (no observations in a habitat) to 1 (all observations in a habitat) and provides a measure of the estimated probability that habitat type *i* would be the next one selected if all habitat types were equally available (Manly et al, 2002). We considered habitat types with the highest selectivity index (*Bi*) for each activity as preferred habitat for the chimpanzees. We then examined if habitat selection ratios were statistically significant using the following equation:

$$-X^2 = \left\{\frac{Wi - 1}{se(Wi)}\right\}^2$$

Where $se(Wi)$ is the standard error of the selection ratio for habitat type *i* (Manly et al, 2002). We further compared if selection ratios for each habitat type were significantly different from each other using the following equation:

$$X^2 = \frac{(Wi - Wj)^2}{var(Wi - Wj)}$$

Where $var(Wi - Wj)$ is the variance of the difference between the selection ratios for habitat type *i* and *j* (Manly et al, 2002). For all chi-square tests, we applied a Z-test with Bonferroni adjusted 95% confidence intervals of the standardised residuals (Byers et al, 1984; Neu et al, 1974; Manly et al, 2002).

3.3.5.2 Distance of feeding events relative to cultivated fields and routes

We used QGis 2.14.0-Essen to calculate the nearest distance (m) of each chimpanzee feeding event point (N = 474) to cultivated fields (range: 5.1 - 681.5 m; mean distance = 352.87 ± 8.29 m) and routes (range: 1.0 - 593.8 m; mean distance = 170.01 ± 5.24 m) for the full year and for the wet and dry seasons (Fig. 3.1). We grouped the distance from feeding event points to cultivated fields and routes into 0-100 m, 101-200 m, >200 m categories to facilitate analyses (sensu Lehman et al, 2006). We used a Pearson chi-square test to examine the null hypothesis that the frequency of chimpanzee feeding events was the same for all distance categories to cultivated fields and routes. We then examined the influence of habitat type and season on feeding event distance to cultivated fields and routes using a two-way analysis of variance (ANOVA). To meet the assumptions for Levene's test for equality of variance and normality distribution of the data, we removed 3 outliers and square root transformed the feeding event point distances to routes, and cube transformed the feeding event point distances to cultivated fields. We carried out all statistical analyses using SPSS version 22 and set the significance level at $P \leq 0.05$.

3.4 RESULTS

3.4.1 Habitat use and preferences

3.4.1.1 Patterns of overall habitat use

Habitat selection ratio (*Wi*) values for the full year for all chimpanzee activities were similar for forest habitat (mature, riverine, secondary, and young secondary forest combined) (*Wi* = 0.74-1.04) and highly disturbed habitat (cultivated fields, coffee plantations and fallow stages 1, 2, and 3 combined) (*Wi* = 0.86-1.29) (Fig. 3.2a). Selection ratio values for the wet season suggested that the chimpanzees used highly disturbed habitat marginally more than forest habitat for all activities other than resting (Forest habitat range *Wi* = 0.76-0.91; Highly disturbed *Wi* = 0.96-1.27) (Fig. 3.2b). However, during the dry season, the chimpanzees used forest habitat more for resting and travelling and overall (all activities combined) and used highly disturbed habitat more for socialising (Fig. 3.2c).

When we examined the Bonferroni adjusted standardised residuals (X^2 tests) for individual habitat types, selection ratios were significantly different between all habitat types, except between young secondary forest and fallow stage 1, and between fallow stage 3 and coffee plantations. Furthermore, selection ratios were significantly different for each of the four activities and overall for all habitat types and all time periods, with the exception of foraging, resting and traveling in fallow stage 1 during the dry season (Table 3.2 and Table 3.S1).

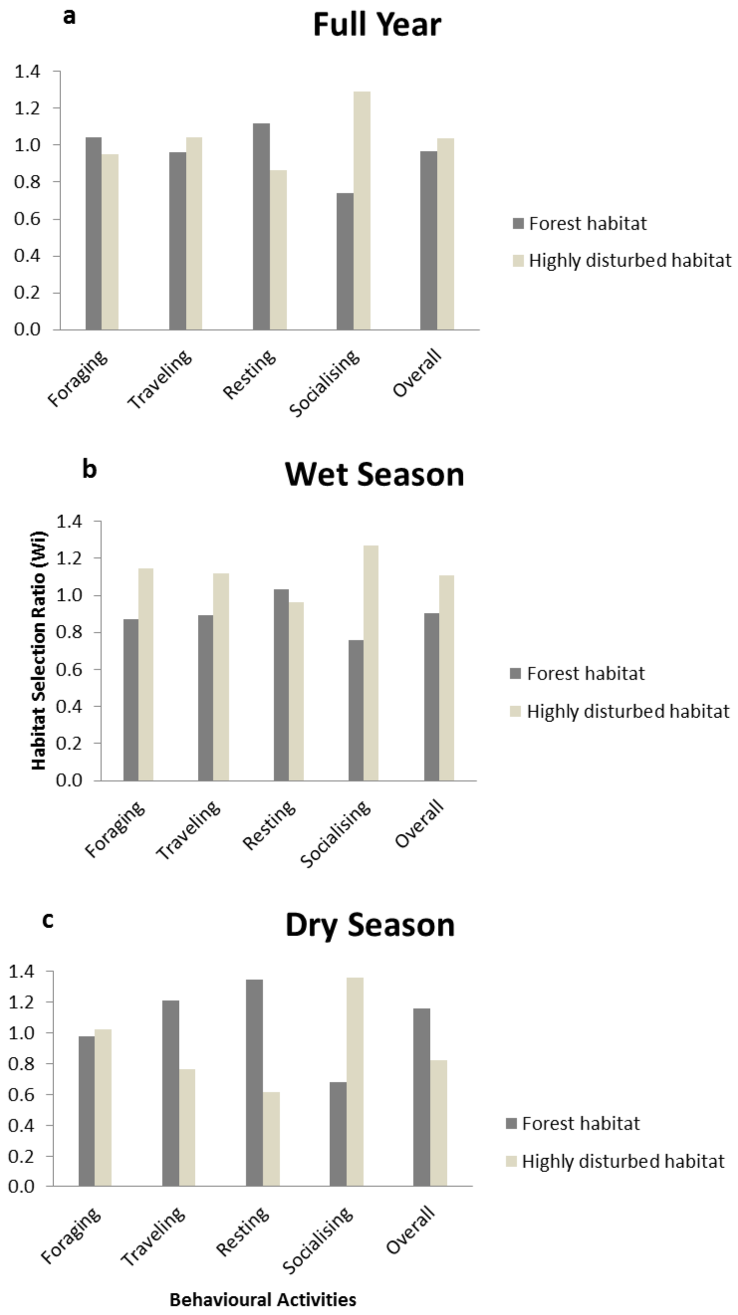

Figure 3.2 Habitat selection ratios (*Wi*) (Manly et al, 2002) for four activities and overall (aggregate of 15 minute scans for each habitat type) for the chimpanzee community at Bossou, Guinea, West Africa. a) Full year (April 2012-March 2013); b) Wet season (March-October); c) Dry season (November-February). Forest habitat (mature, riverine, secondary and young secondary forest) and highly disturbed habitat (fallow stage 1, 2, and 3, coffee plantations, and cultivated fields).

Table 3.2 Chimpanzee habitat selection ratios (*Wi*) (Manly et al, 2002) for each habitat type at Bossou, Guinea, during the wet season (March-October), dry season (November-February) and full year (April 2012-March 2013) for four activities and overall (aggregate of 15 minute scans). * Denotes selection ratios that were not significant. Selection ratios highlighted in dark-grey: *Wi* ≥ 2.00: Highly preferred; Mid-grey: *Wi* = 1.20-1.99: Preferred; Light-grey: *Wi* = 0.90-1.19: Used proportionally to availability; White: *Wi* = 0-0.89: Avoided. Forest habitat: MF: Mature Forest; RVF: Riverine Forest; SF: Secondary Forest; YSF: Young Secondary Forest; Highly-disturbed habitat: F3: Fallow Stage 3; F2: Fallow Stage 2; F1: Fallow Stage 1; CAFE: Coffee Plantation; CF: Cultivated Field

Habitat type	**FORAGING**			**TRAVELLING**			**RESTING**			**SOCIALISING**			**OVERALL**		
	Full Year	**Wet**	**Dry**	**Full Year**	**Wet**	**Dry**	**Full Year**	**Wet**	**Dry**	**Full Year**	**Wet**	**Dry**	**Full Year**	**Wet**	**Dry**
Forest															
MF	3.68	2.62	6.75	2.86	2.29	4.36	2.75	2.01	5.42	2.31	1.63	4.41	2.86	2.11	5.27
RVF	0.41	0.37	0.51	0.55	0.55	0.54	0.47	0.34	0.93	0.61	0.61	0.61	0.49	0.41	0.74
SF	0.94	1.03	0.68	1.34	1.17	1.79	1.20	1.20	1.20	0.82	0.95	0.41	1.16	1.15	1.18
YSF	0.39	0.45	0.22	0.63	0.77	0.28	0.38	0.41	0.28	0.27	0.30	0.18	0.43	0.48	0.26
Highly disturbed															
F3	0.74	0.83	0.48	0.96	0.98	0.89	1.36	1.42	1.15	1.34	1.47	0.97	1.19	1.26	0.9
F2	1.06	1.12	0.87	1.34	1.67	0.48	1.47	1.64	0.83	1.74	2.01	0.88	1.4	1.61	0.76
F1	0.20	0.2	0.19*	0.18	0.25	0*	0.43	0.53	0.06*	0.65	0.30	1.76	0.37	0.41	0.23
CAFE	2.17	2.55	1.06	1.04	1.14	0.77	1.03	1.05	0.95	1.58	1.37	2.25	1.24	1.30	1.05
CF	1.7	1.28	2.99	0.72	0.75	0.67	0.65	0.70	0.48	1.09	1.04	1.27	0.86	0.82	0.99

Overall, mature forest emerged as the most preferred habitat for the chimpanzees with the highest standardised selection ratios (*Bi*) during all time periods (Overall: Wet season: *Bi* = 0.22; Dry season: *Bi* = 0.46; Full year: *Bi* =0.29). Generally, fallow stage 1 was the least preferred habitat type for the chimpanzees for all activities and time periods (Overall: Wet season: *Bi* = 0.04; Dry season: *Bi* = 0.02; Full year: *Bi* =0.04), followed closely by young secondary forest (Overall: Wet season: *Bi* = 0.04; Dry season: *Bi* = 0.02; Full year: *Bi* =0.04) (Table 3.S1).

3.4.1.2 Habitat preference for foraging

For the forest habitat types and given relative habitat availability, selection ratios revealed that the chimpanzees highly preferred mature forest for foraging during all time periods. Generally, chimpanzees used secondary forest relative to its availability for foraging and avoided riverine and young secondary forest during all time periods. Of the highly disturbed habitat types, chimpanzees preferred coffee plantations and cultivated fields for foraging across the full year, with coffee plantations being highly preferred during the wet season and cultivated fields highly preferred during the dry season. Chimpanzees avoided all stages (i.e. 1, 2, and 3) of fallow habitat for foraging (Table 3.2 and Table 3.S1).

3.4.1.3 Habitat preference for other activities

3.4.1.3.1 Travelling

Chimpanzees highly preferred mature forest for travelling, used secondary forest relative to availability, and avoided riverine and young secondary forest for travelling regardless of season. Generally, they used fallow stage 2 and 3 and coffee plantations relative to availability, except during the dry season when they avoided these areas. Chimpanzees avoided fallow stage 1 and cultivated fields across all time periods (Table 3.2 and Table 3.S1).

3.4.1.3.2 Resting

The chimpanzees highly preferred mature forest for resting during all time periods. They used secondary forest relative to availability across all time periods, and used riverine forest relative to availability during the dry season but avoided it during the wet season and full year. They avoided young secondary forest across all time periods. Generally, the chimpanzees used coffee plantations, fallow stage 3 and stage 2 relative to availability for resting. They avoided fallow stage 1 and cultivated fields for resting during all time periods (Table 3.2 and Table 3.S1).

3.4.1.3.3 Socialising

Of the forest habitats, chimpanzees preferred only mature forest for socialising. They used secondary forest relative to availability during the wet season. Of the highly disturbed habitats, the chimpanzees generally preferred socialising in fallow stage 3 and stage 2 and coffee plantations. Generally, chimpanzees used cultivated fields relative to availability and preferred fallow stage 1 for socialising during the dry season but avoided it during the wet season and full year (Table 3.2 and Table 3.S1).

3.4.2 Distance of feeding events in non-cultivated habitat relative to cultivated fields and routes

There was a significant difference between feeding event distance categories to cultivated fields for the full year and both the wet and dry seasons (Full year: X^2= 433.841, df=2, P<0.0001; Wet season: X^2=280.760, df=2, P<0.0001; Dry season: X^2=158.423, df=2, P<0.0001). Inspection of the standardised residuals revealed that the chimpanzees fed less than expected by chance at 0-100 m and 101-200 m and more than expected by chance > 200 m away from cultivated fields during the wet and dry seasons and full year. We also found no effect of habitat type or season on feeding event distance to cultivated fields (2-way ANOVA, F (1, 467) = 0.430, P = 0.512).

There was no significant difference between the observed and expected values for chimpanzee feeding event distance to routes for the wet and dry seasons and full year (Full year: X^2= 1.466, df=2, P=0.480; Wet season: X^2=1.031, df=2, P=0.597; Dry season: X^2=0.437, df=2, P=0.804). However, the 2-way ANOVA revealed a statistically significant interaction between habitat type and season on the distance of feeding events to routes (F (1, 467) = 5.227, P = 0.023). Specifically, the distance of feeding events to routes was greater during the wet season than the dry season in highly degraded habitat. However, there was no effect of season on feeding event distance to routes for forest habitat.

3.5 DISCUSSION

Our study revealed that the chimpanzee community inhabiting the highly heterogeneous anthropogenic landscape of Bossou used different habitat types with varying frequency depending on season and behavioural activity.

3.5.1 Habitat preference for foraging

Our results support the prediction that chimpanzee patterns of habitat use for foraging reflect spatial and temporal food resource availability. Mature forest harbours high densities of chimpanzee food tree species and THV, and the chimpanzees preferentially used this habitat type for foraging throughout the year and especially during the dry season, when wild fruit availability was high (Bryson-Morrison et al, 2016). The chimpanzees also preferentially used cultivated fields for foraging during the dry season, which coincides with the availability of many crops (Hockings et al, 2009). Coffee plantations had the same selection ratio as mature forest during the wet season when wild fruit abundance was lower (Bryson-Morrison et al, 2016). Coffee plantations provide the chimpanzees with easily attainable spatially clumped fruit trees, many of which produce ripe fruit during the wet season, or year round (Bryson-Morrison et al, 2016; Hockings et al, 2009). Furthermore, the chimpanzees generally avoided fallow habitats, which have relatively low food availabilities (Table 3.1) (Bryson-Morrison et al, 2016). Similarly to other chimpanzee communities, Bossou chimpanzees consume a diverse range of foods but maintain a high annual proportion of fruit in their diets (Hockings et al, 2009; Takemoto, 2002; Yamakoshi, 1998), which significantly influenced their habitat use and foraging strategies. These patterns are similar to those reported for other chimpanzee communities (e.g. Caiquene-Cadique, Cantanhez National Park, Guinea-Bissau: Bessa et al, 2015; Bafing Biosphere Reserve, Mali: Duvall, 2008; Budongo, Uganda: Tweheyo et al, 2004; Kahuzi, Democratic Republic of Congo: Basabose, 2005). Our study reveals that Bossou chimpanzees specifically prefer mature forest year round for foraging, although they also rely heavily on agricultural habitat to supplement their diets with cultivars. As we did not record all incursions into cultivated fields, we may have underestimated the importance of this habitat type relative to other habitat types.

3.5.2 Habitat preference for other activities

Our results indicated that Bossou chimpanzees preferred to travel, rest, and socialise in habitat types with less human-induced pressure. Older growth forest (mature and secondary forest) offers greater tree cover (Bryson-Morrison et al, 2016) and little to no human presence, while cultivated fields are relatively open areas (Bryson-Morrison et al, 2016) with high human presence and a high likelihood of antagonistic interactions with humans (Hockings et al, 2007, 2009). Preferential use of mature forest in the dry season, when daily temperatures are high and precipitation low (Humle, 2011), for all activities may also reflect an increased requirement for shade. The chimpanzees are known to display thermoregulatory behaviour during the dry season by increasing terrestriality to take advantage of cooler temperatures on the ground compared to higher positions in the trees (Takemoto, 2004). The high densities of the invasive shrub, *Chromolaena odorata,* which form dense thickets that are difficult to navigate through, may explain chimpanzees' avoidance of stage 1 fallow (Bryson-Morrison, pers. obs.). Nevertheless, our results show that the chimpanzees did not actively avoid all highly disturbed habitat types and used some preferentially, depending on activity and season. Although not examined in the context of specific non-foraging activity patterns, other ecologically flexible primates, such as macaques (e.g. Riley, 2008) and baboons (e.g. Hoffman & O'Riain, 2011), often preferentially use human-modified habitats. The high occurrence of social activity in coffee plantations and cultivated fields reflects increased group cohesiveness and social behaviour previously reported for Bossou chimpanzees foraging on cultivars (Hockings et al, 2012). Consumption of nutritious energy-rich crops in cultivated areas may allow them more time to engage in other activities, such as socialising, as in populations of baboons, vervets, and macaques consuming human food sources (Altmann & Muruthi 1988; Brennan et al, 1985; Schlotterhausen, 2000).

Bossou chimpanzees generally avoided riverine forest habitat. This pattern contrasts with findings from Bulindi, Uganda, where chimpanzees heavily use riverine forest fragments which contain a higher density of feeding trees than the Budongo Forest Reserve, the nearest main forest block (McLennan & Plumptre, 2012). Several factors may explain this difference. The density of chimpanzee food tree species in riverine forest at Bossou is low compared to other forest types (Table 3.1) (Bryson-Morrison et al, 2016). Secondly, riverine forest patches in Bossou are relatively small and often abut cultivated fields, and there is a higher human presence in these areas than within other non-cultivated habitat types. This suggests that the availability of a particular habitat type is not necessarily a good indicator of use by chimpanzees, as habitat quality and perceived risks likely vary across sites.

Chimpanzee avoidance of young secondary forest is more difficult to interpret, particularly as this forest type harbours a high density of chimpanzee food species (Bryson-Morrison et al, 2016). The chimpanzees may be selecting older growth forests for feeding on wild fruits as larger trees are known to produce greater fruit yields (Chapman et al, 1992). More detailed phenological surveys of fruiting patterns between habitat types are needed to test this.

3.5.3 Distance of feeding events to cultivated fields and routes

Our results indicated that the chimpanzees significantly preferred foraging on foods in non-cultivated habitat at > 200m compared to 0-100m and 101-200m from cultivated fields during all time periods, with no effect of habitat type or season. Wild fruit scarcity during the wet season and ease of access to cultivars did not appear to influence distance of feeding events to cultivated fields, contrasting with findings for the chimpanzee community at Sebitoli, Kibale National Park, Uganda (Bortolamiol et al, 2016). Instead our results suggest that the chimpanzees' preference for foraging on foods in non-cultivated habitat at a greater distance from cultivated fields was more likely driven by perceived risks associated with these areas (Hockings, 2007, 2011). The nutritional benefits gained from acquiring wild foods close to cultivated fields may not be enough to offset any risks associated with potential human presence, as has been proposed for cultivar-foraging (Hockings et al, 2009; Naughton-Treves et al, 1998; McLennan & Hockings, 2014). The chimpanzees may therefore be using their environment strategically to balance food acquisition and risk avoidance (Hill, 2016). Future studies should aim to collect more detailed phenological data on the availability of food resources at varying distances to cultivated fields, along with behavioural and/or cortisol measures of stress, to investigate fully the effects of risky areas on chimpanzee foraging behaviour.

We found no significant difference between chimpanzee feeding event distance categories to routes (human made roads and paths). However, the chimpanzees foraged in highly degraded habitat at a greater distance from routes during the wet season than the dry season with no such seasonal effect found for forest habitat. This suggests that the Bossou chimpanzees did not actively avoid foraging close to routes; instead, feeding event distance from routes was likely driven by food availability. Pioneer tree species that produce fruits consumed by the chimpanzees, including *Musanga cecropioides*, semi-domesticated and wild oil palm (*Elaeis guineensis*), and coffee plantations containing fruit orchards and banana plants, are found at the sides of roads and paths (Bryson-Morrison, pers. obs). Road-crossing is risky for wildlife, including primates (Cibot et al, 2015; Gunson et al, 2011; Jaegger et al, 2005; McLennan & Asiimwe, 2016); however, roadsides can also represent areas of high vegetation species richness, attracting wildlife (Forman & Alexander, 1998). Indeed, findings from Sebitoli, Kibale National Park, Uganda indicated that proximity to a tarmac road, where roadside management strategies favour the growth of THV, was one of the main predictors of chimpanzee distribution (Bortolamiol et al*,* 2016).

3.5.4 Implications for chimpanzee conservation in anthropogenic landscapes

Overall, our study clearly indicated that chimpanzees at Bossou show a high preference for mature forest. Local people rarely gather non-timber forest products from, or enter, this single small patch of mature forest as they regard it as sacred (Kortlandt, 1986; Yamakoshi, 2005). We also found chimpanzees rarely use riverine forest at Bossou, probably because this combines relatively low food availability with high human presence. Our results suggest that chimpanzees in human-dominated environments prefer habitat types where a plentiful supply of wild foods is coupled with low human presence for most activities. The availability of such ‘refuges’ may be critical to the long-term persistence of chimpanzee populations within anthropogenic landscapes.

Alongside older-growth forest (mature and secondary forest), the chimpanzees at Bossou preferentially used cultivated habitat for foraging throughout the year. Chimpanzee reliance on crops to supplement wild foods in forest-agricultural mosaics complicates human-chimpanzee coexistence and requires careful management (Hill & Wallace, 2012). Restoration or recovery of abandoned agricultural areas to forest may reduce reliance on cultivated food, but this will likely depend on how important crops are in the diet of a given population, as well as the degree of perceived risk associated with cultivar-foraging in agricultural habitats (Hockings & McLennan, 2012; McLennan & Hockings, 2014). Moreover, reforestation of abandoned agricultural areas can take many years (Aide et al, 2001; Chapman & Chapman, 1999) and young successional habitat types may be the only available habitats for resident chimpanzees in the interim. Our study showed that chimpanzees generally avoided using young regenerating habitat types (fallow and young secondary forest), suggesting that widespread agricultural conversion and subsequent expansion of new fallow areas could prove detrimental for the long-term survival of chimpanzees, as for other primate populations (Ancrenaz et al, 2015; Palm et al, 2013; Wich et al, 2014).

In conclusion, our study reveals that the risks associated with some anthropogenic features may influence important behavioural activities, such as foraging. These findings contribute to our understanding of chimpanzee behavioural responses to human encounters and pressures in their environment. Our study further demonstrates the value of determining which habitat types are avoided or preferred, and potentially necessary, for chimpanzees in anthropogenic landscapes. We suggest that it is crucial to determine relative reliance on available habitat types, as well as agricultural areas, when devising conservation strategies for chimpanzee and other primate populations residing in anthropogenic landscapes.

3.6 REFERENCES

Aide, T.M., Zimmerman, J.K., Pascarella, J.B., Rivera, L., & Marcano-Vega, H. (2000). Forestregeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology,* 8, 328-338.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour,* 49, 227-267.

Altmann, J., & Muruthi, P. (1988). Differences in daily life between semiprovisioned and wild-feeding baboons. *American Journal of Primatology,* 15, 213-221.

Ancrenaz, M., Cheyne, S. M., Humle, T., & Robbins, M. M. (2015). Impacts of industrial agriculture on ape ecology. In: Arcus Foundation (Ed), *State of the apes. Volume II: Industrial agriculture and ape conservation.* (pp 165-192). Cambridge: Cambridge University Press.

Basabose, A. K. (2005). Ranging patterns of chimpanzees in a montane forest of kahuzi, Democratic Republic of Congo. *International Journal of Primatology,* 26, 33-54.

Bessa, J., Sousa, C., & Hockings, K. J. (2015). Feeding ecology of chimpanzees (*Pan troglodytes verus*) inhabiting a forest-mangrove-savanna-agricultural-matrix at Caiquene-Cadique, Cantanhez National Park, Guinea-Bissau. *American Journal of Primatology*, 77, 651-665.

Blake, S., Strindberg, S., Boudjan, P., Makombo, C., Bila-Isia, I., Ilambu, O., Grossmann, F., Bene-Bene, L., de Semboli, B., Mbenzo, V., S'hwa, D., Bayogo, R., Williamson, L., Fay, M., Hart, J. & Maisels, F. (2007). Forest elephant crisis in the Congo Basin. *PLoS Biology,* 5, e111.

Bortolamiol, S., Cohen, M., Jiguet, F., Pennec, F., Seguya, A., & Krief, S. (2016). Chimpanzee non-avoidance of hyper-proximity to humans. *The Journal of Wildlife Management,* 80, 924-934.

Brennan, E., Else, J., & Altmann, J. (1985). Ecology and behaviour of a pest primate: vervet monkeys in a tourist-lodge habitat. *African Journal of Ecology,* 23, 35-44.

Brncic, T., Amarasekaran, B., & McKenna, A. (2010). *Sierra Leone national chimpanzee census*. Freetown Sierra Leone: Tacugama Chimpanzee Sanctuary.

Bryson-Morrison, N., Matsuzawa, T. and Humle, T. (2016). Chimpanzees in an anthropogenic landscape: examining food resources across habitat types at Bossou, Guinea, West Africa. *American Journal of Primatology*, 78, 1237-1249.

Byers, C. R., Steinhorst, R.K., Krausman, P. R. (1984). Clarification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management,* 48, 1050-1053.

Campbell-Smith, G., Campbell-Smith, M., Singleton, I., Linkie, M. (2011). Raiders of the lost bark: orangutan foraging strategies in a degraded landscape. *PloS one,* 6, e20962.

Chapman, C.A., & Chapman, L.J. (1999). Forest restoration in abandoned agricultural land: a case study from East Africa. *Conservation Biology,* 13, 1301-1311.

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

Chapman, C.A., & Peres, C.A. (2001). Primate conservation in the new millennium: the role of scientists. *Evolutionary Anthropology,* 10, 16-33.

Cibot, M., Bortolamiol, S., Seguya, A., & Krief, S. (2015). Chimpanzees facing a dangerous situation: ahigh-traffic asphalted road in the Sebitoli area of Kibale National Park, Uganda. *American Journal of Primatology,* 77, 890-900.

Cowlishaw, G. (1997). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour,* 53, 667-686.

Cyr, N., & Romero, L. (2008). Fecal glucocorticoid metabolites of experimentally stressed captive and free-living starlings: implications for conservation research. *General Comparative Endocrinology*, 158, 20-28.

Duvall, C.S. (2008). Human settlement ecology and chimpanzee habitat selection in Mali. *Landscape Ecology,* 23, 699-716.

Estrada, A. (2013). Socioeconomic contexts of primate conservation: population, poverty, global economic demands, and sustainable land use. *American Journal of Primatology,* 75, 30-45.

Forman, R. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics,* 29, 207-231.

Fourie, N.H., Turner, T.R., Brown, J.L., Pampush, J.D., Lorenz, J.G., & Bernstein, R.M. (2015). Variation in vervet (*Chlorocebus aethiops*) hair cortisol concentrations reflects ecological disturbance by humans. *Primates,* 56, 365-373.

Gabriel, D.N. (2013). Habitat use and activity patterns as an indication of fragment quality in a strepsirrhine primate. *International Journal of Primatology,* 34, 388-406.

Gunson, K. E., Mountrakis, G., & Quackenbush, L. J. (2011). Spatial wildlife-vehicle collision models: a review of current work and its application to transportation mitigation projects. *Journal of Environmental Management,* 92, 1074-1082.

Guzmán, A., Link, A., Castillo, J. A., & Botero, J. E. (2016). Agroecosystems and primate conservation: shade coffee as potential habitat for the conservation of Andean night monkeys in the Northern Andes. *Agriculture, Ecosystems & Environment,* 215, 57-67.

Heiduck, S. (2002). The use of disturbed and undisturbed forest by masked titi monkeys *Callicebus personatus melanochir* is proportional to food availability. *Oryx,* 36, 133-139.

Hickey, J.R., Nackoney, J., Nibbelink, N.P., Blake, S., Bonyenge, A., Coxe, S., Dupain, J., Emetshu, M., Furuichi, T. & Grossmann, F. (2013). Human proximity and habitat fragmentation are key drivers of the rangewide bonobo distribution. *Biodiversity and Conservation,* 22, 3085-3104.

Hicks, T. C., Roessingh, P., & Menken, S. B. J. (2012). Reactions of Bili-uele chimpanzees to humans in relation to their distance from roads and villages. *American Journal of Primatology,* 74, 721-733.

Hill, C.M. (2000). Conflict of interest between people and baboons: crop raiding in Uganda. *International Journal of Primatology,* 21, 299-315.

Hill CM. (2005). People, crops, and primates: a conflict of interests. In: Paterson JD, Wallis J, (Eds.), *Commensalism and conflict: the primate–human interface*. Winnipeg, Manitoba: Higwell Printing.

Hill, C.M., & Wallace, G.E. (2012). Crop protection and conflict mitigation: reducing the costs of living alongside non-human primates. *Biodiversity and Conservation,* 21, 2569-2587.

Hill, C. M. & Webber, A. D. (2010). Perceptions of nonhuman primates in human–wildlife conflict scenarios. *American Journal of Primatology*, 72, 919-924.

Hill, R. A. (2016). Nonhuman primate approaches to landscapes. In: B. David, & J. Thomas (Eds.) *Handbook of Landscape Archaeology.* (pp. 95-101). New York: Routledge.

Hockings, K.J. (2007). *Human-Chimpanzee Coexistence at Bossou, the Republic of Guinea: a Chimpanzee Perspective.* PhD Thesis, University of Stirling, Stirling.

Hockings, K.J. (2011). Behavioral flexibility and division of roles in chimpanzee road-crossing. In: T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.). *The chimpanzees of Bossou and Nimba.* (pp.221-229). London: Springer.

Hockings, K.J., Anderson, J.R., & Matsuzawa, T. (2006). Road-crossing in chimpanzees: a risky business. *Current Biology,* 16, 668-670.

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, 636-646.

Hockings, K.J., Anderson, J.R., & Matsuzawa, T. (2012). Socioecological adaptations by chimpanzees, *Pan troglodytes verus*, inhabiting an anthropogenically impacted habitat. *Animal Behaviour,* 83, 801-810.

Hockings, K.J., Humle, T., Anderson, J.R., Biro, D., Sousa, C., Ohashi, G., & Matsuzawa, T. (2007). Chimpanzees share forbidden fruit. *PLoS One,* 2, e886.

Hockings K.J., & McLennan, M.R. (2012). From forest to farm: systematic review of cultivar feeding by chimpanzees–management implications for wildlife in anthropogenic landscapes. *PLoS One,* 7, e33391

Hockings, K.J., McLennan, M.R., Carvalho, S., Ancrenaz, M., Bobe, R., Byrne, R.W., Dunbar, R.I., Matsuzawa, T., McGrew, W.C., & Williamson, E.A. (2015). Apes in the Anthropocene: flexibility and survival. *Trends in ecology & evolution,* 30, 215-222.

Hockings, K.J., & Sousa, C. (2013). Human-chimpanzee sympatry and interactions in Cantanhez National Park, Guinea-Bissau: current research and future directions. *Primate Conservation,* 26, 57-65.

Hoffman, T. S., & O'Riain, M. J. (2011). The spatial ecology of chacma baboons (*Papio ursinus*) in a human-modified environment. *International Journal of Primatology,* 32, 308-328.

Humle, T. (2011). Location and ecology. In T. Matsuzawa, T. Humle, &Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 13-21). London: Springer.

Humle, T., & Matsuzawa, T. (2004). Oil palm use by adjacent communities of chimpanzees at Bossou and Nimba Mountains, West Africa. *International Journal of Primatology* 25, 551-581.

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

Jaegger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., & von Toschanowitz, K.T. (2005). Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling,* 185, 329-348.

Junker, J., Blake, S., Boesch, C., Campbell, G., Toit, L.D., Duvall, C., Ekobo, A., Etoga, G., Galat-Luong, A., & Gamys, J. (2012). Recent decline in suitable environmental conditions for African great apes. *Diversity and Distributions,* 18, 1077-1091.

Kortlandt, A. (1986). The use of stone tools by wild-living chimpanzees and earliest hominids. *Journal of Human Evolution,* 15, 77-132.

Krief, S., Cibot, M., Bortolamiol, S., Seguya, A., Krief, J.M., & Masi, S. (2014). Wild chimpanzees on the edge: nocturnal activities in croplands. *PLoS One,* 9, e109925.

Lambert, J. E., & Rothman, J. M. (2015). Fallback foods, optimal diets, and nutritional targets: primate responses to varying food availability and quality. *Annual Review of Anthropology,* 44, 493-512.

Lee, R. J. (1997). *The Impact of hunting and habitat disturbance on the population dynamics and behavioral ecology of the crested black macaque* (*Macaca nigra*). Ph.D. Thesis, University of Oregon, Eugene.

Lehman, S. M., Rajaonson, A., & Day, S. (2006). Edge effects and their influence on lemur density and distribution in Southeast Madagascar. *American Journal of Physical Anthropology,* 129, 232-241.

Lehmann, J., Korstjens, A. H., & Dunbar, R. (2007). Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evolutionary Ecology,* 21, 613-634.

Leighton, M. (1993). Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology,* 14, 257-313.

Li, Y. (2004). The effect of forest clear-cutting on habitat use in Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in Shennongjia Nature Reserve, China. *Primates,* 45, 69-72.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., & Erickson, W.P. (2002). *Resource selection by animals: Statistical design and analysis for field studies (2nd Ed.)*. Dordrecht: Kluwer Academic.

Matsuzawa, T., Humle, T., & Sugiyama, Y (Eds.). (2011). *The chimpanzees of Bossou and Nimba*. London: Springer.

Mckinney, T. (2011). The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced capuchins (*Cebus capucinus*). *American Journal of Primatology,* 73, 439-448.

McLennan, M.R. (2013). Diet and feeding ecology of chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: foraging strategies at the forest–farm interface. *International Journal of Primatology,* 34, 585-614.

McLennan, M. R., & Asiimwe, C. (2016). Cars kill chimpanzees: case report of a wild chimpanzee killed on a road at Bulindi, Uganda. *Primates,* 57, 377-388.

McLennan, M.R., & Hockings, K.J. (2014). Wild chimpanzees show group differences in selection of agricultural crops. *Scientific Reports,* 4, 5956.

McLennan, M.R., & Plumptre, A.J. (2012). Protected apes, unprotected forest: composition, structure and diversity of riverine forest fragments and their conservation value in Uganda. *Tropical Conservation Science,* 5, 79-103.

Ménard, N., Motsch, P., Delahaye, A., Saintvanne, A., Le Flohic, G., Dupé, S., et al, (2014). Effect of habitat quality on diet flexibility in Barbary macaques. *American Journal of Primatology,* 76, 679-693.

Muyambi, F. (2005). The impact of tourism on the behaviour of mountain gorillas. *Gorilla Journal*, 30, 14-15.

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, 596-606.

Neu, C.W., Byers, C.R., & Peek, J.M. (1974). A technique for analyses of utilization-availability data. *Journal of Wildlife Management,* 38, 541-545.

O'Brien, T.G., & Kinnaird, M.F. (1997). Behavior, diet, and movements of the Sulawesi crested black macaque. *International Journal of Primatology, 18,* 321-351.

Palm, C.A., Vosti, S.A., Sanchez, P.A., & Ericksen, P.J. (2013). *Slash-and-burn agriculture: the search for alternatives.* New York: Columbia University Press.

Palminteri, S., & Peres, C. A. (2012). Habitat selection and use of space by bald-faced sakis (*Pithecia irrorata*) in Southwestern Amazonia: lessons from a multiyear, multigroup study. *International Journal of Primatology,* 33, 401-417.

Plumptre, A., Rose, R., Nangendo, G., Williamson, E.A., Didier, K., Hart, J., *et al,* (2010). *Eastern chimpanzee (Pan troglodytes schweinfurthii): status survey and conservation action plan 2010-2020*. IUCN, Gland, Switzerland.

Poulsen, J., Clark, C., Mavah, G., & Elkan, P. (2009). Bushmeat supply and consumption in a tropical logging concession in Northern Congo. *Conservation Biology,* 23, 1597-1608.

Porter, L. L., Sterr, S. M., & Garber, P. A. (2007). Habitat use and ranging behavior of *Callimico goeldii*. *International Journal of Primatology,* 28, 1035-1058.

Pozo-Montuy, G., Serio-Silva, J.C., Chapman, C.A., & Bonilla-Sánchez, Y.M. (2013). Resource use in a landscape matrix by an arboreal primate: evidence of supplementation in black howlers (*Alouatta pigra*). *International Journal of Primatology* 34, 714-731.

Raboy, B.E., & Dietz, J.M. (2004). Diet, foraging, and use of space in wild golden-headed lion tamarins. *American Journal of Primatology,* 63, 1-15.

Rangel-Negrín, A., Alfaro, J., Valdez, R., Romano, M., & Serio-Silva, J. (2009). Stress in Yucatan spider monkeys: effects of environmental conditions on fecal cortisol levels in wild and captive populations. *Animal Conservation,* 12, 496-502.

Richards, P.W. (1996). *The tropical rainforest,* second edition. New York: Cambridge University.

Riley, E.P. (2007). The human-macaque interface: Conservation implications of current and future overlap and conflict in Lore Lindu National Park, Sulawesi, Indonesia. *American Anthropologist,* 109, 473-484.

Riley, E.P. (2008). Ranging patterns and habitat use of Sulawesi Tonkean macaques (*Macaca tonkeana*) in a human-modified habitat. *American Journal of Primatology*, 70, 670-679.

Robinson, J.G., Redford, K.H., & Bennett, E.L. (1999). Wildlife harvest in logged tropical forests. *Science,* 284, 595-596.

Saj, T., Sicotte, P., & Paterson, J.D. (1999). Influence of human food consumption on the time budget of vervets. *International Journal of Primatology,* 20, 977-994.

Sakura, O. (1994). Factors affecting party size and composition of chimpanzees (*Pan troglodytes verus*) Bossou, Guinea. *International Journal of Primatology,* 15, 167-183.

Sapolsky, R.M., Romero, L.M., & Munck, A.U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine reviews,* 21, 55-89.

Sawyer, S. C., & Brashares, J. S. (2013). Applying resource selection functions at multiple scales to prioritize habitat use by the endangered cross river gorilla. *Diversity and Distributions,* 19, 943-954.

Schlotterhausen L. (2000). *Town monkeys, country monkeys: a socioecological comparison of a human commensal and wild group of bonnet macaques (Macaca radiata)*. PhD Thesis, New York University, New York.

Schroeder, J., Oke, D., Onyekwelu, J., & Yirdaw, E. (2010). Secondary forests in West Africa: a challenge and opportunity for management. In G. Mery, P. Katila, G. Galloway, R. Alfaro, & M. Kanninen (Eds.), *Forests and Society-Responding to Global Drivers of Change 25* (pp.335-353). Vienna: IUFRO World Series.

Schurr, M.R., Fuentes, A., Luecke, E., Cortes, J., & Shaw, E. (2012). Intergroup variation in stable isotope ratios reflects anthropogenic impact on the Barbary macaques (*Macaca sylvanus*) of Gibraltar. *Primates,* 53, 31-40.

Sha, J.C.M., & Hanya, G. (2013). Diet, activity, habitat use, and ranging of two neighboring groups of food-enhanced long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology* 75, 581-592.

Singh, M., Kumara, H., Kumar, M. A., & Sharma, A. K. (2001). Behavioural responses of lion-tailed macaques (*Macaca silenus*) to a changing habitat in a tropical rain forest fragment in the Western Ghats, India. *Folia Primatologica,* 72, 278-291.

Sugiyama, Y., & Koman, J. (1979). Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates,* 20, 323-339.

Sugiyama, Y., & Koman, J. (1992). The flora of Bossou: its utilization by chimpanzees and humans. *African Study Monographs* 13, 127-169.

Takemoto, H. (2002*). Feeding ecology of chimpanzees in Bossou, Guinea: coping with the seasonal fluctuation of food supply and micrometeorology in the tropical forest*. PhD Thesis (unpublished), Kyoto University, Kyoto.

Takemoto, H. (2004). Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. *American Journal of Physical Anthropology*, 124, 81-92.

Terada, S., Nackoney, J., Sakamaki, T., Mulavwa, M.N., Yumoto, T., & Furuichi, T. (2015). Habitat use of bonobos (*Pan paniscus*) at Wamba: Selection of vegetation types for ranging, feeding, and night-sleeping. *American Journal of Primatology,* 77, 701-713.

Tutin, C. E. (1999). Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé reserve, Gabon. *Primates,* 40, 249-265.

Tweheyo, M., Hill, C.M., & Obua, J. (2005). Patterns of crop raiding by primates around the Budongo Forest Reserve, Uganda. *Wildlife Biology,* 11, 237-247.

Tweheyo, M., Lye, K.A., & Weladji, R.B. (2004). Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management,* 188, 267-278.

Umapathy, G., & Kumar, A. (2000). The demography of the lion-tailed macaque (*Macaca silenus*) in rain forest fragments in the Anamalai Hills, South India. *Primates,* 41, 119-126.

Van Gils, H. & Kayijamahe, E. (2010). Sharing natural resources: mountain gorillas and people in the Parc National des Volcans, Rwanda. *African Journal of Ecology,* 48, 621-627.

Wich, S. A., Gaveau, D., Abram, N., Ancrenaz, M., Baccini, A., Brend, S., Curran, L., Delgado, R.A., Erman, A., & Fredriksson, G.M. (2012). Understanding the impacts of land-use policies on a threatened species: is there a future for the Bornean orangutan? *PLoS One,* 7, e49142.

Wich, S., Garcia-Ulloa, J., Kühl, H., Humle, T., Lee, J.H., & Koh, L. (2014). Will oil palm's homecoming spell doom for Africa's great apes? *Current Biology,* 24*,* 1659-1663.

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., et al, (2014). Lethal aggression in pan is better explained by adaptive strategies than human impacts. *Nature,* 513, 414-417.

Wilson, M.L., Hauser, M.D., & Wrangham, R.W. (2007). Chimpanzees (*Pan troglodytes*) modify grouping and vocal behavior in response to location-specific risk. *Behaviour,* 144, 1621-1653.

Wong, S. N., Saj, T. L., & Sicotte, P. (2006). Comparison of habitat quality and diet of *colobus vellerosus* in forest fragments in Ghana. *Primates,* 47, 365-373.

Wingfield, J., & Romero, L. (2010). Adrenocortical responses to stress and their modulation in free-living vertebrates. *Comprehensive Physiology, Supplement 23: Handbook of Physiology, the Endocrine System, Coping with the Environment: Neural and Endocrine Mechanisms*, 211-234.

Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. *American Journal of Physical Anthropology,* 106, 283-295.

Yamakoshi, G. (2005). What is happening on the border between humans and chimpanzees?: wildlife conservation in West African rural landscapes. In K. Hiramatsu, (Ed.), *Coexistence with nature in a 'Glocalizing' world: Field science perspectives. Proceedings of the 7th Kyoto University International Symposium* (pp. 91-97). Kyoto: Kyoto University.

Yamakoshi, G. (2011). Looking back on three decades of research on Bossou chimpanzees. In T. Matsuzawa, T. Humle, & Y. Sugiyama, (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 13-21). London: Springer.

3.7 SUPPORTING INFORMATION

3.7.1 Appendix 3.S1: Table 3.S1

Table 3.S1 Observed and expected chimpanzee habitat selection with selection ratios (*Wi*) and standardised selection ratios (*Bi*) (Manly *et al,* 2002). Statistical significance of selection ratios was determined using Bonferroni adjusted 95% confidence intervals of the standardised residuals (Byers *et al,* 1984; Neu *et al,* 1974; Manly *et al,* 2002). All selection ratios were significant except for those highlighted in grey. Wet season = March-October; Dry season = November-February; Year = April 2012-March2013. Overall = aggregate of 15 minute scans. MF: Mature Forest; RVF: Riverine Forest; SF: Secondary Forest; YSF: Young Secondary Forest; F3: Fallow Stage 3; F2: Fallow Stage 2; F1: Fallow Stage 1; CAFE: Coffee Plantation; CF: Cultivated Field.

Period	**Behaviour**		**MF**	**RF**	**SF**	**YSF**	**F3**	**F2**	**F1**	**CAFE**	**CF**
Year	**Foraging**	Expected	60.6	136.4	378.8	227.3	227.3	121.2	121.2	121.2	121.2
		Observed	223	56	355	89	169	128	24	263	208
		Wi	3.68	0.41	0.94	0.39	0.74	1.06	0.20	2.17	1.72
		Bi	0.33	0.04	0.08	0.03	0.07	0.09	0.02	0.19	0.15
	Resting	Expected	239.4	538.6	1496	897.6	897.6	478.7	478.7	478.7	478.7
		Observed	658	253	1797	345	1221	702	205	492	311
		Wi	2.75	0.47	1.20	0.38	1.36	1.47	0.43	1.03	0.65
		Bi	0.28	0.05	0.12	0.04	0.14	0.15	0.04	0.11	0.07
	Travelling	Expected	89.8	202.1	561.3	336.8	336.8	179.6	179.6	179.6	179.6
		Observed	257	111	752	213	323	241	32	186	130
		Wi	2.86	0.55	1.34	0.63	0.96	1.34	0.18	1.04	0.72

		Bi	0.30	0.06	0.14	0.07	0.10	0.14	0.02	0.11	0.08
	Socialising	Expected	42.0	94.6	262.8	157.7	157.7	84.1	84.1	84.1	84.1
		Observed	97	58	215	43	212	146	55	133	92
		Wi	2.31	0.61	0.82	0.27	1.34	1.74	0.65	1.58	1.09
		Bi	0.22	0.06	0.08	0.03	0.13	0.17	0.06	0.15	0.10
	Overall	Expected	431.8	971.55	2698.8	1619.3	1619.3	863.6	863.6	863.6	863.6
		Observed	1235	478	3119	690	1925	1217	316	1074	741
		Wi	2.86	0.49	1.16	0.43	1.19	1.41	0.37	1.24	0.86
		Bi	0.29	0.05	0.12	0.04	0.12	0.14	0.04	0.12	0.09
Wet	**Foraging**	Expected	45.0	101.3	281.5	168.9	168.9	90.1	90.1	90.1	90.1
		Observed	118	38	289	76	141	101	18	230	115
		Wi	2.62	0.37	1.03	0.45	0.83	1.12	0.20	2.55	1.28
		Bi	0.25	0.04	0.10	0.04	0.08	0.11	0.02	0.24	0.12
	Resting	Expected	187.4	421.6	1171	702.6	702.6	374.7	374.7	374.7	374.7
		Observed	376	144	1408	290	997	616	199	393	261

		Wi	2.01	0.34	1.20	0.41	1.42	1.64	0.53	1.05	0.70
		Bi	0.25	0.04	0.13	0.04	0.15	0.18	0.06	0.11	0.07
	Travelling	Expected	65.0	146.3	406.5	243.9	243.9	130.1	130.1	130.1	130.1
		Observed	149	81	475	187	240	217	32	148	97
		Wi	2.29	0.55	1.17	0.77	0.98	1.67	0.25	1.14	0.75
		Bi	0.24	0.06	0.12	0.08	0.10	0.17	0.03	0.12	0.08
	Socialising	Expected	31.8	71.6	199	119.4	119.4	63.7	63.7	63.7	63.7
		Observed	52	44	189	36	175	128	19	87	66
		Wi	1.63	0.61	0.95	0.30	1.47	2.01	0.30	1.37	1.04
		Bi	0.17	0.06	0.10	0.03	0.15	0.21	0.03	0.14	0.11
	Overall	Expected	329.3	740.9	2058	1234.8	1234.8	658.6	658.6	658.6	658.6
		Observed	695	307	2361	589	1553	1062	268	858	539
		Wi	2.11	0.41	1.15	0.48	1.26	1.61	0.41	1.30	0.82
		Bi	0.22	0.04	0.12	0.05	0.13	0.17	0.04	0.14	0.09
Dry	**Foraging**	Expected	15.6	35.0	97.3	58.4	58.4	31.1	31.1	31.1	31.1

	Observed	105	18	66	13	28	27	6	33	93
	Wi	6.75	0.51	0.68	0.22	0.48	0.87	0.19	1.06	2.99
	Bi	0.49	0.04	0.05	0.02	0.03	0.06	0.01	0.08	0.22
Resting	Expected	52	117	325	195	195	104	104	104	104
	Observed	282	109	389	55	224	86	6	99	50
	Wi	5.42	0.93	1.20	0.28	1.15	0.83	0.06	0.95	0.48
	Bi	0.48	0.08	0.11	0.02	0.10	0.07	0.01	0.08	0.04
Travelling	Expected	24.8	55.7	154.8	92.9	92.9	49.5	49.5	49.5	49.5
	Observed	108	30	277	26	83	24	0	38	26
	Wi	4.36	0.54	1.79	0.28	0.89	0.48	0	0.77	0.67
	Bi	0.45	0.06	0.18	0.03	0.09	0.05	0	0.08	0.07
Socialising	Expected	10.2	23.0	63.8	38.3	38.3	20.4	20.4	20.4	20.4
	Observed	45	14	26	7	37	18	36	46	26
	Wi	4.41	0.61	0.41	0.18	0.97	0.88	1.76	2.25	1.27
	Bi	0.35	0.05	0.03	0.01	0.08	0.07	0.14	0.18	0.10

Overall	Expected	102.5	230.7	640.8	384.5	384.5	205.0	205.0	205.0	205.04
	Observed	540	171	758	101	372	155	48	216	202
	Wi	5.27	0.74	1.18	0.26	0.97	0.76	0.23	1.05	0.99
	Bi	0.46	0.06	0.10	0.02	0.08	0.07	0.02	0.09	0.09

Chapter 4 THE MACRONUTRIENT COMPOSITION OF CHIMPANZEE WILD AND CULTIVATED PLANT FOODS

4.1 ABSTRACT

Agricultural expansion continues to encroach on tropical forests and primates exposed to agricultural areas frequently incorporate cultivars into their diets. A better understanding of the drivers behind primate cultivar-foraging is required for informing conservation efforts for sustainable human-primate coexistence. We aimed to build on existing knowledge of primate diets in anthropogenic landscapes by using standard chemical analyses to estimate the macronutrient content of 25 wild and 16 cultivated foods consumed by chimpanzees (*Pan troglodytes verus*) in a forest-agricultural mosaic at Bossou, Guinea, West Africa. We compared these to recently published results for chimpanzees (*P. t. schweinfurthii*) in a disturbed habitat at Bulindi, Uganda, East Africa. We also provided the first macronutrient measures of all oil palm (*Elaeis guineensis*) food parts (except flowers) known to be consumed by chimpanzees. The composition of wild fruit, leaves and pith were consistent with previous reports for primate diets. Cultivated fruits were higher in digestible carbohydrates and energy and lower in insoluble fibre than wild fruits, while wild fruits were higher in protein. We found no differences in macronutrients between cultivated and wild pith. All oil palm food parts were relatively rich in carbohydrates, protein, lipids, and/or fermentable fibre fractions; adding nutritional support for the importance of oil palms for West African chimpanzees. We found little differences in the macronutrient composition of cultivated fruit or cultivated and wild pith between Bossou and Bulindi, although we found evidence that wild fruits differed in macronutrient, but not energy, content. Our results build on current understanding of chimpanzee feeding ecology within forest-agricultural mosaics and provide additional support for the assumption that cultivars offer primates energetic benefits over wild foods.

Key words: *Pan troglodytes verus; Elaeis guineensis; forest-agricultural mosaic; crop-foraging; human-wildlife coexistence*

4.2 INTRODUCTION

The world's most biodiversity rich forests are increasingly being converted to agricultural land for subsistence and large-scale industrial farming in order to meet the demands of an ever-growing human population (Laurance et al, 2014). Such agricultural expansion brings new challenges for wildlife aiming to meet their nutritional and energetic needs from the surrounding environment. Deforestation reduces the distribution and availability of wild food resources while agricultural practises introduce spatially clumped and often predictably available cultivated foods. Many wildlife species respond to these changes by altering their foraging strategies to incorporate cultivars into their diets, allowing them to exploit anthropogenic landscapes, e.g. African elephants (*Loxodonta africana*) (Hoare, 2001); baboons (*Papio* spp.) (Hill, 2000), macaques (*Macaca* sp.) (Priston & McLennan, 2013) and other non-human primates (Humle & Hill, 2016); wild boar (*Sus scrofa*) (Keuling et al, 2009); raccoon (*Procyon lotor*) (Beasley & Rhodes, 2008). Cultivar-foraging (also often termed "crop-raiding") affects local livelihoods through crop losses and damages (Hill, 1997, 2005), while species that consume cultivars frequently face significant risks from negative interactions and/or hostile behaviours from farmers (Hockings & Humle, 2009). As a result, cultivar-foraging is one of the principle threats to human-wildlife coexistence within anthropogenic landscapes (e.g. Hoare, 2001; Hockings & Humle, 2009; McKenzie & Ahabyona, 2012; Redpath et al, 2013). Understanding the drivers behind cultivar consumption by wildlife is essential for effective conservation planning and mitigation strategies (Dostaler et al, 2011; Osborn, 2004; Rode et al, 2006).

The behavioural and ecological flexibility and broad dietary repertoire of many primate species, means that they readily exploit cultivars when available (e.g. baboon (*Papio* spp.) (Hill, 2000: Strum, 2010); macaque (*Macaca* sp.) (Priston & McLennan, 2013); vervet (*Chlorocebus* sp.) (Brennan et al, 1985); capuchin (*Cebus* sp.) (McKinney, 2011); orangutan (*Pongo* sp.) (Campbell-Smith et al, 2011)). Studies examining primate feeding ecology within human-impacted environments have revealed diverse cultivar-foraging strategies depending on various factors such as type, availability, and proximity of cultivated resources, habitat quality and wild food availability, and perceived risks associated with cultivar-foraging (Bryson-Morrison et al, 2017; Reynolds, 2005; Hockings et al, 2009; Naughton-Treves et al, 1998; McLennan, 2013). Where cultivars are fully incorporated into the diets, primates often display changes to activity budget and ranging patterns, spending less time foraging and travelling and more time resting (e.g. Altmann & Muruthi, 1988; Saj et al, 1999; Strum, 2010; Warren et al, 2011). A more effective immune response to parasite infections (e.g. Chapman et al, 2006) and a reduction in physiological stress (Lodge et al, 2013) has also been reported for primates that consume crops. Finally, alterations to life history traits have also been recorded, such as shorter inter-birth intervals, reduced infant mortality, and heavier bodyweight in adulthood (e.g. Sugiyama & Fujita, 2011; Lodge et al, 2013; Strum, 2010; Warren et al, 2011). These behavioural, ecological and physiological advantages to primates that frequently consume cultivars are often attributed to increased nutritional and energetic gains compared to wild plant foods.

Humans have selected cultivated foods to be palatable, easily digestible and energy rich with low levels of potentially toxic and/or digestion inhibiting secondary compounds (Milton, 1999). Until recently, few studies had determined the nutritional composition of wild and cultivated foods in the diets of primates. Cultivated potato and maize consumed by baboon (*Papio anubis*) were easier to digest than wild plant foods due to lower levels of insoluble fibre (Forthman Quick & Demment, 1988). Similarly, cultivated cacao fruit consumed by Tonkean macaques (*Macaca tonkeana*) were lower in insoluble fibre and higher in carbohydrate energy than wild fruit foods (Riley et al, 2013). The first comprehensive study to quantify the maconutrient content of multiple cultivated and wild foods in the diets of wild primates, found that cultivated fruit and pith eaten by chimpanzees (*Pan troglodytes schweinfurthii*) were lower in insoluble fibre and secondary compounds and higher in carbohydrates than wild food equivalents (McLennan & Ganzhorn, 2017). These results suggest that cultivars are indeed high quality foods in terms of providing a rich source of easily digestible carbohydrate energy. However, cultivated foods were found to be low in other macronutrients, particularly protein and lipids, compared to wild foods (McLennan & Ganzhorn, 2017).

Chimpanzees (*Pan troglodytes*) are found in anthropogenically disturbed habitats throughout their range in West, Central and East Africa (Humle et al, 2016) and frequently incorporate cultivars into their diets (Hockings & Humle, 2009). Chimpanzees consume a diverse range of plant food types as well as limited amounts of animal products (Nishida & Uehara, 1983; Reynolds, 2005; Sugiyama & Koman, 1992; Tutin & Fernandez, 1993). However, regardless of habitat type, chimpanzees are predominantly frugivorous and maintain a high proportion of fruit in their diets even when fruit availability is low (Ghiglieri, 1984; Watts et al, 2012; Wrangham et al, 1998). Generally, the macronutrient composition of chimpanzee diets reflects their preference for ripe fruit, with relatively high levels of easily digestible carbohydrates and lower levels of insoluble fibre (Conklin-Brittain et al, 1998; Hohmann et al, 2010; Matsumoto-Oda & Hayashi, 1999; Reynolds et al, 1998). Pith, particularly from terrestrial herbaceous vegetation (THV), also provides chimpanzees with moderate to high levels of carbohydrates as well as energy from digestible fibre fractions (Matsumoto-Oda & Hayashi 1999; Wrangham et al, 1991, 1998). Young leaves provide the greatest amounts of protein of plant foods frequently consumed by chimpanzees (Carlson et al, 2013; Takemoto, 2003). Chimpanzee diets are considered high quality (i.e. generally higher in macronutrients and lower in indigestible fibre and secondary compounds) (Conklin-Brittain et al, 1998). However, the macronutrient and secondary compound content of wild fruit and leaves varies between chimpanzee sites (Hohmann et al, 2010).

In the present study, we aimed to build on existing knowledge of primate diets in anthropogenic landscapes by describing the nutritional aspects of wild and cultivated foods consumed by a chimpanzee (*P. t. verus*) community inhabiting the forest-agricultural mosaic at Bossou, Guinea, West Africa. Presently, there is limited information on the nutritional characteristics of foods in the diets of West African chimpanzees inhabiting anthropogenic landscapes (Takemoto, 2003). This chimpanzee community are ideally situated for our study as Bossou has been rated as the site facing the greatest degree of human-impact (Wilson et al, 2014). Furthermore, over 30 years of research has produced a comprehensive list of over 200 plant food species (246 plant parts) consumed by the chimpanzees (Humle et al, 2011). They also occasionally eat insects, honey, bird eggs, and tree pangolin (*Manis tricuspis*), however, hunting for animal prey is relatively rare at Bossou compared to chimpanzees at other sites (Humle, 2011). The Bossou chimpanzees have foraged on cultivars for generations and consume 17 different fruit and non-fruit crop varieties (Hockings, 2011; Hockings et al, 2009). Cultivars account for a relatively large proportion of feeding time (6.4-14%: Hockings et al, 2009; Takemoto, 2002). The chimpanzees also frequently feed from the semi-domesticated or wild oil palm (*Elaeis guineensis*), exploiting more food parts (i.e. fruit, nut kernel, pith, petiole, flower, and heart) than any other known chimpanzee community (Humle & Matsuzawa, 2004). Oil palm is native to West Africa and is found at high densities in human-impacted landscapes where it is maintained and utilised by people predominantly for the production of palm oil for domestic and commercial use (Humle & Matsuzawa, 2004). The oil palm is heavily utilised by the chimpanzees at Bossou for food (up to 15.9% of annual feeding time: Yamakoshi, 1998) and nesting (Humle & Matsuzawa, 2001). Recent evidence suggests that oil palm trees are also an important food and nesting resource for other chimpanzee communities residing in human-impacted areas across West Africa (Guinea-Bissau: Bessa et al, 2015, Sousa et al, 2011; Cote d'Ivoire: Humle & Matsuzawa, 2004; Sierra Leone: Humle, unpublished data). The macronutrient content of oil palm fruit and nut kernel, both of which are used in the production of palm oils, has been previously described (Agunbiade et al, 1999; Akpanabiatu et al, 2001; Bora et al, 2002; Kok et al, 2011). However, there is as yet no published data detailing the nutritional composition of other oil palm parts (i.e. petiole, pith, flower, and heart) that serve as potentially important food sources for chimpanzees.

Specifically, we examined and compared the macronutrient and energy content of wild and cultivated foods, including oil palm food parts, which constituted the Bossou chimpanzee diet. We further compared the macronutrient and energy content of cultivated and wild foods from Bossou with published results for wild and cultivated foods that constituted the diet of the chimpanzee community at Bulindi, Uganda (McLennan & Ganzhorn, 2017). Following findings for Bulindi chimpanzees (McLennan & Ganzhorn, 2017), we predicted that Bossou chimpanzee cultivated foods would be higher in easily digestible carbohydrates and energy, and lower in insoluble fibre, protein, and lipids, than equivalent wild foods. Given the differences in macronutrient content of available foods between chimpanzees sites (Hohmann et al, 2010); we predicted that there would be differences in macronutrient composition between Bossou chimpanzee and Bulindi chimpanzee wild and cultivated foods.

4.3 METHODS

4.3.1 Study site and population

We present data collected from April 2012 to March 2013 from the semi-isolated chimpanzee community that inhabits the anthropogenic landscape surrounding the village of Bossou, Republic of Guinea, West Africa (latitude 7°38’71.7’N and longitude 8°29’38.9’W). During our study, the community size ranged between 12-13 individuals with 6 adult females and 4 adult males. The chimpanzee community’s home range is approximately 15 km^2, although they spend most of their time in the four small hills (70-150 m high) that surround Bossou village and constitute their 6 km^2 core area (Humle, 2011). Local people practise slash and burn agriculture within and at the edges of these small hills, resulting in a highly heterogeneous forest-agricultural mosaic composed of regenerating, riverine, and mature forest as well as fallow land, coffee plantations and cultivated fields (Bryson-Morrison et al, 2016; Humle, 2011). The climate in this region is classified as tropical wet seasonal with a long rainy season from March to October, when wild fruit availability is low, and a short dry season from November to February, when wild fruit availability is high (Bryson-Morrison et al, 2016; Hockings, 2007; Humle, 2011; Takemoto, 2002; Yamakoshi, 1998).

4.3.2 Sample collection and nutritional analyses

Our sample collection protocols and nutritional analyses followed Rothman et al, (2012). We collected food samples during focal feeding bout observations of adult individuals (N = 10) (total observation: 568 hours), and endeavoured to collect samples from the same tree, plant or food patch fed on by the focal individual. When this was not possible, we selected nearby conspecific plants and collected parts of the same maturation stage as those consumed. With permission, we collected fruit from cultivated fruit tree orchards and food parts from banana plants from coffee plantations. However, we did not collect crops from cultivated fields. Instead, cultivars were either donated to us by our local research assistants or were bought from Bossou village market. All sampled cultivars were grown in Bossou and were known to have been harvested within 1-2 days of us buying and processing them. Oil palm petiole from young leaf fronds and palm heart were collected opportunistically from trees that were known to have recently fallen (<3 days). Due to the diversity of the chimpanzee diet, we were unable to sample all wild foods. Instead, we aimed to preferentially sample fruit, pith and gum most important to overall diet, as well as all cultivated plant parts (i.e. nut kernel, petiole, palm heart, and tuber) that were observed to be eaten. We used previously reported macronutrient concentrations for leaves (Takemoto, 2003). In total, we sampled foods representing 90.7% of overall food intake (measured as g dry matter) (Table 4.1). We collected 224 food samples (150 wild samples; 74 cultivar samples) representing 36 species (25 wild species; 11 cultivar species) (Table 4.1). We combined fruit samples from *Ficus* species (i.e. 6 species) as we were unable to obtain large enough sample sizes of individual species for nutritional analyses. We processed samples in the same way as the chimpanzees by only selecting parts observed to be eaten and swallowed. Samples were weighed as soon as possible after collection (wet weight) and dried in a dehydrator set at 45°C. Samples were weighed again after drying and stored in the dark in sealed and labelled plastic bags with desiccant. Once transported back to the UK, we ground all samples through a 1 mm screen using a Fritsch Pulverisette 19 at Sparsholt College Nutritional Laboratory, Hampshire, England. Particularly oily samples were freeze dried in order to aid in the grinding process. Samples representing the same plant part and species were mixed prior to analyses to account for spatial and temporal variation in chemical composition (Rothman et al, 2012).

We used standard wet chemistry procedures (Association of Official Analytical Chemists, 1990) to estimate macronutrient content. A portion of each sample was dried at 105°C in an oven for 24 hours to calculate dry matter before nutritional analyses were performed. We estimated total nitrogen (N) content using Kjeldahl digestion (using a Gerhardt Vapodest 50), and calculated crude protein (CP) by multiplying N by 6.25 (Rothman et al, 2012). Crude protein values overestimate the amount of available protein within food samples as total nitrogen includes digestible and indigestible fibre-bound protein (Rothman et al, 2008). As we did not have the facilities to determine available protein (AP) we used CP measures. However, McLennan & Ganzhorn, (2017) found that CP and AP were highly correlated in their sample of wild and cultivated chimpanzee foods. Furthermore, CP and AP were correlated in leaves from Uganda (Wallis et al, 2012). We determined neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) using detergent fibre analysis (Van Soest, 1991). However, it must be noted that our fibre results for high lipid foods (>10% lipids by dry matter) may be overestimated as we did not pre-extract our samples before performing fibre analyses (Rothman et al, 2012). We determined ash by burning a portion of the sample at 500°C. We used ether extract (extracted using a Gerhardt Soxtherm) to estimate lipid content. We calculated total non-structural carbohydrates (TNC) using the following formula:

$$\%TNC = 100 - (\%CP + \%Lipid + \%Ash + \%NDF)$$

This calculation is widely used to give a crude estimate of TNC but it does not account for other fractions present such as vitamins and secondary compounds (Rothman et al, 2012). We calculated energy gain using the standard physiological metabolisable energy (ME) equation:

$$ME = ((4\ Kcal/g \times TNC) + (4\ Kcal/g \times CP) + (9\ Kcal/g \times Lipid) + (1.6\ Kcal/g \times NDF))/100$$

Where components are multiplied by their physiological fuel values derived from human diets (National Research Council, 2003). NDF is multiplied by the physiological fuel value for fibre digestion in chimpanzees (Conklin-Brittain et al, 2006).

4.3.3 Comparison of macronutrient and energy content of cultivated and wild foods between Bossou, Guinea and Bulindi, Uganda

We used macronutrient and energy content data from McLennan & Ganzhorn (2017) for wild (N = 28) and cultivated (N = 15) fruit and pith consumed by the Bulindi chimpanzee community. We also used macronutrient and energy content data on crops grown at Bulindi that were also consumed by the Bossou chimpanzees, but were never observed to be eaten by the Bulindi chimpanzees (N = 5). As the Bulindi chimpanzees are unhabituated to researcher presence, the food species and food parts consumed were largely determined by examining faecal and feeding traces (McLennan & Ganzhorn, 2017), as opposed to continual direct observations of feeding behaviour used in the present study. As such, there are likely to be differences in the plant parts included for nutritional analyses, such as the seeds of fruits, between the present study and that conducted by McLennan & Ganzhorn (2017).

4.3.4 Statistical analysis

For analyses, we included oil palm food parts with cultivars given that a large majority of trees found at Bossou are semi-domesticated and actively maintained and utilised by local people. We compared the nutritional proportions of plant parts between cultivated and wild fruits and pith eaten by the Bossou chimpanzees using independent samples t-test as our data met the assumptions of the Levene's Test for Equality of Variances and normality distribution.

We used non-parametric tests to examine differences in macronutrient and energy content between Bossou and Bulindi chimpanzee foods as not all of these data were normally distributed. We compared the macronutrient and energy content of the same species of cultivated ripe fruit and pith grown at both Bossou and Bulindi (N = 5) (i.e. eaten by Bossou chimpanzees and grown in Bulindi, but not necessarily eaten by Bulindi chimpanzees) using Wilcoxon signed ranks test. We examined the macronutrient and energy content of cultivated fruit (N = 11) and pith (N = 4) actually consumed by Bulindi chimpanzees with cultivated fruit (N = 9) and pith (N = 3) consumed by the Bossou chimpanzees (i.e. cultivars eaten by both chimpanzee communities but not necessarily the same species) using Mann-Whitney U tests. We also used Mann-Whitney U tests to compare the macronutrient and energy content of wild chimpanzee fruit (Bossou: N = 17; Bulindi: N = 21) and pith (Bossou: N = 8; Bulindi: N = 7). We used SPSS version 22.0 and set the significance level at $p \leq 0.05$.

4.4 RESULTS

4.4.1 Bossou chimpanzee cultivated and wild fruit compared

Cultivated fruit (N = 9) was significantly higher in TNC and metabolisable energy (ME) than wild fruit (N = 17) (TNC: t (24) = 3.803, $P \leq 0.001$; ME: t (24) = 2.195, $P < 0.05$) (Table 4.1; Fig. 4.1a). Whereas wild fruits were significantly higher in ADF, NDF, and CP than cultivated fruits (ADF: t (24) = -3.710, $P \leq 0.001$; NDF: t (24) = -3.471, $P \leq 0.002$; CP: t (24) = -3.344, $P < 0.003$) (Table 4.1; Fig. 4.1a). We found no significant difference in ADL, lipid or ash composition between cultivated and wild fruit (ADL: t (24) = -0.846, P = 0.406; Lipid: t (24) = -0.425, P = 0.675; Ash: t (24) = -1.380, P = 0.180) (Table 4.1; Fig. 4.1a).

Table 4.1 Macronutrient and energy composition of cultivated and wild foods consumed by a chimpanzee community inhabiting the forest-agricultural mosaic of Bossou, Guinea, West Africa

	Species	**Part**	**NDF**	**ADF**	**ADL**	**Lipid**	**Ash**	**CP**	**TNC**	**ME**
Cultivar	*Citrus sinensis*	Fruit	8.62	7.87	5.75	2.29	3.75	5.68	79.66	376
	Zea mays	Fruit	53.81	3.26	2.11	2.54	1.63	10.30	31.72	277
	**Theobroma cacao*	Fruit	22.70	20.88	5.40	31.45	3.51	10.93	31.42	489
	Ananas comosus	Fruit	9.06	4.28	3.52	0.09	2.83	2.49	85.53	367
	Musa sinensis	Fruit	4.65	2.62	0.65	0.19	3.89	5.66	85.62	374
	Musa sinensis	Pith	41.28	27.47	3.42	2.80	18.63	20.08	17.21	240
	Citrus reticula	Fruit	12.80	11.03	6.39	6.23	4.80	7.55	68.61	381
	Mangifera indica	Fruit	7.80	2.88	2.32	0.62	2.14	2.29	87.15	376
	Carica papaya	Fruit	12.60	11.70	6.49	0.09	8.26	3.94	75.11	337
	Oryza sp.	Pith	54.93	34.79	3.65	1.18	12.87	3.45	27.56	223
	Manihot esculenta	Tuber	8.44	2.37	1.89	0.40	1.39	1.34	88.44	376
	**Elaeis guineensis*	Fruit	50.29	40.97	16.89	30.32	2.00	4.42	12.98	423
	Elaeis guineensis	Heart	30.94	20.18	2.39	4.03	12.13	18.56	34.35	297
	Elaeis guineensis	Petiole	30.64	20.66	1.69	3.68	12.65	20.11	32.92	294

	Elaeis guineensis	Pith	51.28	41.69	7.93	1.15	2.89	1.55	43.13	271
	Elaeis guineensis	Nut	57.48	/	/	42.82	2.00	11.12	23.20[1]	615
Wild	**Parkia bicolor*	Fruit	14.50	5.94	3.53	14.04	3.59	18.83	49.04	421
	**Megaphrynium macrostachyum*	Fruit	68.62	23.38	10.55	1.11	6.46	12.61	11.20	215
	**Ficus sp.*	Fruit	59.41	55.27	22.51	4.33	8.23	10.30	17.74	246
	**Pseudospondias microcarpa*	Fruit	38.81	33.46	15.60	4.64	9.31	9.78	37.46	293
	**Canarium schwenfurthii*	Fruit	60.96	50.09	17.72	12.30	3.05	5.65	18.05	303
	Spondias mombin	Fruit	51.36	41.75	22.07	4.17	5.02	10.03	29.43	278
	**Myrianthus libericus*	Fruit	44.86	37.25	17.16	11.47	2.88	19.18	27.35	310
	Myrianthus arboreus	Fruit	41.08	33.65	13.93	22.69	2.30	19.35	14.59	406
	**Macarenga barteri*	Fruit	40.26	32.95	8.52	19.46	4.16	8.98	27.14	384
	**Morus mesozygia*	Fruit	20.29	19.26	7.77	9.58	7.16	13.27	49.70	371
	**Monodora tenuifolia*	Fruit	48.17	32.97	16.35	23.34	1.81	12.17	14.51	394
	**Discophylium cumminsii*	Fruit	35.68	31.72	5.30	18.03	11.23	14.92	20.14	360
	Musanga cecropioides	Fruit	64.26	60.54	14.97	3.56	3.72	8.67	23.52	258
	**Antiaris africana*	Fruit	32.67	15.80	7.10	2.99	5.15	12.18	47.01	316

**Aningeria altissima*	Fruit	33.33	19.92	8.39	12.38	3.79	8.72	41.77	367
**Landolphia sp.*	Fruit	32.94	24.33	13.21	1.64	3.04	4.52	57.87	317
Albizia zygia	Gum	29.30	3.44	1.86	0.08	7.82	6.26	56.55	299
Aframomum latifolium	Pith	61.21	43.57	5.15	0.66	12.84	6.70	18.59	205
Costus afer	Pith	48.43	32.34	7.67	1.35	8.86	10.15	31.21	244
Gongronema latifolium	Pith	34.09	27.61	8.49	3.22	13.38	3.82	45.49	281
Hypselodelphis Sp.	Pith	31.29	25.13	5.95	1.88	9.96	18.25	38.62	294
Maranthochloa macrophylla	Pith	37.64	24.71	3.91	2.67	13.93	22.54	23.22	267
Megaphrynium macrostachyum	Pith	33.57	19.36	2.38	3.50	13.67	26.47	22.80	282
Pennisetum purpureum	Pith	53.79	33.80	1.72	1.98	15.24	15.29	13.69	220
Thaumatococus daniellii	Pith	36.69	22.46	2.02	2.53	13.99	23.82	22.96	269
Species combined	Leaf[2]	37.00	/	/	2.70	12.00	25.00	23.30	277

ADF = acid detergent fibre, ADL = acid detergent lignin, NDF = neutral detergent fibre, CP = crude protein, TNC = total non-structural carbohydrates, ME = metabolisable energy. Macronutrients expressed on a percentage dry matter basis. Energy = Kcal/100g.* = seeds included. [1]Mean TNC value of oil palm nuts taken from Akpanabiatu et al (2001). [2]Overall mean values for young leaves consumed by the chimpanzee at Bossou taken from Takemoto (2003).

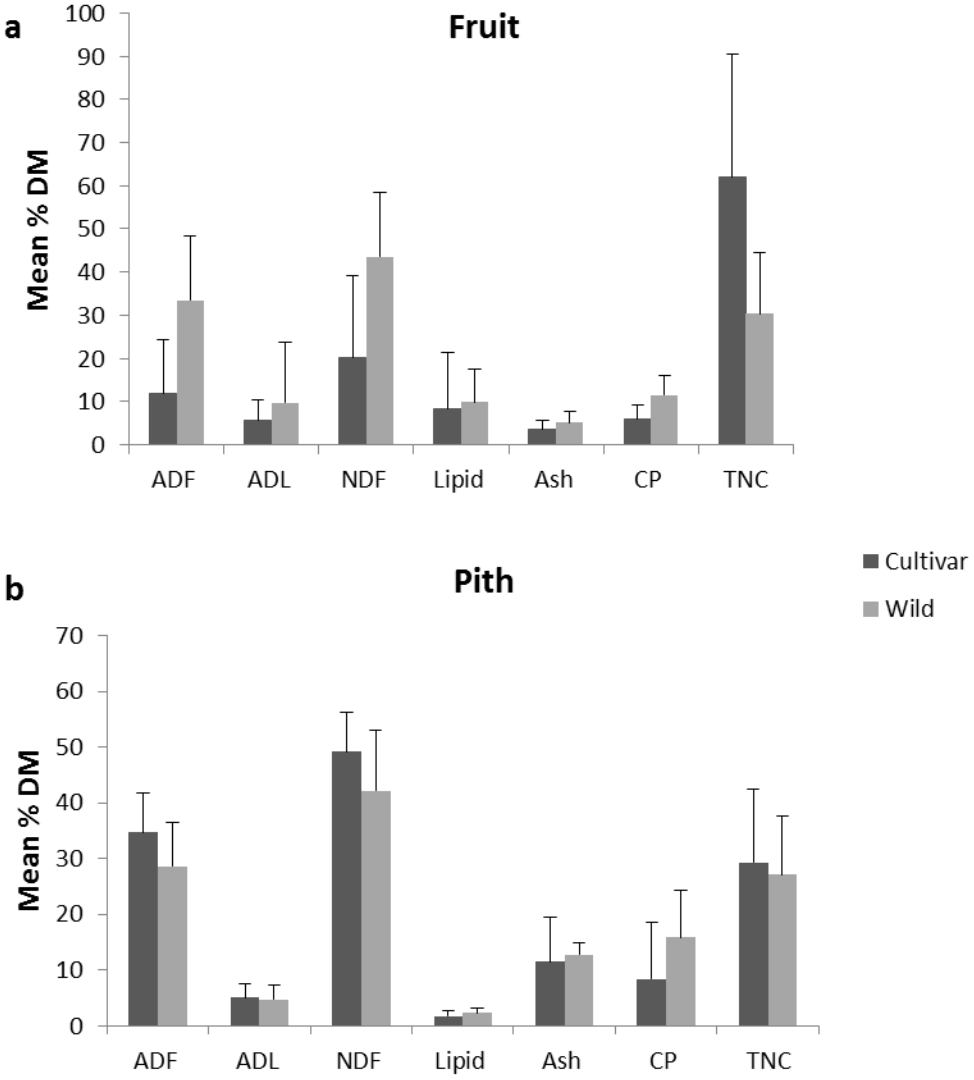

Figure 4.1 Mean plus SD of macronutrient density expressed as % dry matter (DM) of wild and cultivated fruit and pith consumed by a chimpanzee community inhabiting the forest-agricultural mosaic of Bossou, Guinea, West Africa. a) Fruit: cultivar (N = 9) and wild (N = 17); b) Pith: cultivar (N = 3) and wild (N = 8). ADF = acid detergent fibre, ADL = acid detergent lignin, NDF = neutral detergent fibre, CP = crude protein, TNC = total non-structural carbohydrates. Oil palm fruit and pith included with cultivar

4.4.2 Bossou chimpanzee cultivated and wild pith compared

Overall, cultivated pith (N = 3) was higher in fibre (ADF, ADL and NDF) and TNC, while wild pith (N = 8) was higher in CP (Table 4.1, Fig. 4.1b). However, we found no significant difference between individual macronutrients and ME density of cultivated and wild pith (NDF: t (9) = 1.020, P = 0.334; ADF: t (9) = 1.174, P = 0.270; ADL: t (9) = 0.194, P =0.851; Lipid: t (9) = -0.801, P = 0.444; Ash: t (9) = -0.445, P = 0.667; CP: t (9) = -1.263, P = 0.238; TNC: t (9) = 0.293, P = 0.776; ME: t (9) = -0.639, P = 0.539).

4.4.3 Oil palm food parts

The macronutrient composition of oil palm nut kernel and fruit from Bossou falls within the range reported by other studies (Table 4.2). Although the exact composition of nut kernel varies, all were high in lipids and moderate to high in CP and TNC. Oil palm fruit was high in NDF, lipids, and TNC (Table 4.2). Pith was relatively low in lignin (ADL: <8% dry matter (DM)) and high in fermentable fibre fractions (NDF: > 50% DM) and TNC (> 40% DM). Both the petiole and heart were high in ash (around 12% DM), CP (≥ 19% DM), and TNC (≥ 33% DM) and lower in fibre than other oil palm parts (around 30% DM) (Table 4.1; Fig. 4.2a). Oil palm nut kernel was higher in ME than all other sampled food parts, and only cacao fruit was higher in ME than oil palm fruit (Table 4.1; Fig. 4.2b). Petiole, pith and heart contained similar amounts of ME, which were within the ranges found for other sampled foods (Table 4.1; Fig. 4.2b).

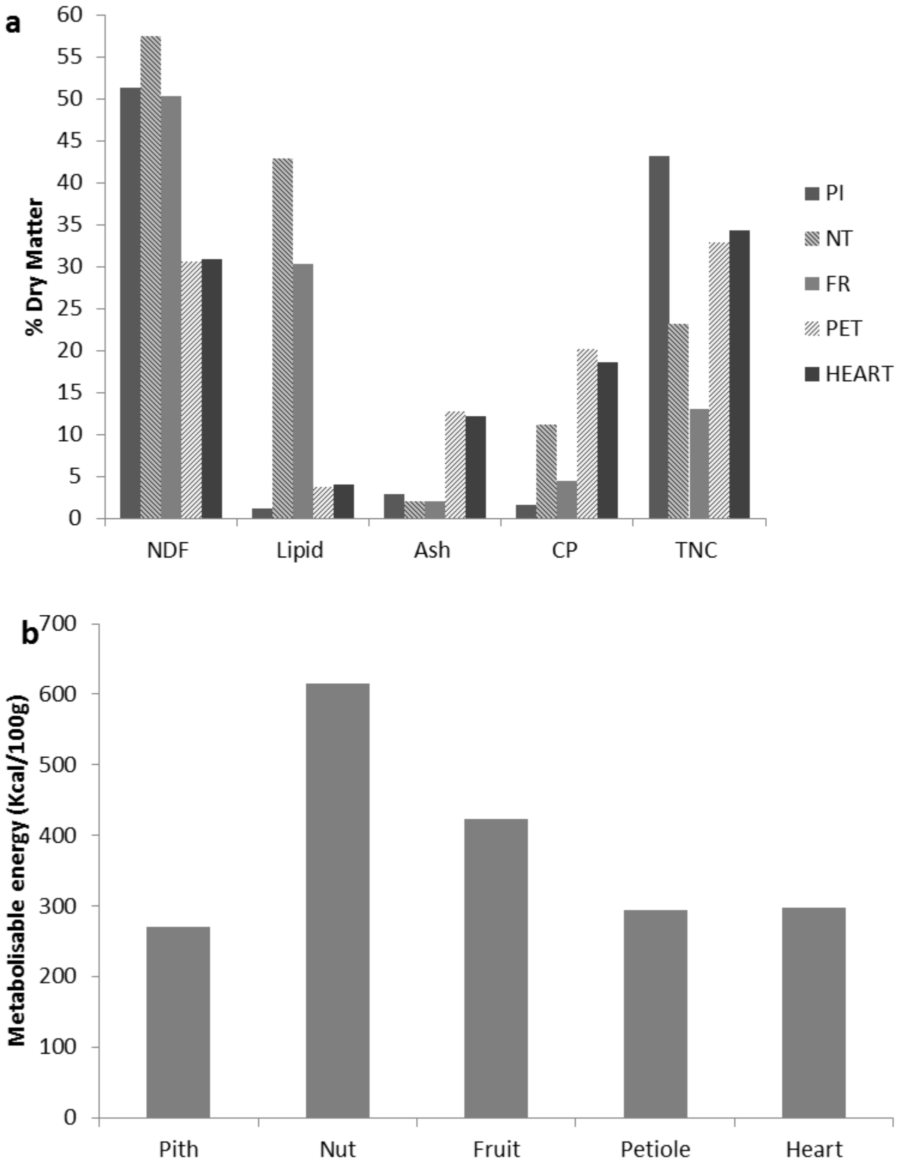

Figure 4.2 (a) Macronutrient density and (b) metabolisable energy of oil palm (*Elaeis guineensis*) parts consumed by a community of chimpanzees inhabiting the forest-agricultural mosaic of Bossou, Guinea, West Africa. NDF = neutral detergent fibre, CP = crude protein, TNC = total non-structural carbohydrates. PI = pith; NT = nut kernel; FR = fruit; PET = petiole

Table 4.2 Published results of the nutritional composition of oil palm (*Elaeis guineensis*) nut kernel and fruit

	Sample origin	**NDF**	**Lipid**	**Ash**	**CP**	**TNC**	
Kernel	Commercial[1]	45.6	47	2.6	13.6	/	Agunbiade et al (1999)
	Nigeria[2]	/	42	1.8	8.1	25.4	Akpanabiatu et al (2001)
	Nigeria[2]	/	41	1.5	7.9	21	Akpanabiatu et al (2001
	Malaysia[3]	/	54.9	1.9	7.8	18.1	Kok et al (2011)
	Brazil	/	32.6	1.7	10.9	35.1	Bora et al (2002)
	Bossou, Guinea	57.5	42.8	2.0	11.1	/	This study
Fruit	Brazil[4]	/	73.2	1.9	3.4	13.3	Bora et al (2002)
	Bossou,[5] Guinea	50.3	30.3	2.0	4.4	13.0	This study

NDF = neutral detergent fibre, CP = crude protein, TNC = total non-structural carbohydrates. Macronutrients expressed on a percentage dry matter basis.[1]Commercial sample of West African origin. [2]Dura variety. [3]Tenera hybrid. [4]Pulp only. [5]Whole fruit

4.4.4 Comparisons of Bossou and Bulindi cultivated and wild foods

4.4.4.1 Cultivated foods

We found no significant differences in CP, lipids, TNC, fibre fractions (NDF and ADF) or ME for cultivars grown at Bossou and Bulindi (Wilcoxon signed-rank test: CP: Z = -0.663, P = 0.508; Lipids: Z = -0.102, P = 0.919; TNC: Z = -0.459; P = 0.646; NDF: Z = -0.153, P = 0.878; ADF: Z = -1.580, P = 0.114; ME: Z = -.255, P = 0.799). However, we found a significant difference in ash content between Bossou and Bulindi cultivars (Z = -2.803, P = 0.005), with cultivars grown at Bossou higher in ash.

We found no differences in any of the macronutrient fractions or ME content for cultivated fruit (Mann-Whitney U test: CP: U = 42, P = 0.569; Lipids: U = 44, P = 0.676; TNC: U = 36, P = 81; Ash: U = 41, P = 0.552; NDF = 38, P = 0.412; ADF = U = 35, P = 0.295; ME: U = 38, P = 0.412) consumed by Bulindi and Bossou chimpanzees (Fig. 4.3). We found a significant difference in ADF content of cultivated pith (U = 0, P = 0.034), with pith from Bulindi lower in ADF than pith from Bossou (Fig. 4.4). We found no differences in all other macronutrients and ME between Bossou and Bulindi cultivated pith (CP: U = 5, P = 0.857; Lipids: U = 2, P = 0.157; TNC: U = 2, P = 0.157; Ash: U = 4, P = 0.480; NDF: U = 2, P = 0.157; ME: U = 1, P = 0.077) (Fig. 4.4).

4.4.4.2 Wild foods

We found significant differences in CP, lipids, TNC, NDF, and ADF content between Bossou and Bulindi chimpanzee wild fruits (CP: U = 58, P > 0.001; Lipids: U = 46, P > 0.001; TNC: U = 13, P > 0.001; NDF: U = 28, P > 0.001; ADF: U = 26, P > 0.001), but no differences between ash and ME content (Ash: U = 136, P = 0.220; ME: U = 148, P = 0.383) (Fig. 4.5). Specifically, Bossou chimpanzee wild fruits were higher in CP, lipids, NDF and ADF, while Bulindi wild fruits were higher in TNC. We found no significant differences in macronutrient and ME content between Bossou and Bulindi wild pith (CP: U = 15, P = 0.132; Lipids: U = 18, P = 0.247; TNC: U = 19, P = 0.298; Ash: U = 28, P = 1.000; NDF: U = 24.5, P = 0.685; ADF: U = 21, P = 0.418; ME: U = 25, P = 0.779) (Fig. 4.6).

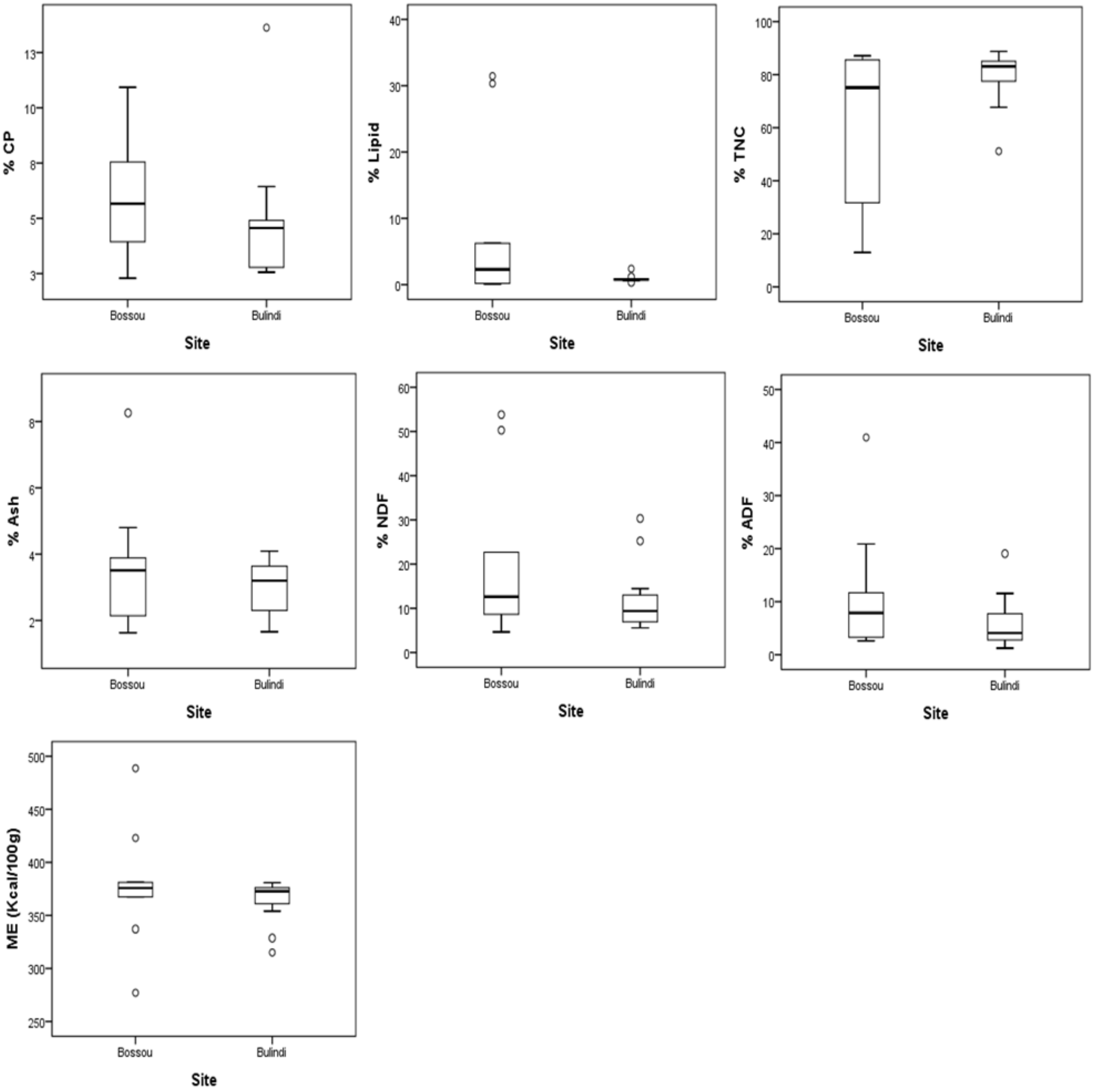

Figure 4.3 Macronutrient and energy comparison of cultivated fruits eaten by chimpanzees in Bossou, Guinea (N = 9) this study (2012-2013) and Bulindi, Uganda (N= 11) taken from McLennan & Ganzhorn (2017). Horizontal lines are medians; boxes span first to third quartiles; whiskers depict minimum and maximum values; circles are outliers. CP: crude protein; TNC: total non-structural carbohydrates; fibre fractions: NDF, ADF; ME: metabolisable energy. Macronutrients expressed as % dry matter; ME expressed as Kcal/100g

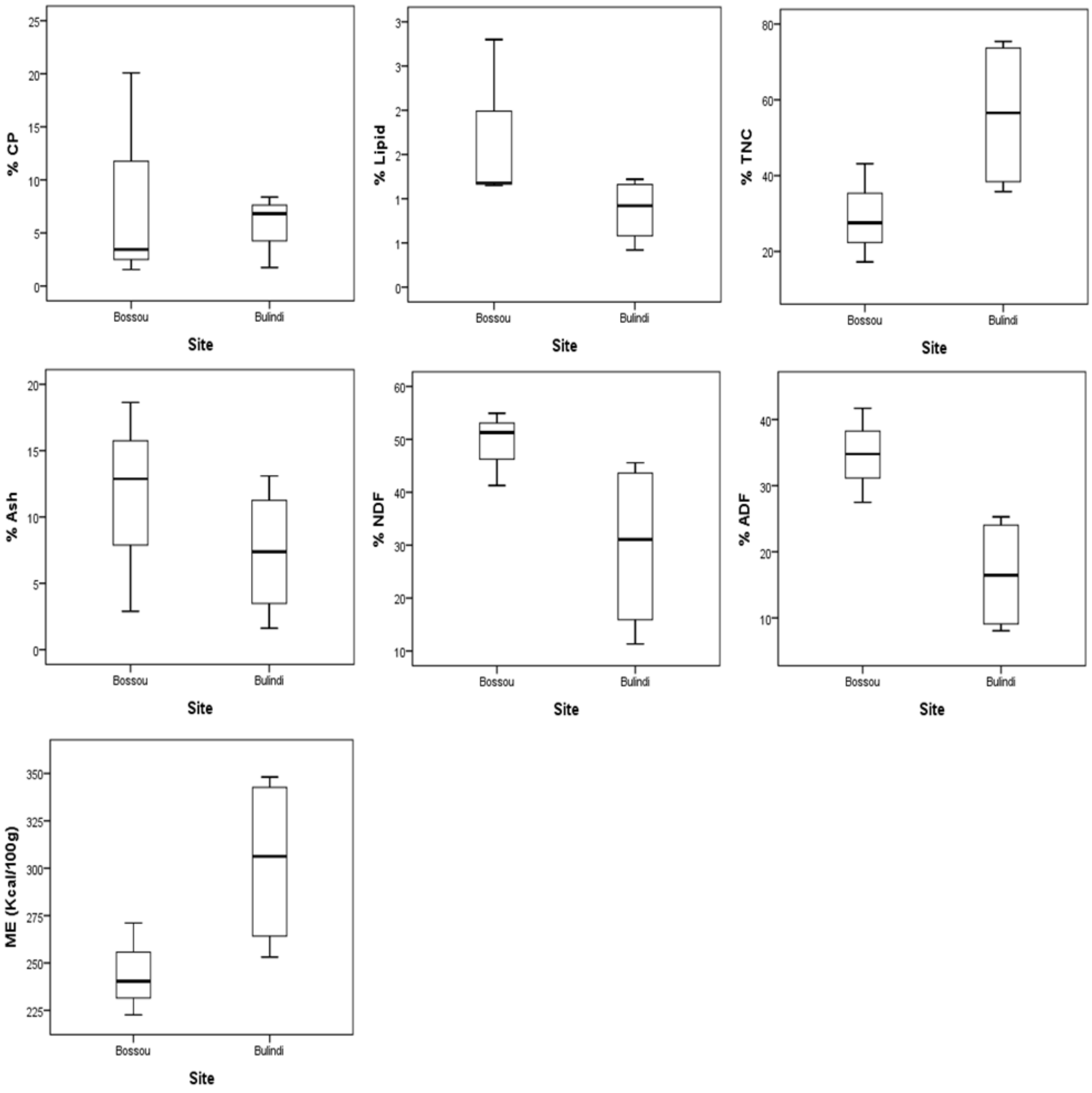

Figure 4.4 Macronutrient and energy comparison of cultivated pith eaten by chimpanzees in Bossou, Guinea (N= 3) this study (2012-2013) and Bulindi, Uganda (N= 4) taken from McLennan & Ganzhorn (2017). Horizontal lines are medians; boxes span first to third quartiles; whiskers depict minimum and maximum values; circles are outliers. CP: crude protein; TNC: total non-structural carbohydrates; fibre fractions: NDF, ADF; ME: metabolisable energy. Macronutrients expressed as % dry matter; ME expressed as Kcal/100g

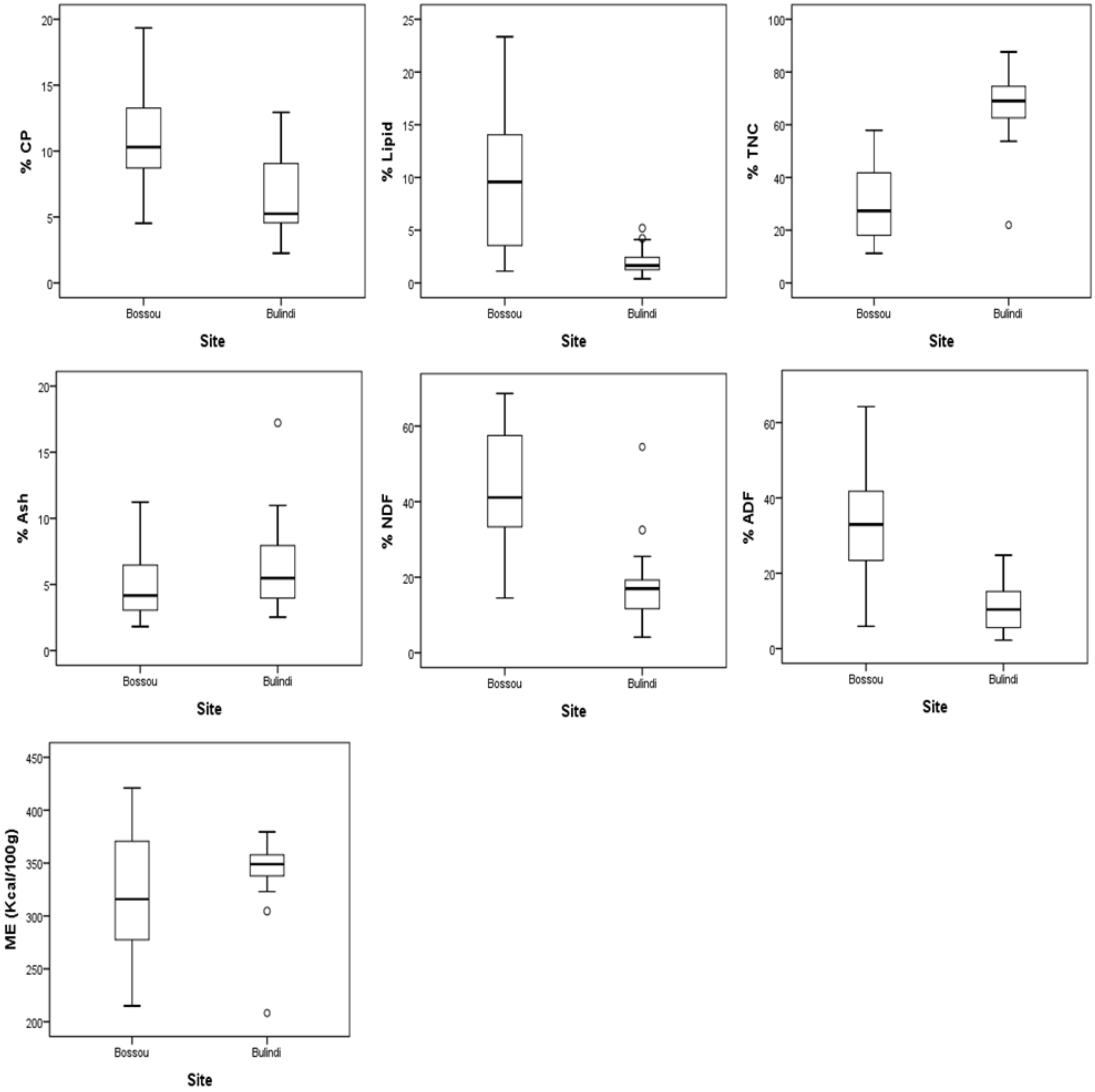

Figure 4.5 Macronutrient and energy comparison of wild fruit eaten by chimpanzees in Bossou, Guinea (N= 17) this study (2012-2013) and Bulindi, Uganda (N= 21) taken from McLennan & Ganzhorn (2017). Horizontal lines are medians; boxes span first to third quartiles; whiskers depict minimum and maximum values; circles are outliers. CP: crude protein; TNC: total non-structural carbohydrates; fibre fractions: NDF, ADF; ME: metabolisable energy. Macronutrients expressed as % dry matter; ME expressed as Kcal/100g

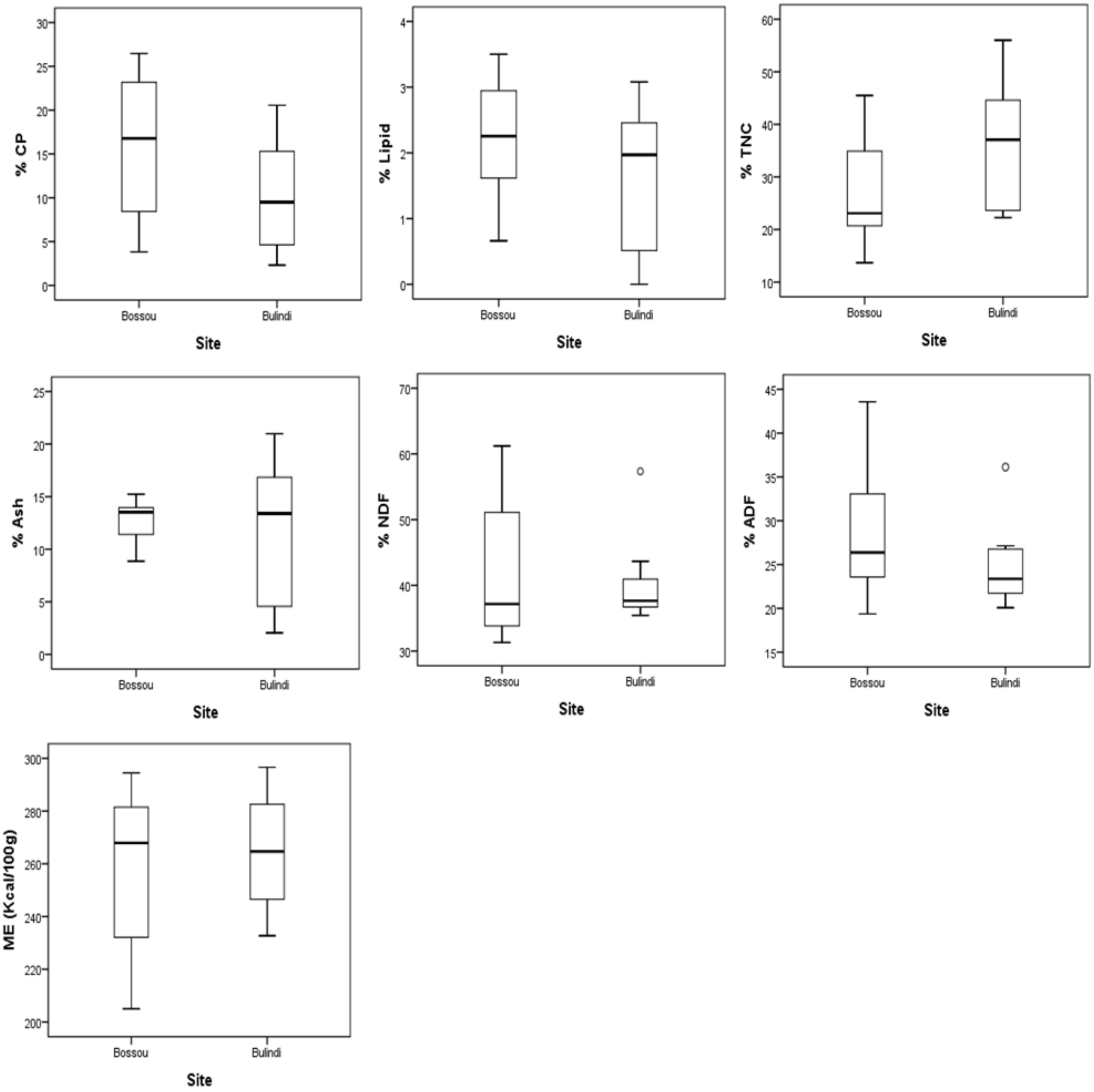

Figure 4.6 Macronutrient and energy comparison of wild pith eaten by chimpanzees in Bossou, Guinea (N= 8) this study (2012-2013) and Bulindi, Uganda (N= 7) taken from McLennan & Ganzhorn (2017). Horizontal lines are medians; boxes span first to third quartiles; whiskers depict minimum and maximum values; circles are outliers. CP: crude protein; TNC: total non-structural carbohydrates; fibre fractions: NDF, ADF; ME: metabolisable energy. Macronutrients expressed as % dry matter; ME expressed as Kcal/100g

4.5 DISCUSSION

Overall, our results add to those found for the Bulindi chimpanzee community (McLennan & Ganzhorn, 2017) in supporting the widespread view that cultivar-foraging has energetic benefits by providing primates with access to foods low in insoluble fibre and high in easily digestible carbohydrate energy (e.g. Hockings et al, 2009; Lodge et al, 2013; Naughton-Treves et al, 1998).

The nutritional composition of wild plant parts consumed by the Bossou chimpanzees were similar to those reported previously for other chimpanzee communities (Conklin-Brittain et al, 1998; Hohmann et al, 2010; Matsumoto-Oda & Hayashi, 1999) and for primates more generally (Lambert & Rothman, 2015). Foods varied in their nutrient content; ripe fruit provided easily digestible carbohydrates (TNC), pith and gum provided carbohydrate energy mostly from fermentable fibre (i.e. NDF) (Wrangham et al, 1991), while leaves provided high amounts of protein. Fruit contained the highest proportions of lipids of wild foods, as is consistent with other studies of great ape diets (Conklin-Brittain et al, 1998; Reiner et al, 2014; but see McLennan & Ganzhorn, 2017).

Primate diets are generally considered to contain limited amounts of lipids (Lambert & Rothman, 2015). However, the Bossou chimpanzees rely heavily on oil palm fruit and nut kernel (Humle & Matsuzawa, 2004; Yamakoshi & Sugiyama, 1995), both of which were extremely high in lipids. Oil palm fruit and nut kernel likely constitute high quality foods for the chimpanzees given that lipids provide twice the energy of carbohydrates and protein (National Research Council, 2003). Pith from oil palm leaf fronds were similar to wild pith in providing good sources of energy from fermentable fibre. The chimpanzees also frequently consume the petiole, from young leaf fronds, and the palm heart (up to 9.6% of feeding time, Yamakoshi, 1998). Our results showed that these parts are nutrient dense foods rich in both protein and carbohydrates and relatively low in insoluble fibre. Oil palm trees clearly provide the chimpanzees with high quality food sources, all of which are available year round (Bryson-Morrison et al, 2016). These findings provide nutritional support for the oil palm serving as a potentially critical resource for chimpanzee populations residing in human-impacted landscapes across West Africa (Bessa et al, 2015; Brncic et al, 2010; Humle & Matsuzawa, 2004; Yamakoshi, 1998).

Similarly to Bulindi, we found that Bossou chimpanzee wild fruit were generally higher in protein and fibre than cultivated fruit. However, unlike Bulindi, we found that Bossou chimpanzees cultivated and wild pith were nutritionally similar. Bulindi chimpanzees consumed pith from sugar cane and yam, cultivars not grown at Bossou, both of which contained particularly high levels of sugar akin to cultivated fruits (McLennan & Ganzhorn, 2017). Bulindi chimpanzees may be selecting cultivated pith for carbohydrate energy (McLennan & Ganzhorn, 2017) while cultivated pith consumption by Bossou chimpanzees may be influenced by nutritional factors other than macronutrient and energy content. For example, cultivars consumed by elephants in Kibale National Park, Uganda were found to be higher in sodium than wild foods (Rode et al, 2006). Rice pith, which is highly selected by Bossou chimpanzees when seasonally available (Hockings et al, 2009), may serve as an important source of sodium. Previous studies have reported on plant food parts that grow in wet areas, such as the pith of herbaceous swamp plants, as providing sodium and other minerals in primate diets (gorilla: Magliocca & Gautier-Hion, 2002; chimpanzee: Reynolds et al, 2009, 2012; black & white colobus: Oates, 1978). Analyses of the micronutrient content of rice pith and other foods consumed from wet areas, such as algae, are required for understanding the role of these plant parts in the Bossou chimpanzee diet.

Our prediction that Bossou and Bulindi wild and cultivated foods would differ in macronutrient composition was partially supported by our findings that wild fruit varied in most nutrient components. The nutritional composition of wild plant parts in primate diets have been shown to vary spatially and temporally both within and between sites (Chapman et al, 2003; Ganzhorn, 1995; Houle et al, 2014; Rothman et al, 2009; Worman & Chapman, 2005). Plant chemistry is influenced by environmental effects including temperature variability, light intensity, water availability, salt levels, soil type, seasonality, and plant maturation stage (Chapman et al, 2003; Sams, 1999; Woolf & Ferguson, 2000). We found that cultivars grown at Bossou were higher in ash, a crude measure of minerals, and environmental effects, along with fertilisation practises, significantly influences the mineral content of cultivated plant foods (Martinez-Ballesta et al, 2010). The similarity in other macronutrient components between Bossou and Bulindi crops are most likely due to high genetic selectivity by humans (Milton, 1999). However, we must be cautious in our interpretation of these results due to differences in sample processing methods between our study and that conducted at Bulindi (McLennan & Ganzhorn, 2017). During sample processing, we retained all food parts seen to be actively eaten and swallowed by the chimpanzees and as such many of our fruit samples contained seeds which may have elevated protein, lipid and fibre estimates (Conklin & Wrangham, 1994; Milton, 2008). Nevertheless, we found no difference in energy content of wild and cultivated chimpanzee foods between Bossou and Bulindi, suggesting that dietary quality may reflect selection preferences rather than habitat ecology, as found for chimpanzees and bonobos (*Pan paniscus*) at other sites (Hohmann et al, 2010).

4.5.1 Conclusions and future directions

Our study adds to knowledge on the nutritional composition of foods eaten by chimpanzees in a range of different habitats. We reported on the nutritional dimensions of both wild and cultivated foods, building on current understanding of chimpanzee feeding ecology and diet within forest-agricultural mosaics. Such information is essential for helping to unravel the drivers behind cultivar-foraging for the effective management of human-wildlife coexistence and the development of conservation initiatives for chimpanzees, and other primates, residing in anthropogenic landscapes. Furthermore, the nutritional profiles of foods selected by wild primates are important for informing captive facilities on species specific dietary needs.

However, the nutritional compositions of consumed foods are unable to provide details of nutrient prioritisation and balancing of selected diets (Felton et al, 2009; Garber et al, 2015;

Righini et al, 2015). Such information is important if we are to fully understand the strategies primates employ to meet their nutrient and energetic needs (Righini et al, 2015). Thus, our future priorities are to employ new analytical frameworks (Simpson & Raubenheimer, 2012; Raubenheimer et al, 2015) to examine the effects of seasonal fruit availability and cultivar consumption on chimpanzee nutrient prioritisation and intake.

4.6 REFERENCES

Agunbiade, J., Wiseman, J. and Cole, D. J. (1999) Energy and nutrient use of palm kernels, palm kernel meal and palm kernel oil in diets for growing pigs, *Animal Feed Science and Technology*, 80: 165–181.

Akpanabiatu, M., Ekpa, O., Mauro, A. and Rizzo, R. (2001) Nutrient composition of Nigerian palm kernel from the dura and tenera varieties of the oil palm (Elaeis guineensis), *Food Chemistry*, 72: 173–177.

Altmann, J. and Muruthi, P. (1988) Differences in daily life between semiprovisioned and wild-feeding baboons, *American Journal of Primatology*, 15: 213–221.

Association of Official Analytical Chemists (1990) *Official Methods of Analysis*. VA: Association of Official Analytical Chemists.

Beasley, J. and Rhodes, O.E. (2008) Relationship between raccoon abundance and crop damage, *Human-Wildlife Conflicts*, 2: 248-259.

Bessa, J., Sousa, C. and Hockings, K. J. (2015) Feeding ecology of chimpanzees (Pan troglodytes verus) inhabiting a forest-mangrove-savanna-agricultural matrix at Caiquene-Cadique, Cantanhez National Park, Guinea-Bissau, *American Journal of Primatology*, 77: 651–665.

Bora, P. S., Rocha, R. V., Narain, N., Moreira-Monteiro, A. and Moreira, R. (2003) Characterization of principal nutritional components of Brazilian oil palm (Eliaes guineensis) fruits, *Bioresource Technology*, 87: 1–5.

Brennan, E. J., Else, J. G. and Altmann, J. (1985) Ecology and behaviour of a pest primate: vervet monkeys in a tourist-lodge habitat, *African Journal of Ecology*, 23: 35–44.

Brncic, T., Amarasekaran, B. and McKenna, A. (2010) Sierra Leone national chimpanzee census, *Freetown Sierra Leone: Tacugama*.

Bryson-Morrison, N., Matsuzawa, T. and Humle, T. (2016) Chimpanzees in an anthropogenic landscape: Examining food resources across habitat types at Bossou, Guinea, West Africa, *American Journal of Primatology*, 78: 1237-1249.

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T. and Humle, T. (2017) Activity and Habitat Use of Chimpanzees (Pan troglodytes verus) in the Anthropogenic Landscape of Bossou, Guinea, West Africa, *International Journal of Primatology*: doi: 10.1007/s10764-016-9947-4.

Campbell-Smith, G., Campbell-Smith, M., Singleton, I. and Linkie, M. (2011) Raiders of the lost bark: Orangutan foraging strategies in a degraded landscape, *PloS one,* 6: e20962.

Carlson, B. A., Rothman, J. M. and Mitani, J. C. (2013) Diurnal Variation in Nutrients and Chimpanzee Foraging Behavior, *American Journal of Primatology,* 75: 342–349.

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

Chapman, C. A., Speirs, M. L., Gillespie, T. R., Holland, T. and Austad, K. M. (2006) Life on the edge: gastrointestinal parasites from the forest edge and interior primate groups, *American journal of primatology*, 68: 397–409.

Conklin-Brittain, N.L., Knott, C.D. and Wrangham, R. (2006) Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison., in G. Hohmann, M.M. Robbins, and C. B. (ed.) *Feeding Ecology in Apes and Other Primates*. Cambridge: Cambridge University Press, 445–472.

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

Conklin, N. Lou and Wrangham, R. W. (1994) The value of figs to a hind-gut fermenting frugivore: a nutritional analysis, *Biochemical systematics and ecology,* 22: 137–151.

Dostaler, S., Ouellet, J.-P., Therrien, J.-F. and Côté, S. D. (2011) Are feeding preferences of white-tailed deer related to plant constituents?, *The Journal of Wildlife Management,* 75: 913–918.

Felton, A., Felton, A., Lindenmayer, D. and Foley, W. (2009) Nutritional goals of wild primates, *Functional Ecology*, 23: 70-78.

Forthman-Quick, D. L. and Demment, M. W. (1988) Dynamics of exploitation: Differential energetic adaptations of two troops of baboons to recent human contact, *Ecology and Behavior of Food-Enhanced Primate Groups. New York: Liss*, 25–51.

Ganzhorn, J. U. (1995) Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations, *Ecology*, 76: 2084–2096.

Garber, P. A., Righini, N. and Kowalewski, M. M. (2015) Evidence of Alternative Dietary Syndromes and Nutritional Goals in the Genus Alouatta, in Kowalewski, M. M., Garber, P. A., Cortés-Ortiz, L., Urbani, B., and Youlatos, D. (eds) *Howler Monkeys: Behavior, Ecology, and Conservation*. New York, NY: Springer, 85–109.

Ghiglieri, M.P. (1984)*. The Chimpanzees of Kibale Forest: A Field Study of Ecology and Social Structure.* New York: Columbia University Press.

Hill, C. (2000) Conflict of interest between people and baboons: crop raiding in Uganda, *International Journal of Primatology*, 21: 299-315.

Hill, C. (2005) People, crops and primates: a conflict of interests, *Commensalism and conflict: The human-primate*. Norman, Oklahoma: American Society of Primatologists, 40-59.

Hill, C. M. (1997) Crop-raiding by wild vertebrates: The farmer's perspective in an agricultural community in western Uganda, *International Journal of Pest Management*, 43: 77–84.

Hoare, R. (2001) Management implications of new research on problem elephants, *Pachyderm*, 30: 44-48.

Hockings, K. J. (2007) *Human-Chimpanzee Coexistence at Bossou, the Republic of Guinea: a Chimpanzee Perspective.* University of Stirling.

Hockings, K. J. (2011) The Crop-Raiders of the Sacred Hill, in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The Chimpanzees of Bossou and Nimba*. London: Springer, 211–220.

Hockings, K. J., Anderson, J. R. and 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: 636–646.

Hockings, K. J. and Humle, T. (2009) *Best practice guidelines for the prevention and mitigation of conflict between humans and great apes.* Gland, Switzerland: IUCN/SSC Primate Specialist Group.

Hohmann, G., Potts, K., N'Guessan, A., Fowler, A., Mundry, R., Ganzhorn, J. U. and Ortmann, S. (2010) Plant foods consumed by Pan: Exploring the variation of nutritional ecology across Africa, *American Journal of Physical Anthropology*, 141: 476–485.

Houle, A., Conklin-Brittain, N. L. and Wrangham, R. W. (2014) Vertical stratification of the nutritional value of fruit: Macronutrients and condensed tannins, *American Journal of Primatology*, 76: 1207-1232.

Humle, T. (2011) Location and Ecology, in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The Chimpanzees of Bossou and Nimba*. London: Springer, 13–21.

Humle, T. and Hill, C. (2016) People-primate interactions: Implications for primate conservation', in Wich., S. A., and Marshall, A. J. (eds) *An Introduction to Primate Conservation*. Oxford: Oxford University Press, 219-240.

Humle T, Koops K, Cherif P. (2011). Appendix B: Plant food list of Bossou chimpanzees. In: Matsuzawa T, Humle T, Sugiyama Y, (eds). *The chimpanzees of Bossou and Nimba*. London: Springer: 406–411.

Humle, T. and Matsuzawa, T. (2004) Oil Palm Use by Adjacent Communities of Chimpanzees at Bossou and Nimba Mountains, West Africa, *International Journal of Primatology*, 25: 551–581.

Humle, T., Maisels, F., Oates, J.F., Plumptre, A. and Williamson, E. . (2016) *Pan troglodytes*, *The IUCN Red List of Threatened Species*. Available at: http://www.iucnredlist.org (Accessed: 21 February 2017).

Keuling, O., Stier, N. and Roth, M. (2009) Commuting, shifting or remaining?: Different spatial utilisation patterns of wild boar Sus scrofa L. in forest and field crops during summer, *Mammalian Biology - Zeitschrift für Säugetierkunde*, 74: 145–152.

Kok, S., Ong-Abdullah, M., Ee, G. C. and Namasivayam, P. (2011) Comparison of nutrient composition in kernel of tenera and clonal materials of oil palm (Elaeis guineensis Jacq.), *Food Chemistry*, 129: 1343–1347.

Lambert, J. E. and Rothman, J. M. (2015) Fallback Foods, Optimal Diets, and Nutritional Targets: Primate Responses to Varying Food Availability and Quality, *Annual Review of Anthropology,* 44: 493–512.

Laurance, W. F., Sayer, J. and Cassman, K. G. (2014) Agricultural expansion and its impacts on tropical nature, *Trends in Ecology & Evolution*, 29: 107–116.

Lodge, E., Ross, C., Ortmann, S. and MacLarnon, A. M. (2013) Influence of diet and stress on reproductive hormones in Nigerian olive baboons, *General and comparative endocrinology*, 191: 146–154.

Mackenzie, C.A. and Ahabyona, P. (2012). Elephants in the garden: Financial and social costs of crop raiding. *Ecological Economics*, *75*: 72-82.

Magliocca, F. and Gautier-Hion, A. (2002) Mineral content as a basis for food selection by western lowland gorillas in a forest clearing., *American journal of primatology*, 57: 67–77.

Martínez-Ballesta, M. C., Dominguez-Perles, R., Moreno, D. A., Muries, B., Alcaraz-López, C., Bastías, E., García-Viguera, C. and Carvajal, M. (2010) Minerals in plant food: effect of agricultural practices and role in human health. A review, *Agronomy for Sustainable Development,* 30: 295–309.

Matsumoto-Oda, A. and Hayashi, Y. (1999) Nutritional aspects of fruit choice by chimpanzees., *Folia primatologica; international journal of primatology*, 70: 154–62.

Mckinney, T. (2011) The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced Capuchins (Cebus capucinus), *American Journal of Primatology*, 73: 439–448.

McLennan, M. R. (2013) Diet and Feeding Ecology of Chimpanzees (Pan troglodytes) in Bulindi, Uganda: Foraging Strategies at the Forest–Farm Interface, *International Journal of Primatology,* 34 :585-614.

McLennan, M. and Ganzhorn, J. (2017) Nutritional Characteristics of Wild and Cultivated Foods for Chimpanzees (Pan troglodytes) in Agricultural Landscapes, *International Journal of Primatology*: doi:10.1007/s10764-016-9940-y

Milton, K. (1999) Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us, *Nutrition,* 15: 488–498.

Milton, K. (2008) Macronutrient Patterns of 19 Species of Panamanian Fruits from Barro

Colorado Island, *Neotropical Primates,* 15: 1–7.

National Research Council (2003) *Nutrient requirements of nonhuman primates*. (2nd ed.). Washington, DC: National Academies Press.

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

Nishida, T & Uehara, S. (1983) Natural Diet of Chimpanzees (Pan troglodytes schweinfurthii): Long-Term Record from the Mahale Mountains, Tanzania, *African study monographs*, 3: 109–130.

Oates, J. F. (1978) Water-Plant and Soil Consumption by Guereza Monkeys (Colobus guereza): A Relationship with Minerals and Toxins in the Diet?, *Biotropica*, 10: 241.

Osborn, F. V (2004) Seasonal variation of feeding patterns and food selection by crop-raiding elephants in Zimbabwe, *African Journal of Ecology*, 42: 322–327.

Priston, N. E. C. and McLennan, M. R. (2013) Managing Humans, Managing Macaques: Human–Macaque Conflict in Asia and Africa, in *The Macaque Connection*. New York, NY: Springer, 225–250.

Raubenheimer, D., Machovsky-Capuska, G.E., Chapman, C.A. and Rothman, J.M. (2015) Geometry of nutrition in field studies: an illustration using wild primates, *Oecologia*, 177: 223-234.

Redpath, S. M., Young, J., Evely, A., Adams, W. M., Sutherland, W. J., Whitehouse, A., Amar, A., Lambert, R. A., Linnell, J. D. C., Watt, A. and Gutiérrez, R. J. (2013) Understanding and managing conservation conflicts, *Trends in Ecology & Evolution*, 28: 100–109.

Reiner, W. B., Petzinger, C., Power, M. L., Hyeroba, D. and Rothman, J. M. (2014) Fatty acids in mountain gorilla diets: implications for primate nutrition and health, *American journal of primatology*, 76: 281–288.

Reynolds, V. (2005) T*he chimpanzees of the Budongo forest: Ecology, behaviour and conservation.* Oxford: Oxford University Press.

Reynolds, V., Lloyd, A. W., Babweteera, F. and English, C. J. (2009) Decaying Raphia farinifera Palm Trees Provide a Source of Sodium for Wild Chimpanzees in the Budongo Forest, Uganda, *PLoS ONE*, 4: e6194.

Reynolds, V., Lloyd, A. and English, C. (2012) Adaptation by Budongo Forest chimpanzees (Pan troglodytes schweinfurthii) to loss of a primary source of dietary sodium, *African Primates*, 7: 156–162.

Reynolds, V., Plumptre, A. J., Greenham, J. and Harborne, J. (1998) Condensed tannins and sugars in the diet of chimpanzees (Pan troglodytes schweinfurthii) in the Budongo Forest, Uganda, *Oecologia*, 115: 331–336.

Righini, N., Garber, P. A. and Rothman, J. M. (2015) The effects of plant nutritional chemistry on food selection of Mexican black howler monkeys (Alouatta pigra): The role of lipids, *American journal of primatology*: doi:10.1002/ajp.22524.

Riley, E. P., Tolbert, B. and Farida, W. R. (2013) Nutritional content explains the attractiveness of cacao to crop raiding Tonkean macaques, *Current Zoology*. Oxford University Press, 59: 160–169.

Rode, K. D., Chapman, C. A., McDowell, L. R. and Stickler, C. (2006) 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. and 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 : 441–449.

Rothman, J. M., Chapman, C. A., Hansen, J. L., Cherney, D. J. R. and 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: 729–742.

Rothman, J. M., Chapman, C. A. and Pell, A. N. (2008) Fiber-bound nitrogen in gorilla diets: implications for estimating dietary protein intake of primates, *American journal of primatology*, 70: 690–694.

Rothman, J. M., Chapman, C. A. and Van Soest, P. J. (2012) Methods in Primate Nutritional Ecology: A User's Guide, *International Journal of Primatology*, 33: 542–566.

Saj, T., Sicotte, P. and Paterson, J. D. (1999) Influence of Human Food Consumption on the Time Budget of Vervets, *International Journal of Primatology*, 20: 977–994.

Sams, C. E. (1999) Preharvest factors affecting postharvest texture, *Postharvest Biology and Technology*, 15: 249–254.

Simpson, S.J. and Raubenheimer, D. (2012) *The nature of nutrition: a unifying framework from animal adaptation to human obesity*. Princeton University Press.

Van Soest, P. J., Robertson, J. B. and Lewis, B. A. (1991) Methods for Dietary Fiber, Neutral Detergent Fiber, and Nonstarch Polysaccharides in Relation to Animal Nutrition, *Journal of Dairy Science*, 74: 3583–3597.

Sousa, J., Barata, A. V, Sousa, C., Casanova, C. C. N. and Vicente, L. (2011) Chimpanzee oil-palm use in southern Cantanhez National Park, Guinea-Bissau, *American Journal of Primatology*, 73: 485–497.

Strum, S. C. (2010) The development of primate raiding: implications for management and conservation, *International Journal of Primatology*, 31: 133–156.

Sugiyama, Y. and Fujita, S. (2011) The Demography and Reproductive Parameters of Bossou Chimpanzees, in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The Chimpanzees of Bossou and Nimba*. London: Springer, 23–34.

Sugiyama, Y. and Koman, J. (1992) The Flora of Bossou: its Utilization by Chimpanzees and Humans, *African Study Monographs*, 13: 127–169.

Takemoto, H. (2002) *Feeding Ecology of Chimpanzees in Bossou, Guinea: Coping with the Seasonal Fluctuation of Food Supply and Micrometeorology in the Tropical Forest*. (Unpublished PhD thesis). Kyoto: Kyoto University.

Takemoto, H. (2003) Phytochemical determination for leaf food choice by wild chimpanzees in Guinea, Bossou, *Journal of chemical ecology*, 29: 2551–2573.

Tutin, C. E. G. and Fernandez, M. (1993) Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the lopé reserve, gabon, *American Journal of Primatology*, 30: 195–211.

Wallis, I. R., Edwards, M. J., Windley, H., Krockenberger, A. K., Felton, A., Quenzer, M., Ganzhorn, J. U. and Foley, W. J. (2012) Food for folivores: nutritional explanations linking diets to population density, *Oecologia*, 169: 281–291.

Warren, Y., Higham, J. P., Maclarnon, A. M. and Ross, C. (2011) Crop-raiding and Commensalism in Olive Baboons: The Costs and Benefits of Living with Humans', in Sommer, V. and Ross, C. (eds) *Primates of Gashaka: Socioecology and Conservation in Nigeria's Biodiversity Hotspot*. New York, NY: Springer, 359–384.

Watts, D. P., Potts, K. B., Lwanga, J. S. and 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: 130–144.

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: 689–697.

Wilson, M.L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I.C., Hashimoto, C., Hobaiter, C.L., Hohmann, G., Itoh, N., Koops, K. and Lloyd, J.N. (2014) Lethal aggression in Pan is better explained by adaptive strategies than human impacts, *Nature*, 513: 414-417.

Woolf, A. B. and Ferguson, I. B. (2000) Postharvest responses to high fruit temperatures in the field, *Postharvest Biology and Technology*, 21: 7–20.

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

Wrangham, R. W., Conklin, N. L., Chapman, C. A., Hunt, K. D., Milton, K., Rogers, E., Whiten, A.

and Barton, R. A. (1991) The Significance of Fibrous Foods for Kibale Forest Chimpanzees, *Philosophical Transactions of the Royal Society of London.Series B: Biological Sciences*, 334: 171–178.

Yamakoshi, G. (1998) Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use, *American Journal of Physical Anthropology*, 106: 283–295.

Yamakoshi, G. and Sugiyama, Y. (1995) Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: A newly observed tool-using behavior, *Primates*, 36: 489–500.

Chapter 5 THE ROLE OF CROPS IN CHIMPANZEE DIETS: SEX DIFFERENCES, SEASONALITY, AND MACRONUTRIENT BALANCING FROM WILD AND CULTIVATED FOODS

5.1 ABSTRACT

Many primates frequently face seasonal fluctuations in spatial and temporal food availability, which can significantly affect their ability to meet nutritional requirements. Anthropogenic disturbances and influences, such as agriculture, human presence and infrastructures, can further impact seasonal food availability, dietary composition and nutrition. Chimpanzees, and many other primates, residing in anthropogenic landscapes frequently incorporate cultivars into their diets. However, the nutritional drivers behind cultivar consumption are poorly understood. We examined variations in chimpanzee (*Pan troglodytes verus*) macronutrient intake from wild and cultivated foods between sexes and seasons over a 1-year period in Bossou, Guinea, West Africa. We used the geometric framework of nutrition to examine proportional contributions of macronutrients to the diet and nutrient balancing. We conducted focal observations of adult individuals and nutritional analyses of plant foods. We found no sex differences in wild or cultivated food or macronutrient intakes; however, females showed higher total foods (i.e. wild and cultivated combined), digestible fibre (NDF), and protein intakes when controlling for metabolic body mass. There were no differences in wild or cultivated food intake between seasons; however lipid and protein intake from cultivars were higher in the low fruit availability season. Bossou chimpanzees maintained a constant proportional intake of protein while allowing carbohydrates and lipid intakes to vary. Furthermore, they were able to maintain a consistent balance of protein to non-protein (carbohydrates, lipids, and NDF) energy across the year. Our results suggest that chimpanzees in this human-dominated landscape suffered little seasonal constraints in food quality or availability and were able to combine their consumption of available wild and cultivated foods to achieve a balanced diet. These findings contribute significantly to our understanding of primate nutritional requirements and their ability to meet these requirements in disturbed environments.

Keywords: *West Africa; cultivars; nutritional geometry; nutritional ecology; anthropogenic landscape; human-primate coexistence*

5.2 INTRODUCTION

Most primate species are found in tropical forests characterised by fluctuations in the spatial and temporal availability of plant foods (Janson & Chapman, 1999; van Schaik et al, 1993; van Schaik & Pfannes, 2005). The density, distribution and overall fitness of primate populations are significantly influenced by the availability and nutritional quality of foods (Chapman & Chapman, 2002; Ganzhorn, 1992, 2002; Kay et al, 1997; Koenig et al, 1997; Van Schaik et al, 1993; Worman & Chapman, 2005) and primates in seasonal environments must adapt their foraging behaviours, habitat use and diets in order to meet their nutritional requirements (Lambert & Rothman, 2015).

Anthropogenic influences within human-dominated landscapes can further impact seasonal variation in primate food availability. Human-induced habitat degradation alters the availability and distribution of food resources and this, along with the presence of agricultural areas, roads, settlements and people, can significantly affect primate habitat use and feeding behaviours (e.g. Bryson-Morrison et al, 2016, 2017; Bortolamiol et al, 2016; Duvall, 2008; Gabriel, 2013; McKinney, 2011; Riley, 2008; Terada et al, 2015). Although changes in the diets of primates inhabiting anthropogenic environments are fairly well documented (e.g. Chapman & Chapman, 1999; Irwin, 2008; Lee, 1997; Menard et al, 2014; Riley, 2007; Tutin, 1999; Wong et al,. 2006), few studies have examined the nutritional composition of diets within such landscapes. When faced with habitat disturbance after a hurricane, black howler monkeys (*Alouatta pigra*) consumed greater proportions of mature leaves and selected plant foods high in minerals (Behie & Pavelka, 2012). Collared brown lemurs (*Eulemur collaris*) in a degraded fragment consumed mature leaves lower in carbohydrates and higher in fibre and fruits that were lower in carbohydrates but higher in lipids than those eaten by a nearby group inhabiting an intact area of forest (Donati et al, 2011). Lemur species showed high encounter rates in a lightly-logged deciduous forest that had high fruit production and protein concentrations in leaves (Ganzhorn, 1995).

Various models have been used to explain diet selection in primates, including energy/protein maximisation, toxin/fibre minimisation and nutrient balancing (reviewed in Felton et al, 2009a). Recent advances in primate nutritional ecology have highlighted the use of nutritional frameworks for a better understanding of how foraging decisions and food intakes relate to nutrient and energy requirements (Raubenheimer et al, 2015; Righini, 2017). A small number of studies have recently used the geometric framework for nutrition (Raubenheimer et al, 2009;

Simpson & Raubenheimer, 2012) to examine primate nutritional strategies and prioritisation when faced with reductions in food availability (Felton et al, 2009b; Rothman et al, 2011; Irwin et al, 2015). However, there is limited information of how changes in primate food availability and shifts in dietary composition in disturbed environments influence nutritional intakes (Irwin et al, 2015). Rode et al (2006a) found that intakes of key minerals, protein, and lipids were lower in redtail monkey (*Cercopithecus ascanius*) groups inhabiting heavily logged areas compared to groups in more intact areas of Kibale National Park, Uganda (KNP). One study to date has employed the geometric framework of nutrition to investigate nutrient balancing in primates across a gradient of human-disturbances (Irwin et al, 2015). This study demonstrated that sifaka (*Propithecus diadema*) groups had similar relative dietary contributions of macronutrients but groups inhabiting highly-impacted areas had lower food and nutrient intakes in the high food availability season compared to those in nearby intact forest (Irwin et al, 2015). An increased understanding of nutritional intakes in primates would allow for better land use management and conservation planning for populations residing in anthropogenic landscapes.

To our knowledge no study has yet quantified macronutrient intakes in cultivar-foraging primates inhabiting highly disturbed anthropogenic landscapes. A 30-day study of a female baboon (*Papio ursinus*) that consumed “human-derived” foods from garbage bins and gardens, as well as exotic plant species, demonstrated nutrient balancing and a constant relative intake of protein despite variation in the nutritional composition of foods in the diet (Johnson et al, 2013). Female olive baboons (*P. anubis*) in a troop that consumed cultivars had higher energy intake rates than those in a nearby troop that consumed only wild foods in Gashaka-Gumti National Park, Nigeria (Lodge et al, 2013). Cultivar-foraging (often termed “crop-raiding”) is widely documented in primate species that have access to agricultural areas in human-disturbed environments, e.g. baboons (*Papio* spp.) (Hill, 2000; Strum, 2010); macaques (*Macaca* spp.) (Prison & McLennan, 2013); vervets (*Chlorocebus* spp.) (Brennan et al, 1985); capuchins (*Cebus* spp.) (McKinney, 2011); orangutans (*Pongo* spp.) (Campbell-Smith et al, 2011); chimpanzees (*Pan troglodytes*) (Hockings et al, 2009; McLennan, 2013). Crops have been selected by humans to provide rich sources of easily digestible energy (Milton, 1999) and are generally higher in carbohydrates and lower in insoluble fibre than wild plant foods consumed by primates (Chapter 4; McLennan & Ganzhorn, 2017). The propensity of primates to forage on cultivars, despite the considerable risks involved (e.g. potential injury and mortality as a result of human mitigation or retaliation strategies), is often attributed to the increased energy and nutritional gains compared to wild plant foods (e.g. Lodge et al, 2013; Hockings et al, 2009; Naughton-Treves et al, 1998; Strum, 1991). Studies examining cultivar-foraging in relation to food availability have found that cultivar consumption often increases during periods when preferred wild foods are scarce, although some crops may be selected regardless of wild food availability (Hockings et al, 2009; McLennan, 2013; Naughton-Treves et al, 1998). Determining how primates balance their nutritional intakes through their consumption of wild and cultivated foods can provide invaluable insights into the role of crops in meeting nutritional needs (Chiyo et al, 2005; Lambert & Rothman, 2015; Osborn, 2004; Rode et al, 2006b).

Chimpanzees are an ideal model for examining nutrient intakes from wild and cultivated foods in primate diets. Chimpanzees are found in many habitat types, including forest-agricultural mosaics, across their range in West, Central and East Africa (Hockings & McLennan 2012, 2016). Regardless of habitat type, they maintain a high proportion of ripe fruit in their diets even during fruit scarce seasons (Ghiglieri 1984; Hockings et al, 2009; Takemoto, 2003; Watts et al. 2012; Wrangham et al. 1998; Yamakoshi, 1998). Generally, chimpanzee diet composition reflects preferences for foods higher in macronutrients and lower in insoluble fibre and plant secondary metabolites (PSMs) (Conklin-Brittain et al, 1998; Hohmann et al, 2010; Matsumoto-Oda & Hayashi, 1999; Remis, 2002; Reynolds et al, 1998; Wrangham et al, 1998). Chimpanzees readily integrate cultivars into their diets and are known to exploit a wide range of crop species and plant parts, although ripe fruits are preferentially selected (Hockings & McLennan, 2012). Sex differences in chimpanzee cultivar-foraging have been documented, with males spending more time feeding on crops than females (Hockings et al, 2009). These differences have been attributed to males being more likely to partake in risker behaviours than females (Hockings, 2011). Variation in primate foraging choices between sexes can also be a result of differences in nutritional requirements (Ganzhorn, 2002; Koch et al, 2016; Koenig et al, 1997; Rothman et al, 2008b; Vogel et al, 2016). The larger body size of males in many primate species means that they have higher maintenance costs and therefore greater energy needs on an absolute basis, while pregnancy and lactation increases energy requirements in females (Key & Ross, 1999). Furthermore, nutritional and energetic needs vary as a function of body mass and smaller individuals have higher relative metabolic rates (Rothman et al, 2008b). Chimpanzees, particularly the West African sub-species, have relatively low body mass sexual dimorphism (males are approximately 10% heavier than females: Smith & Jungers, 1997) and research has shown little variation in absolute macronutrient and energy intakes between males and females (N'guessan et al, 2009; Pokempner, 2009). However, when accounting for metabolic body mass, one study conducted in Tai National Park, Côte d'Ivoire found that female chimpanzees maintained energy and protein intake across seasons while male intake varied (N'guessan et al, 2009). Another study demonstrated that females had higher intakes of non-structural carbohydrates than males relative to body mass in chimpanzees in KNP (Pokempner, 2009).

To investigate the role of cultivars in chimpanzee diets, we examined nutrient intakes and foraging behaviour between sexes and seasons of a group of chimpanzees (*P. t. verus*) inhabiting the forest-agricultural mosaic at Bossou in Guinea, West Africa. Crops are fully integrated into the Bossou chimpanzee diets and they regularly consume 17 cultivar species (Hockings et al, 2009). Specifically, we examined variation in food and macronutrient intakes from wild and cultivated foods between males and females during the high fruit availability (HFA) and low fruit availability (LFA) seasons derived from phenology data for the study period (Bryson-Morrison et al, 2016). We used right-angled mixture triangles to quantify relative contributions of macronutrients to the diet and bivariate plots to examine nutrient balancing (Raubenheimer et al, 2015). We made the following predictions relating to sex and seasonal differences in macronutrient intake from wild and cultivated foods:

1. Total energy and macronutrient intake from all foods (i.e. wild and cultivated foods combined) will vary between sexes. Following previous findings for chimpanzees, we predicted that males and females would have similar nutrient and energy intakes on an absolute basis but females would show higher energy and macronutrient intakes once metabolic body mass (MBM) is controlled for (N'guessan et al, 2009; Pokempner, 2009).
2. Males will have higher dietary and macronutrient intakes from cultivars than females. Male chimpanzees at Bossou cultivar-forage more than females (Hockings, 2011) and will therefore consume a greater proportion of cultivars across the year. Conversely, we predicted that females will feed more on wild foods and thus have a higher intake of macronutrients from wild foods.
3. Total food and macronutrient intake (i.e. from wild and cultivated foods combined) will be lower in LFA season, given that chimpanzee food and energy intake has been found to decrease when fruits are scarce (Pokempner, 2009).
4. Dietary and macronutrient intake from cultivars will be higher in the LFA season as the chimpanzees generally consume more crops when fruit availability is lower (Hockings et al, 2009).

We did not make any specific predictions related to nutrient balancing in chimpanzees given the relatively recent use of nutritional geometry in primate research (Felton et al, 2009b; Irwin et al, 2015; Johnson et al, 2013; Johnson et al, 2015; Rothman et al, 2011) and the consequent lack of comparative studies with other chimpanzee communities.

5.3 METHODS

5.3.1 Study site and chimpanzee population

Four small hills (70-150 m high) surround the village of Bossou in the Republic of Guinea, West Africa (latitude 7°38'71.7'N and longitude 8°29'38.9'W) and constitute the 6 km^2 core area of the semi-isolated resident chimpanzee community (home range approximately 15 km^2) (Humle, 2011). During our study, the community size ranged between 12-13 individuals with 6 adult females and 4 adult males. Local people practise slash and burn agriculture within and around the chimpanzees home range which has resulted in a highly heterogeneous landscape composed of regenerating, riverine, and mature forest as well as fallow land, coffee plantations and cultivated fields (Bryson-Morrison et al, 2016; Humle, 2011). The climate in this region is classified as tropical wet seasonal with a long rainy season from March to October and a short dry season from November to February (Humle, 2011).

5.3.2 Food availability

Fruit availability is generally higher during the dry season (Hockings et al, 2009; Takemoto, 2002; Yamakoshi 1998) and phenology data from our 1 year study period (April 2012-March 2013) revealed specifically that December through to May showed the highest fruit availabilities (HFA season) and June to November the lowest (LFA season) (Bryson-Morrison et al, 2016). The Bossou chimpanzees consume over 200 different plant species (Humle et al, 2011), and like other chimpanzee populations ripe fruit constitutes the majority of the diet

(Hockings et al, 2009; Takemoto, 2002; Yamakoshi, 1998). When fruit is scarce, the chimpanzees rely heavily on food parts from the semi-domesticated or wild oil palm tree (*Elaeis guineensis*) (i.e. fruit, nut kernel, pith, petiole, flower, and heart), fruit from *Musanga cercropiodes* (Takemoto, 2002; Yamakoshi, 1998), and cultivars, including cassava (*Manihot esculenta*) tuber, banana (*Musa sinensis*) pith and fruit, and succulent fruit varieties such as papayas (*Carica papaya*), oranges (*Citrus sinensis*), mandarins (*C. reticulata*) and mangos (*Mangifera indica*) (Hockings et al, 2009). Most cultivars, and particularly succulent fruits, are preferentially consumed when fruit availability is low although some crops including rice (*Oryza sp*.) pith, mangos, and maize (*Zea mays*) are highly seasonal and the chimpanzees forage on these according to their availability (Hockings et al, 2009). Past studies have used proportion of time spent feeding to describe the feeding behaviour of the Bossou chimpanzees; here we present diet composition based on food ingested (g dry matter (DM)) which is more accurate for determining nutrient intake (Aristizabal et al, 2016).

5.3.3 Observational data and feeding behaviour

We used continuous focal follows (Altmann, 1974) for a maximum of 6 hours per day from 0630-1230 hours (N = 331 hours) or 1230-1830 hours (N = 237 hours) (total observations: 568 hours) to comply with site regulations that limit the time spent observing the chimpanzees. Each day, we randomly selected a focal individual from a predetermined list to record all feeding bouts (N = 927). We defined a feeding bout (i.e. actively consuming and swallowing food items) as feeding on a single food type and plant part from the same individual tree or food patch. For each feeding bout, we recorded start and stop time, intake rate (number of individual food items), species consumed, plant part (RF: ripe fruit; UF: unripe fruit; YL: young leaves; ML: mature leaves; PET: petiole; PI: pith; SD: seed; FL: flower; NT: nut; HRT: heart; TB: tuber; GM: gum), other food types (including: algae; mushrooms; ants; larvae; soil; meat; honey; palm wine), habitat type, and whether the food was wild or cultivated. Cultivars, or crops, are plants that have been selectively bred and domesticated by people (Spencer & Cross, 2007). We defined food parts from oil palms as cultivars as many trees are semi-domesticated and we were unable to distinguish these from any wild oil palms still present at Bossou. We did not follow the chimpanzees into cultivated fields when they foraged on cultivars to minimise the risk of our presence being viewed negatively by farmers. However, whenever possible, we observed the chimpanzees feeding from a distance using binoculars in order to record the start and stop time of the feeding bout, the intake rate, and to identify the plant part consumed. Although our observational data on chimpanzee cultivar feeding is likely to be underestimated, given that we are comparing sexes and seasons we do not expect it to affect significantly our analyses.

5.3.4 Plant food collection, processing and nutritional analyses

Due to the high diversity of chimpanzee diets, we were unable to collect samples of all wild plant foods the group fed on. We focused on important wild plant food items (i.e. those that constituted ≥ 1% of food intake: N = 25 species), including ripe fruit and pith, and all cultivated food parts (i.e. ripe fruit, pith, nut kernel, petiole, palm heart and tuber: N = 11 species) (Table

5.1). We used previously reported macronutrient concentrations for leaves (Takemoto, 2003). We collected food samples across both seasons from the same trees or food patches where they were consumed by the chimpanzees. When this was not possible, we collected samples of similar phenophase from nearby conspecifics (sensu Irwin et al, 2014). We processed all samples in the same way as the chimpanzees by only selecting parts observed to be eaten and swallowed. Samples were then weighed (wet weight), dried in a dehydrator and weighed again (dry weight) (Rothman et al, 2012). We stored all samples in labelled and sealed plastic bags with desiccant before transporting to the Nutritional Laboratory, Sparsholt, College, UK for nutritional analyses to determine neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL), crude protein (CP), lipids, and ash (as g dry matter (DM)) via standard methods (Rothman et al, 2012). Total non-structural carbohydrates (TNC) were determined by difference, subtracting the contributions of crude protein, lipids, NDF, and ash from the total plant mass (Rothman et al, 2012) and we determined metabolisable energy (ME) by summing each component after multiplying it by its physiological fuel value (Conklin-Brittain et al, 2006; National Research Council, 2003). As we did not have the facilities to conduct available protein analyses, we estimated available protein (AP) from CP values using conversion coefficients derived from the portion of unavailable CP in similar chimpanzee fruit and leaf food items (Conklin-Brittain et al, 1999) and gorilla piths from Uganda (Rothman et al, 2008a) (sensu Vogel et al, 2016). Further details of sample collection, processing, and analyses can be found in Chapter 4. Here we used NDF, AP, lipid, TNC and ME in all analyses.

5.3.5 Food and nutrient intake calculations

We calculated food intake (g DM) for each focal observation by multiplying each feeding bout length by the corresponding intake rate for the plant part/species combination (g DM per minute). We used predefined units for each plant part (e.g. a single leaf or fruit or the average number for small leaves or fruit; the approximate length of pith or tuber) to count what was being consumed during each feeding bout (Chivers, 1998). For food items that we were unable to collect intake rates, we used the average intake rate calculated from similar plant parts (Rothman et al, 2011). We used food consumed in grams to calculate percentages of plant food items (i.e. leaves, fruit, pith, other) in the chimpanzees diet. Following Rothman et al (2008b), we calculated each focal individual's mean daily nutrient intake using the following equation:

$$N_{g,j,k} = \frac{\sum_{i=1}^{I} F_{i,g} U_i Q_{i,j}}{M_g}(TA_k)$$

Where $N_{g,j,k}$ = intake of macronutrient *j* (grams of DM for nutrients; Kcal for energy) by focal individual *g* of sex class *k*, $F_{i,g}$ = number of intake units of plant part *i* fed on by individual *g*, U_i = average intake unit mass of the consumed plant part (g/DM), $Q_{i,j}$ = nutrient concentration (percent DM) or energy (Kcal/g) from macronutrient *j* in consumed plant part *i*, M_g = the number of minutes individual *g* was engaged in feeding bouts, *T* = a constant daylight value of 720 minutes, A_k = average monthly proportion of time spent feeding by males and females. In order to obtain the average nutrient intake for each focal individual, we averaged these estimated daily nutrient intakes over a 2-month period (Rothman et al, 2008b). For food items where we did not have nutritional information, we used macronutrient and energy values averaged across all sampled species for the same plant part (Irwin et al, 2014). In total, we had nutritional data for foods representing 90.7% of food intake. In order to examine if nutrient intake differed between sexes, we divided these absolute estimates of average nutrient intake by the estimated metabolic body mass (MBM = $M^{0.762}$) which includes a scaling factor calculated using field metabolic rates of eutherians (Nagy, 1994). We used West African chimpanzees' body mass values of 46.3 Kg for adult males and 41.6 Kg for adult females (Smith & Jungers, 1997).

5.3.6 Statistical analyses

We did not examine the influence of age on intakes as we found no significant difference between the ages of adult males (N=4; Mean age: 29.0±19.2) or adult females (N=6; Mean age: 45.7±15.9) ($t(8) = -1.521$, $P = 0.167$) and the one juvenile individual present within the community disappeared during our study period, therefore we present data for adult individuals only. For statistical analyses of dietary intake, we selected only the focal observations of ≥ 4 hrs (45 focal observations; Females: 26 observations, Males: 19 observations; HFA season: 21 observations, LFA season: 24 observations). We pooled all morning and afternoon observations as we found no difference in the time spent feeding during the morning (0630-1230 hrs) and afternoon hours (1230-1830 hrs) ($t(22) = 0.712$, $P = 0.484$). We used General Linear Models (GLM) to compare total macronutrient and energy intake and macronutrient and energy intake from wild and cultivated foods between sexes. We also used GLM to investigate the influence of season (i.e. HFA & LFA periods) on total macronutrient and energy intake and macronutrient and energy intake from wild and cultivated foods. We set sex and seasons as fixed factors and macronutrient (i.e. AP, TNC, lipids, NDF measured in grams DM) and energy intake (ME, measured in Kcal) as dependent variables. We used focal ID (N = 10) as random factors to control for individuals. Kolmogorov-Smirnov Tests revealed that not all of our data were normally distributed. To achieve normality, we square-root transformed NDF intake from wild foods, AP, TNC, and ME intake from crops, and food, TNC, NDF, and ME intake from all foods combined, and log transformed lipid and NDF intake from crops, and lipid and AP intake from all foods.

We plotted 3-way right-angled mixture triangles (RMT) to observe the contribution of AP, carbohydrates (TNC + digestible fibre (NDF)) and lipids to energy intake (Raubenheimer, 2011). We used linear regression and coefficient of determination (R^2) values to examine nutrient balancing. We used bivariate plots to examine intake of AP vs. non-protein energy (NPE: TNC + NDF + lipids) (Rothman et al, 2011).

5.4 RESULTS

5.4.1 Plant Diet Composition and Feeding Patterns

Overall, the chimpanzees consumed 95 identified plant species including 83 wild and 12 cultivated species, comprising 134 different plant parts (Wild: N = 112; Cultivated: N = 22). Eighteen of these species accounted for 85% of the annual diet (based on food intake) including 13 wild and 5 cultivated species. Furthermore, the top 7 consumed plant species, i.e. *Musanga cecropioides* (wild; fruit and leaves), mango (*Mangifera indica*) (cultivar; fruit), fig (*Ficus* *annomani*) (wild; fruit), orange (*Citrus sinensis*) (cultivar; fruit), banana (*Musa sinensis*) (cultivar; fruit and pith), and oil palm (*Elaeis guineensis*) (cultivar; fruit, nut, petiole and pith) accounted for 59% of the annual diet. This pattern was consistent across both the HFA (December-May) and LFA (June-November) seasons with 17 species (11 wild and 6 cultivated species) and 14 species (9 wild and 5 cultivated species) comprising around 85% of the diet, respectively (Table 5.1).

Based on food intake, the chimpanzees' annual and seasonal diet was composed of a high proportion of ripe fruit, particularly during the HFA season (Annual: 72.2%; HFA season: 78.1%; LFA season: 67.3%). Unripe fruit consumption was negligible (Annual: 2.2%; HFA season: 1.9%; LFA season: 2.4%). Leaves were the next most consumed plant part, particularly during the LFA season (Annual: 14%; HFA season: 10.5%; LFA season: 16.9%). Pith was consumed evenly throughout the year (Annual: 5.4%; HFA season: 5.7%; LFA season: 5.2%), and "other" plant parts (i.e. petiole, nut kernel, gum, algae, and tuber) were consumed in higher proportions during the LFA season (Annual: 6.2%; HFA season: 3.8%; LFA season: 8.2%). The chimpanzees consumed cultivated foods relatively evenly throughout the year (Annual: 29.2%; HFA season: 29.7%; LFA season: 28.7%); however, the contribution of oil palm food parts varied across seasons (Annual: 5%; HFA season: 1.7%; LFA season: 7.7%).

Important analysed chimpanzee plant foods (i.e. ≥1% of intake) showed considerable variation in AP (1.5 - 20.5%), TNC (13.0 - 88.4%), NDF (4.6 - 61.2%), lipids (0.1 - 42.8%), and the ratio of

AP to NPE (0.01 - 0.46) (Table 5.1). Further details of the macronutrient composition of all analysed chimpanzee foods can be found in Chapter 4.

5.4.2 Food intake

We found no sex differences in absolute intake of wild, cultivated, or all foods (i.e. wild and cultivated) combined (Table 5.2 and Fig. 5.1). We also found no sex differences in wild or cultivated food intake when MBM was controlled for. However, females showed a significantly higher MBM intake of all foods than males (Table 5.2 and Fig. 5.2). We found no seasonal differences in intake of all, wild, or cultivated foods and no sex*season interactions (Table 5.2 and Fig. 5.3).

5.4.3 Macronutrient and energy intakes

We found no sex differences in absolute macronutrient intakes from wild, cultivated or all foods combined (Table 5.2 and Fig. 5.1). However, when we controlled for MBM, we found that females showed a higher intake of AP from all foods combined, and a higher intake of NDF from wild foods and all foods combined than males (Table 5.2 and Fig. 5.2) We found no other sex differences in MBM macronutrient intakes from wild, cultivated, or all foods combined (Table 5.2 and Fig. 5.2). We found no differences in macronutrient intakes from all foods combined between the HFA and LFA seasons (Table 5.2 and Fig. 5.3). However, we found that lipid and AP intake from cultivated foods were significantly higher in the LFA season than the HFA (Table 5.2 and Fig. 5.3). We found no other seasonal differences in macronutrient intakes from wild and cultivated foods and no sex*season interactions (Table 5.2 and Fig. 5.3).

Table 5.1 Seasonal percentage intake and macronutrient concentrations of the most important plant foods (≥ 1% intake) consumed by the chimpanzee community at Bossou, Guinea

	Species	Part	HFA % intake	LFA % intake	AP	TNC	NDF	Lipid	AP:NPE
Wild	*Ficus* spp.[1]	RF	15.5	11.8	6.6	17.7	59.4	4.3	0.13
Wild	*Musanga cecropioides*	RF	11.8	34.2	5.6	23.5	60.5	3.6	0.10
Wild	*Parkia bicolor*	RF	11.3	-	12.1	49.0	14.5	14.0	0.14
Wild	*Landolphia sp.*	RF	7.4	-	2.9	57.9	32.9	1.6	0.04
Wild	Species combined[2]	YL	7.4	10.6	20.5	23.3	37.0	2.7	0.46
Wild	*Aframomum latifolium*	PI	3.6	3.5	4.9	18.6	61.2	0.7	0.11
Wild	*Pseudospondias microcarpa*	RF	2.6	-	6.3	37.5	38.8	4.6	0.10
Wild	*Antiaris africana*	RF	2.2	-	7.8	47.0	32.7	3.0	0.12
Wild	*Aningeria altissima*	RF	1.1	-	5.6	41.8	33.3	12.4	0.07
Wild	*Spondias mombin*	RF	-	1.2	6.4	29.4	51.4	4.2	0.11
Cultivar	*Mangifera indica*	RF	14.3	1.3	1.5	87.1	7.8	0.6	0.02
Cultivar	*Musa sinensis*	RF	5.5	4.7	3.7	85.6	4.6	0.2	0.04
Cultivar	*Manihot esculenta*	TB	3.4	4.2	1.3	88.4	8.4	0.4	0.01
Cultivar	*Citrus sinensis*	RF	2.5	7.7	3.7	79.7	8.6	2.3	0.04
Cultivar	*Oryza sp.*	PI	1.3	-	2.6	27.6	54.9	1.2	0.05
Cultivar	*Ananas comosus*	RF	1.0	-	1.6	85.5	9.1	0.1	0.02
Cultivar	*Elaeis guineensis*	PT	-	2.7	16.5	32.9	30.6	3.7	0.31
Cultivar	*Elaeis guineensis*	NT	-	1.0	7.9	23.2	57.5	42.8	0.06
Cultivar	*Elaeis guineensis*	RF	1.4	3.7	2.8	13.0	50.3	30.3	0.03

RF = ripe fruit; YL = young leaves; PI = pith; TB: = tuber; PT = petiole; NT = nut kernel. HFA = high fruit availability season (December-May), LFA = low fruit availability season (June-November) derived from phenology data of the study period (April 2012-March 2013) (Bryson-Morrison et al, 2016). AP = available protein; TNC = total non-structural carbohydrates; NDF = neutral detergent fibre. AP: NPE = available protein to non-protein energy ratio of foods. Macronutrients expressed as % dry matter. [1] Average macronutrient values for *Ficus* spp. ripe fruit (HFA season ≥1% food intake: *Ficus annomani* (4.9%); *F. umbellata* (4.4%); *F. thonningii* (1.6%); *F. mucuso* (1.2%); *F. variifolia* (1.2%) unknown *Ficus* sp. (1.2); *F. sur* (1.0%); LFA season ≥1% food intake: *F. annomani* (8.5%); *F. mucuso*

(1.2%); *F. umbellata* (1.1%); *F. barteri* (1.0%)). [2]Average macronutrient values for young leaves taken from Takemoto, (2003); (HFA season ≥1% food intake: *Antiaris africana* (2.1%); *Polypodium aureum* (2.1%); *Leptoderris fasciculata* (2.0%); *F. exasperata* (1.2%); LFA season ≥1% food intake: *F. exasperata* (4.4%); *Cryptosepaium tetraphyllum* (2.2%); *Bosquea angolensis* (2.1%); *F. umbellata* (1.1%); *Justicia sp.* (1.0%))

Table 5.2 General Linear Model (GLM) results for sex and seasonal variations in food (g/dry matter), macronutrient (g/dry matter) and energy (Kcal) intakes with and without controlling for metabolic body mass (MBM) for chimpanzee adult individuals (Females: N=6; Males: N=4) at Bossou, Guinea. Significant results are highlighted in bold. AP = available protein; TNC = total non-structural carbohydrates; NDF = neutral detergent fibre

	All Foods				**All Foods (MBM)**				**Cultivar**				**Cultivar (MBM)**				**Wild**				**Wild (MBM)**			
	df	***R^2***	***F***	***P***	**df**	***R^2***	***F***	***P***	**df**	***R^2***	***F***	***P***	**df**	***R^2***	***F***	***P***	**df**	***R^2***	***F***	***P***	**df**	***R^2***	***F***	***P***
Food Intake																								
Sex	1	0.928	1.346	0.253	1	0.928	4.150	**0.048**	1	0.574	0.689	0.411	1	0.572	1.207	0.278	1	0.794	1.814	0.185	1	0.797	3.345	0.075
Season	1	0.928	0.013	0.909	1	0.928	0.015	0.903	1	0.574	0.010	0.920	1	0.572	0.007	0.932	1	0.794	0.118	0.733	1	0.797	0.123	0.727
Sex*Season	1	0.928	0.142	0.709	1	0.928	0.139	0.711	1	0.574	0.115	0.737	1	0.572	0.107	0.745	1	0.794	0.053	0.819	1	0.797	0.059	0.809
AP Intake																								
Sex	1	0.9	2.7	0.1	1	0.9	14.	**0.0**	1	0.7	1.7	0.1	1	0.7	2.9	0.0	1	0.7	1.2	0.2	1	0.7	2.4	0.1

		89	55	05		88	109	**01**		36	52	93		38	04	96		91	02	79		92	45	26
Season	1	0.989	2.594	0.115	1	0.988	2.334	0.134	1	0.736	5.973	**0.019**	1	0.738	5.889	**0.020**	1	0.791	1.300	0.261	1	0.792	1.298	0.261
Sex*Season	1	0.989	0.073	0.788	1	0.988	0.000	0.987	1	0.736	0.154	0.697	1	0.738	0.233	0.632	1	0.791	0.088	0.769	1	0.792	0.117	0.734
Lipid Intake																								
Sex	1	0.962	0.055	0.816	1	0.957	2.520	0.120	1	0.793	2.034	0.162	1	0.697	0.218	0.643	1	0.888	0.742	0.394	1	0.890	2.544	0.118
Season	1	0.962	0.166	0.686	1	0.957	0.220	0.642	1	0.793	5.654	**0.023**	1	0.697	6.846	**0.012**	1	0.888	3.737	0.060	1	0.890	3.531	0.067
Sex*Season	1	0.962	0.008	0.929	1	0.957	0.000	0.985	1	0.793	1.856	0.181	1	0.697	0.531	0.470	1	0.888	0.054	0.817	1	0.890	0.025	0.875
TNC Intake																								
Sex	1	0.859	0.614	0.438	1	0.857	1.923	0.173	1	0.698	0.448	0.507	1	0.698	1.089	0.303	1	0.759	1.703	0.199	1	0.760	2.983	0.092
Season	1	0.859	0.908	0.346	1	0.857	0.834	0.366	1	0.698	0.324	0.573	1	0.698	0.293	0.591	1	0.759	0.536	0.468	1	0.760	0.521	0.474
Sex*Season	1	0.859	0.254	0.617	1	0.857	0.201	0.656	1	0.698	0.259	0.614	1	0.698	0.233	0.632	1	0.759	0.000	0.998	1	0.760	0.001	0.978

NDF Intake																								
Sex	1	0.915	1.413	0.241	1	0.917	4.089	**0.05**	1	0.968	0.069	0.794	1	0.868	1.521	0.225	1	0.896	2.096	0.155	1	0.899	4.805	**0.034**
Season	1	0.915	1.833	0.183	1	0.917	1.864	0.180	1	0.968	1.412	0.243	1	0.868	1.843	0.182	1	0.896	0.396	0.533	1	0.899	0.426	0.517
Sex*Season	1	0.915	0.015	0.905	1	0.917	0.029	0.866	1	0.968	0.699	0.409	1	0.868	0.131	0.719	1	0.896	0.232	0.633	1	0.899	0.265	0.610
Energy Intake																								
Sex	1	0.916	0.928	0.341	1	0.915	3.143	0.084	1	0.747	0.449	0.507	1	0.748	1.200	0.280	1	0.791	1.750	0.193	1	0.794	3.230	0.080
Season	1	0.916	0.041	0.840	1	0.915	0.037	0.849	1	0.747	0.025	0.876	1	0.748	0.030	0.864	1	0.791	0.025	0.876	1	0.794	0.023	0.880
Sex*Season	1	0.916	0.112	0.740	1	0.915	0.104	0.749	1	0.747	0.152	0.698	1	0.748	0.155	0.696	1	0.791	0.011	0.916	1	0.794	0.010	0.922

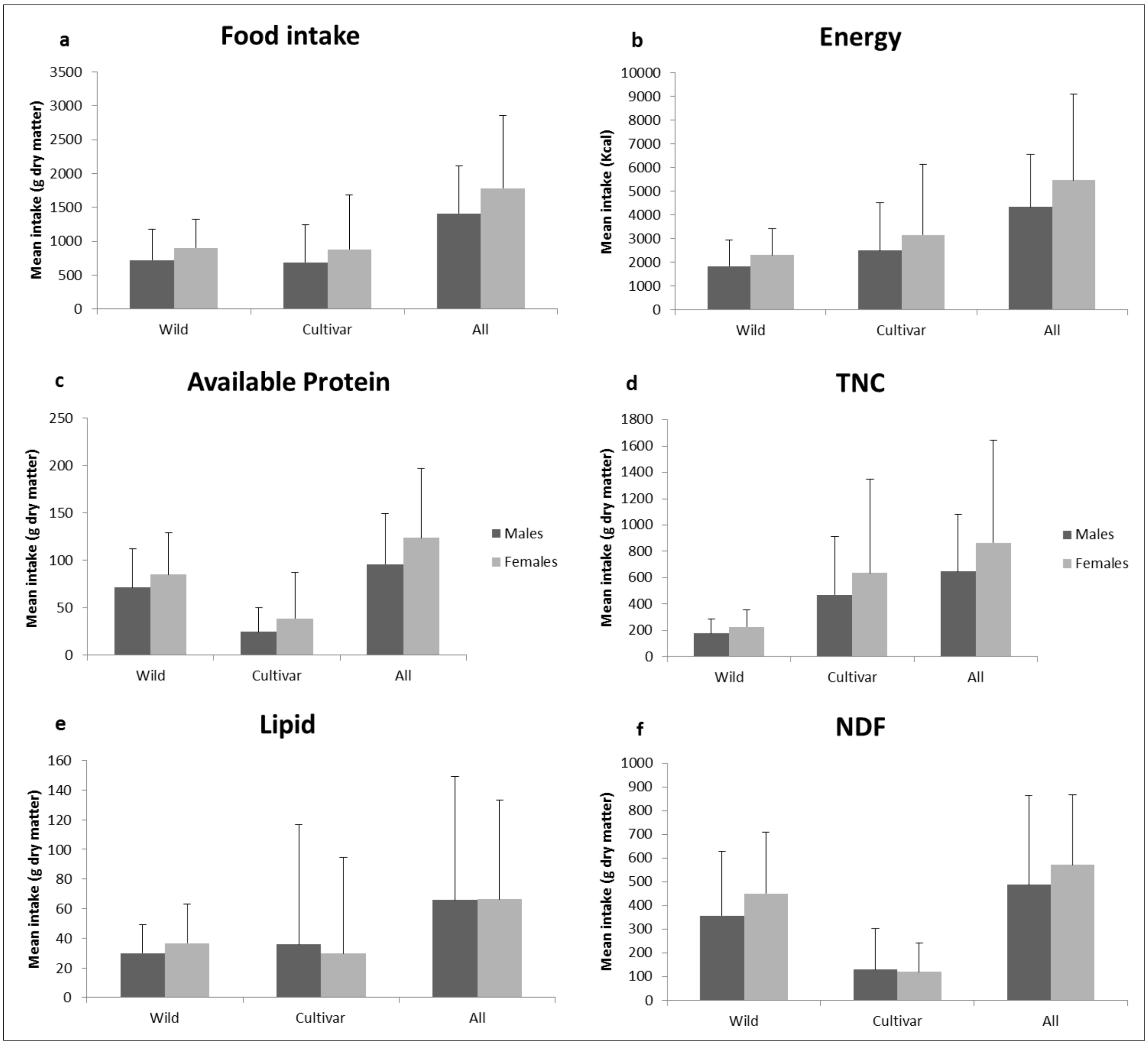

Figure 5.1 Mean (+SD) daily intake by male (N = 4) and female (N = 6) chimpanzees in Bossou, Guinea of: a, food; b, metabolisable energy; c, available protein; d, total non-structural carbohydrates (TNC); e, lipids; f, neutral detergent fibre (NDF). Wild = wild plant foods; Cultivar = cultivated plant foods; All = wild and cultivated foods combined. See Table 5.2 for statistics

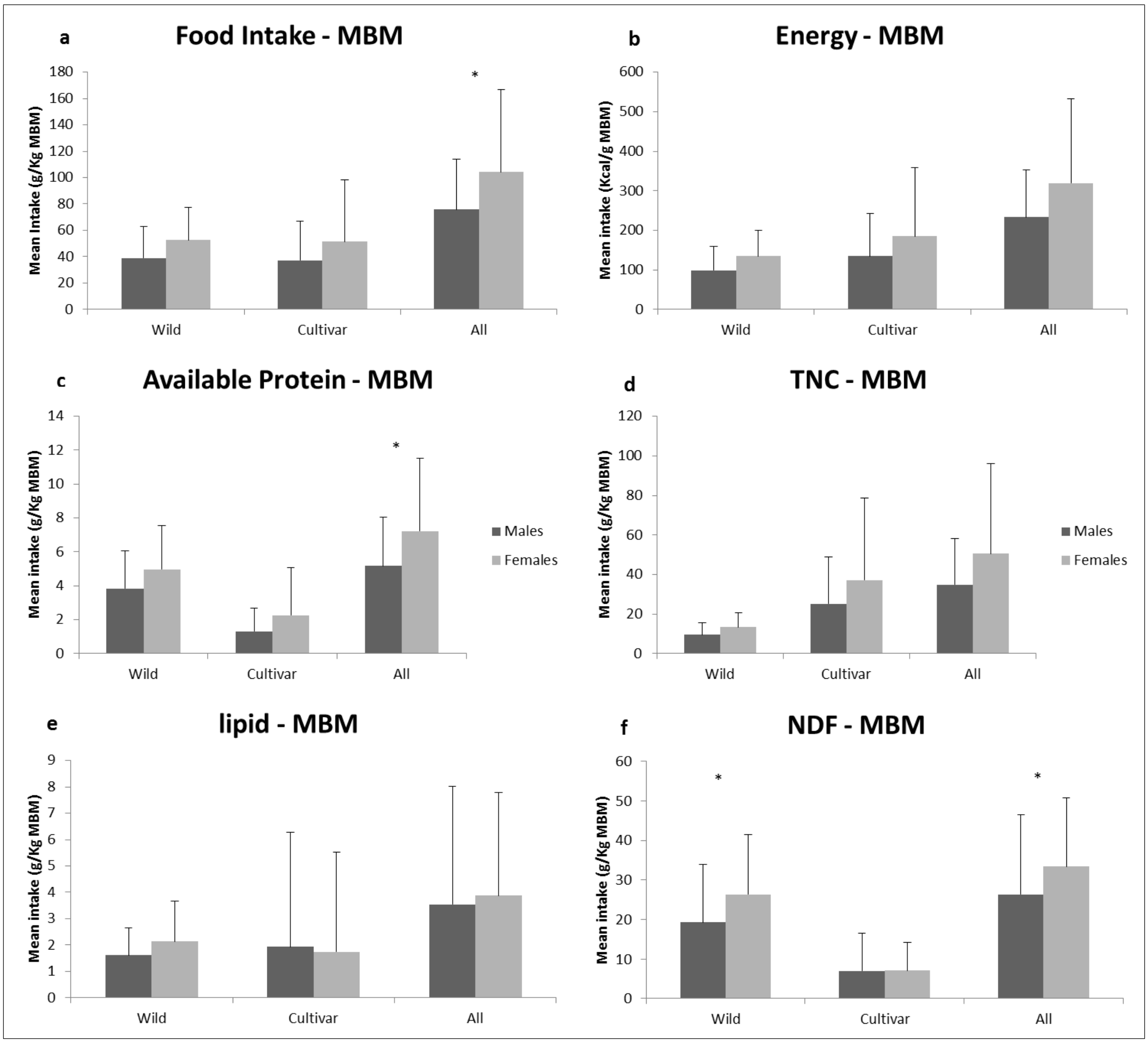

Figure 5.2 Mean (+SD) daily intake by male (N = 4) and female (N = 6) chimpanzees in Bossou, Guinea after accounting for metabolic body mass (MBM) of: a, food; b, metabolisable energy; c, available protein; d, total non-structural carbohydrates (TNC); e, lipids; f, neutral detergent fibre (NDF). Wild = wild plant food; Cultivar = cultivated plant food; All = wild and cultivated foods combined. * denotes significant results. See Table 5.2 for statistics

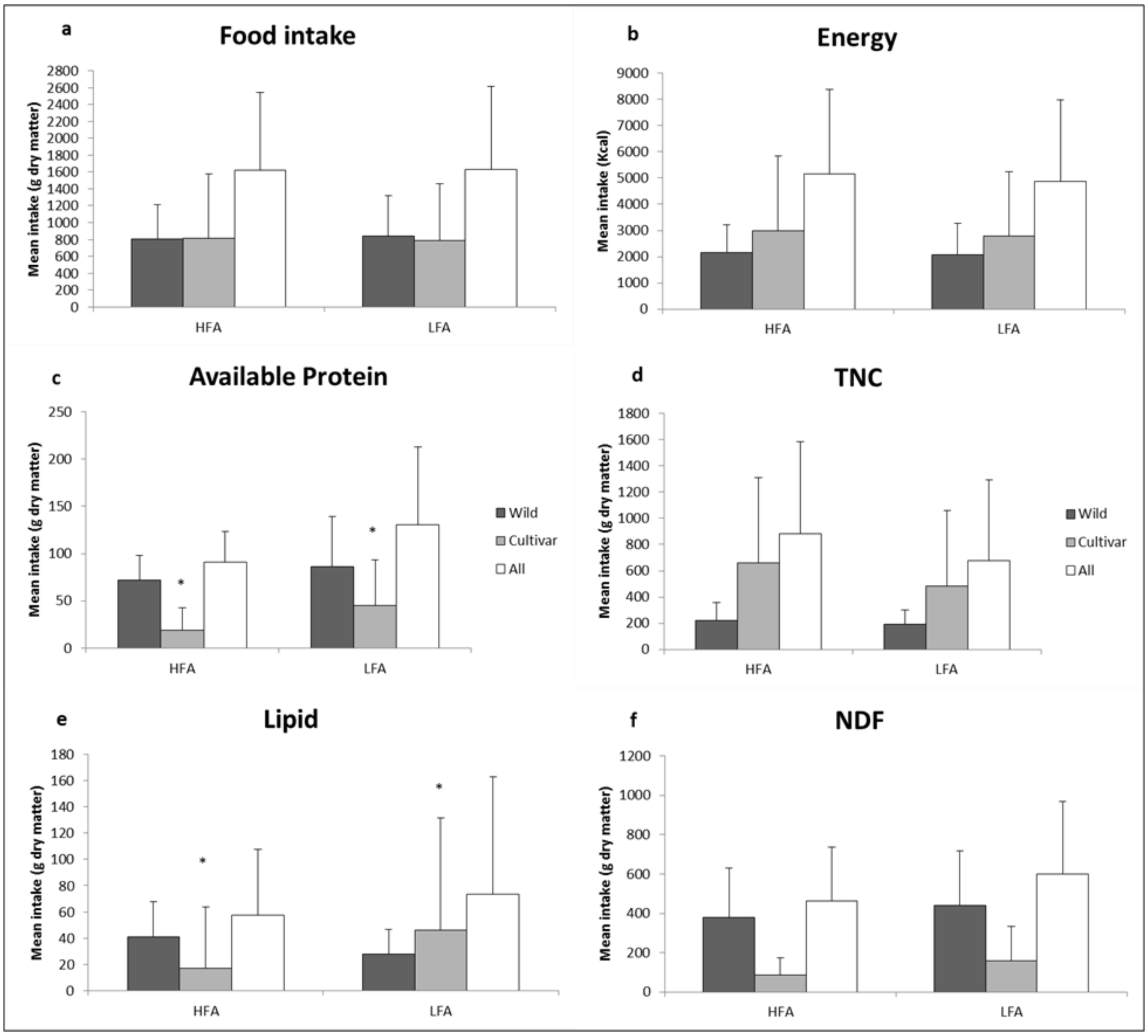

Figure 5.3 Mean (+SD) seasonal intake by adult chimpanzees (N = 10) in Bossou, Guinea of: a, food; b, metabolisable energy; c, available protein; d, total non-structural carbohydrates (TNC); e, lipids; f, neutral detergent fibre (NDF). HFA = high fruit availability season (December - May), LFA = low fruit availability season (June - November) derived from phenology data of the study period (April 2012-March 2013) (Bryson-Morrison et al, 2016). Wild = wild plant foods; Cultivar = cultivated plant foods; All = wild and cultivated foods combined. * denotes significant results. See Table 5.2 for statistics

5.4.4 Relative contribution of macronutrients to the diet

The RMT showed limited scatter of mean daily dietary intakes around the regression line of diet composition (all foods combined) (y= -0.702x + 66.489, R^2=0.74), indicating that the chimpanzees maintained a relatively constant proportional intake of available protein across the year, while allowing carbohydrate (TNC + NDF) and lipid intakes to vary as shown by the greater scatter along the line (Fig.5.4).

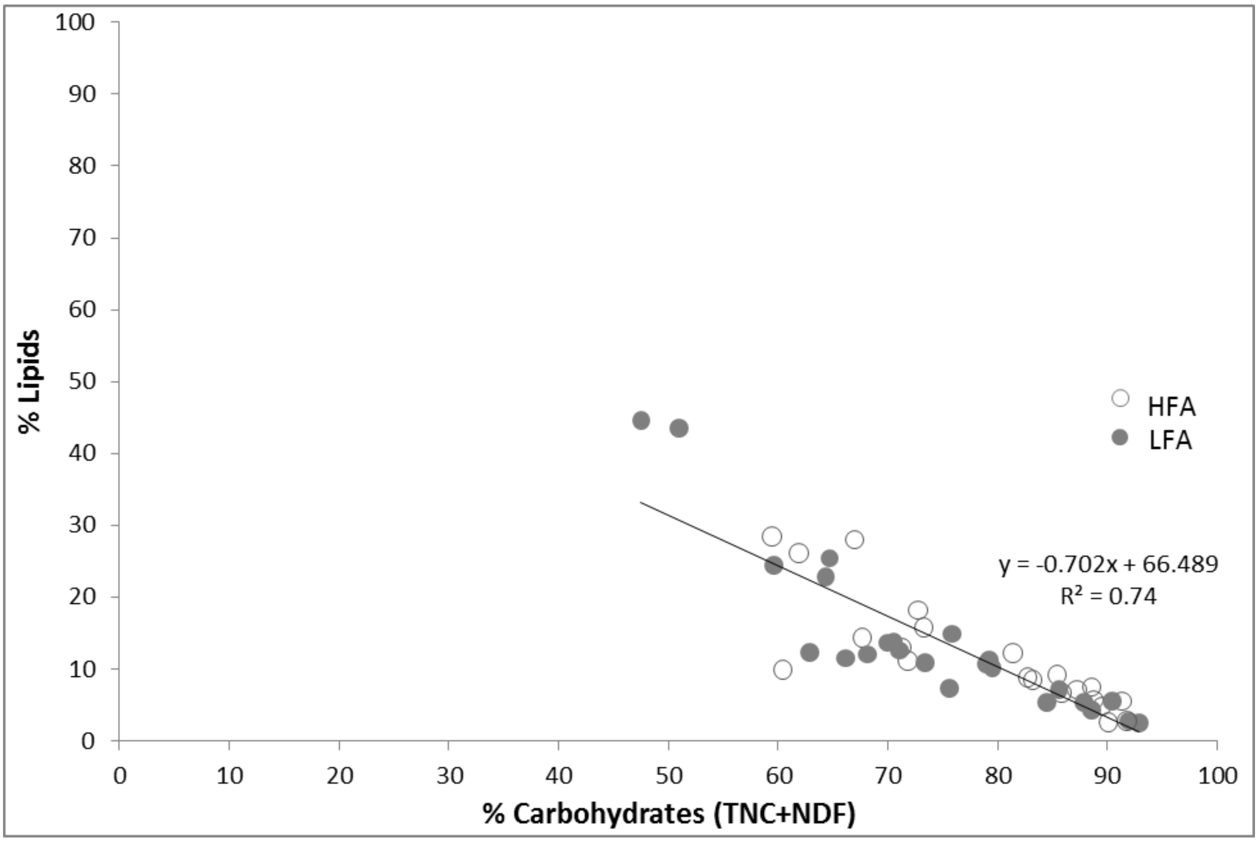

Figure 5.4 Right-angled mixture triangle (RMT) showing the relative contributions of carbohydrate, lipid, and available protein to metabolisable energy intake. Available protein contribution is the implicit axis. The line is the linear regression of diet composition (y = -0.702x + 66.489, R^2=0.74). HFA = high food availability season (December-May), LFA = low food availability season (June-November) derived from phenology data of the study period (April 2012-March 2013) (Bryson-Morrison et al, 2016)

The dietary ratio of AP to NPE across the year was 0.13 ± 0.08 SD, which corresponds to 9% daily energy intake from protein. We found no significant difference in the balance of AP to NPE between the sexes, seasons or any sex*season interactions (R^2=0.94; Sex: *F*=0.366, *P*=0.55; Season: *F*=2.627, *P*=0.11; Sex*Season: *F*=0.004, *P*=0.95) indicating that the chimpanzees maintained a relatively constant AP: NPE ratio throughout the year (Fig. 5.5).

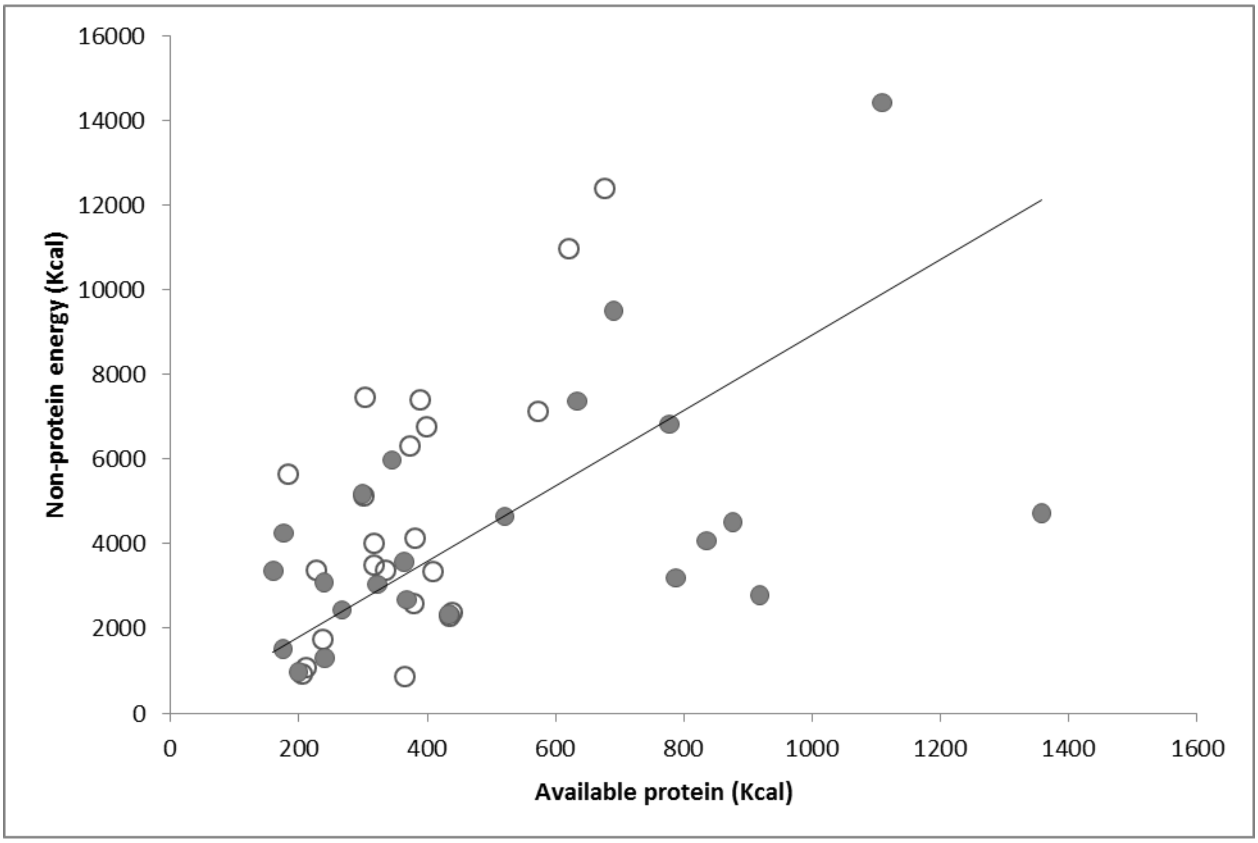

Figure 5.5 Average daily intakes of available protein (AP) vs. non-protein energy (NPE: carbohydrates + lipids + NDF) based on focal follows of individual adult chimpanzees (N = 10) from April 2012-March 2013 in Bossou, Guinea. White circles = high fruit availability season (December-May), Grey circles = low fruit availability season (June-November) derived from phenology data of the study period (April 2012-March 2013) (Bryson-Morrison et al, 2016). The line indicates the AP to NPE balance

5.5 DISCUSSION

5.5.1 Overview of diet composition

In agreement with other studies, we found that the chimpanzees fed predominantly on fruit throughout the year and increased their consumption of leaves and other plant parts when fruit availability was lower (Hockings et al, 2009; Watts et al, 2012; Takemoto, 2002; Wrangham et al, 1998; Yamakoshi, 1998). Although the chimpanzees consumed a high diversity of plant species across the year, the majority of the diet was comprised of food parts from only 18 species. There were no seasonal differences in cultivated food consumption, and crops accounted for around 29% of dietary intake across the year. Interestingly, the proportional contribution of cultivars to the diet was much greater than in previous years, including when calculated using comparative time based measurements (20% of feeding time: this study; 14% of feeding time: Hockings et al 2009; 6.4% of feeding time: Takemoto, 2002). These findings suggest that the Bossou chimpanzees have increased their cultivar consumption over time. A recent study examining cultivar consumption between chimpanzee communities showed that chimpanzees exploited a greater diversity of crops with longer exposure to agricultural environments (McLennan & Hockings, 2014). However, detailed long-term feeding and phenology data would be required to verify if annual differences in cultivar consumption are a direct response to temporal and/or spatial fluctuations in food availability or if the Bossou chimpanzees are adapting their foraging strategies over time to include more cultivars.

5.5.2 Sex differences in food and macronutrient intake

Our first prediction was supported by our findings of no differences in male and female absolute nutrient and energy intakes when accounting for all foods consumed (i.e. wild and cultivated foods combined). This is similar to reports for other chimpanzee populations (Pokempner, 2009) and orangutans (*Pongo pygmaeus wurmbii*) (Vogel et al, 2016), but contrasts with those for mountain gorillas (*Gorilla beringei*) where silverback males had higher nutrient and energy intakes than females (Rothman et al, 2008b). Reduced feeding competition has been suggested to explain the absence of sex differences in feeding time and intake in orangutans, which are largely solitary (Knott, 1998; Vogel et al, 2016), and chimpanzees, where flexible fission-fusion societies enable individuals to forage in small parties (Wrangham & Smuts, 1980). Indeed, we also found no difference in time spent foraging between males and females, with both sexes foraging for 15% of overall observation time (mean foraging time per month, males: 8.33±0.76%, females: 8.33±2.88%).

Nevertheless, differences in male and female food and nutrient intakes emerged once we accounted for metabolic body mass (MBM). Our first prediction was further supported by our findings that, on an equivalent basis, female chimpanzees showed higher intakes of protein and NDF from all foods than males. Females are expected to have increased energy requirements than males due to higher reproductive costs, particularly during pregnancy and lactation (Key & Ross, 1999). However, this is unlikely in the Bossou chimpanzees as they are an aging population with only one reproductively active female (Sugiyama & Fujita, 2011). Indeed, we found no sex differences in energy intake despite females consuming more overall food per unit of $M^{0.762}$ than males. The increased intake of protein and NDF per unit of $M^{0.762}$ in females is likely a consequence of their tendency towards a greater reliance on wild foods (Fig 5.2) that were relatively high in these nutrients (Table 5.1 and Chapter 4).

This is further supported by our finding that females showed higher intakes of NDF from wild foods than males.

Contrary to our predictions, we did not find any sex differences in food and nutrient intakes from cultivars. Previous research at Bossou showed that males were more likely to forage on cultivars than females (Hockings et al, 2009). However these sex differences were most strongly associated with "guarded "crops (i.e. those found in cultivated fields or near the village) that carry a high degree of risk from human presence and potential negative interactions (Hockings, 2011). No such associations were found for "abandoned" crops found in non-cultivated areas, such as fallow land and secondary forest (Hockings, 2011). We did not distinguish between guarded and abandoned cultivars and a relatively large proportion of the chimpanzees' cultivated food intake was from mango fruits and oil palm food parts which were found in high densities in non-cultivated habitats (Bryson-Morrison et al, 2016; Hockings et al, 2009). Overall, these results demonstrate that cultivars contributed equally to the dietary and macronutrient intakes of both males and females. Furthermore, males and females displayed strikingly similar dietary composition and foraging strategies, contrasting with previous studies of other chimpanzee (Murray et al, 2006; Pandolfi et al, 2003; Pokempner, 2009) and primate populations (Doran-Shehy et al, 2009; Koch et al, 2016). Evidence suggests that sex differences in chimpanzee foraging behaviour and diets are more pronounced in habitats with greater temporal and spatial fluctuations in food availability (Bean, 1999). Thus, the year-round availability of nutritious wild and cultivated foods at Bossou (Bryson-Morrison et al, 2016; Chapter 4) may reduce feeding competition and the need for males and females to select different diets and foraging behaviours (Bean, 1999). Although beyond the scope of our present study, a detailed examination of male and female behaviour, such as day journey length, sociality, party size, and time spent in food patches, would provide further insights into the foraging strategies employed by the different sexes.

5.5.3 Seasonal variation in food and macronutrient intake

Contrary to our prediction, food and nutrient intakes did not decrease during the fruit scarce season, contrasting with previous reports for other chimpanzee populations. Chimpanzees in KNP faced a 46% seasonal reduction in energy intake (Conklin-Brittain et al, 2006) and a significant decrease in food intake when fruits were scarce (Pokempner, 2009). Energy balance was greater in seasons dominated by higher quality fruit species in the chimpanzee community at Tai National Park, Cote d'Ivoire (N'guessan et al, 2009). Decreases in energy and/or nutrient intakes during periods of low food availability have also been documented in other primate species including orangutans (Conklin-Brittain et al, 2006; Knott, 1998, 2005; Vogel et al, 2016), Verreaux's sifakas (*Propithecus verreauxi*) (Koch et al, 2016) and diademed sifakas (*Propithecus diadema*) (Irwin et al, 2014). In mountain gorillas, no seasonal differences were found in overall energy consumption but individual macronutrient intakes varied with the contribution of fruit to the diet (Rothman et al, 2008b). The absence of seasonal differences in energy and nutrient intake suggests that the Bossou chimpanzees were able to meet their nutritional requirements across the year by consuming a combination of wild and cultivated foods. During periods of low food availability, many chimpanzee communities rely heavily on foods with relatively low nutritional value, such as fibrous fruits, leaves and piths (Doran, 1997; N'guessan et al, 2009;

Pokempner, 2009; Wrangham et al, 1991). However, during the LFA season, Bossou chimpanzee's fed intensively (i.e. 58.2% of food intake) on nutritious food parts (i.e. relatively high in protein, carbohydrates and/or lipids) from wild *Musanga cecropioides* trees, and cultivated species such as oil palm (*E. guineensis*), orange (*C. sinensis*), banana (*M. sinensis*), and cassava (*Manihot esculenta*) (Table 5.1). The chimpanzees consumed more AP and lipids from cultivars during the LFA season which coincided with higher proportional intake of oil palm parts rich in these macronutrients. The oil palm, which is found at high densities throughout Bossou and provides food sources year-round (Bryson-Morrison et al, 2016; Humle & Matsuzawa, 2004; Yamakoshi & Sugiyama, 1995), may be particularly important in enabling the chimpanzees to meet their nutritional requirements during the LFA season (Yamakoshi, 1998).

5.5.4 The role of cultivars in nutrient balancing

Chimpanzee diets showed a consistent contribution of protein to metabolisable energy (ME), while carbohydrates and lipids were used as interchangeable sources of ME across the year (Fig. 5.4). Bossou chimpanzees were able to maintain this balance despite seasonal differences in dietary composition and availability of wild and cultivated foods. This is similar to patterns found in chimpanzees in KNP where crude protein contribution to the diet did not vary with fruit abundance (Conklin-Brittain et al, 1998). Frugivorous spider monkeys also maintained a constant protein intake across seasons (Felton et al, 2009b). Our estimate of chimpanzee dietary protein content (9%) is lower than that reported for mountain gorillas (19-30%) (Rothman et al, 2011) but very similar to diademed sifakas (9.5%) (Irwin et al, 2015) and spider monkeys (9.5%) (Felton et al, 2009b). Chimpanzee diets fall just below the recommended range for human diets (10-35%) (National Academy of Sciences, 2005). Additionally, Bossou chimpanzees' non-protein energy to protein balance of 10:1 NPE: AP was in agreement with other findings for nutrient balancing in primates with varying frugivorous/folivorous diets (Felton et al, 2009b; Irwin et al, 2015; Johnston et al, 2013; Johnston et al. 2015; Rothman et al, 2011; Simpson & Raubenheimer, 2012). In comparison with these studies, chimpanzees, which are primarily frugivorous, displayed the highest non-protein energy to protein balance at 10:1 NPE: AP, likely due to the large amounts of ripe fruits in the diet which are generally rich in non-protein energy (Lambert & Rothman, 2015). This balance most closely resembles that of other species that preferentially consume ripe fruit (8:1 NPE: AP balance in spider monkeys (Felton et al, 2009b) and diademed sifikas (Irwin et al, 2015)). Omnivorous chacma baboons maintain a balance of 5:1 NPE: AP (Johnston et al, 2013), while seasonally frugivorous/folivorous mountain gorillas maintain a balance of 3:1 and 2:1 NPE: AP (Rothman et al, 2011) and highly folivorous guerezas (*Colobus guereza*) maintain a balance of 1.55:1 NPE: AP (Johnson et al, 2015).

Other studies employing the geometric framework of nutrition to primate diets have revealed variations in nutrient prioritisation when faced with constraints in food availability. When unable to maintain a balanced AP: NPE ratio, spider monkeys prioritise protein intake while allowing NPE intake to vary (Felton et al, 2009b), as did humans in free-choice experiments (Simpson & Batley, 2003). Mountain gorillas allow protein intake to vary between seasons while maintaining their intake of NPE (Rothman et al, 2011). Diademed sifikas appear to maintain their nutrient balance but experience extreme reductions in food intakes and energy when seasonal food quality and availability is low (Irwin et al, 2015). We found little variation in the seasonal ratio of AP to NPE, and the chimpanzees were able to maintain a balanced nutrient intake across the year. These results, along with our findings of no seasonal reductions in food, macronutrient or energy intakes, strongly suggest that the chimpanzees suffered little seasonal constraints in food quality or availability and were able to combine their consumption of available wild and cultivated foods to achieve a balanced diet. However, whether chimpanzees in less disturbed habitats have similar macronutrient balancing to the chimpanzees at Bossou is currently unknown. Diademed sifaka groups in habitats with varying degrees of disturbance showed similar relative contributions of macronutrients to the diets, despite differences in the amounts of food, energy and macronutrients ingested (Irwin et al, 2015). Comparing the macronutrient intakes of Bossou chimpanzees with populations residing in less disturbed habitats that consume little to no cultivars will help to determine if cultivar-foraging decisions are driven by specific macronutrient preferences, as has been proposed for grizzly bears (*Ursus arctos*) foraging on anthropogenic foods (Coogan & Raubenheimer, 2016). Knowledge of the macronutrient requirements of chimpanzees, and other primate species, would allow the development of a nutritionally explicit predictive framework for understanding foraging decisions relative to the foods available within a given environment (Coogan & Raubenheimer, 2016). Such information has important implications for managing primate-people coexistence in anthropogenic areas where the sharing of food resources can cause negative interactions and impacts to local livelihoods and food security (Hill, 2005).

5.5.5 Conclusions

Overall, our study demonstrated that the Bossou chimpanzees experienced little sex and seasonal variation in diet quality within this human-disturbed landscape and were able to maintain a balanced macronutrient intake across the year by consuming a variety of wild and cultivated foods. This suggests that the chimpanzees have adapted their foraging strategies and habitat use in order to meet their nutritional needs from the surrounding environment. These findings not only contribute to our current understanding of primate nutritional requirements, but also the ability of disturbed environments to meet these requirements. Such information is critical for developing sound conservation and management strategies aimed at balancing the needs of people and primates within anthropogenic landscapes.

5.6 REFERENCES

Altmann, J. (1974) Observational study of behavior: sampling methods, *Behaviour* 3: 227–266.

Aristizabal, J. F., Rothman, J. M., García-Fería, L. M. and Serio-Silva, J. C. (2016) Contrasting time-based and weight-based estimates of protein and energy intake of black howler monkeys (Alouatta pigra), *American Journal of Primatology*: doi: 10.1002/ajp.22611.

Bean, A. (1999) Ecology of sex differences in great ape foraging., in Lee, P. C. (ed.) *Comparative Primate Socioecology*. Cambridge: Cambridge University Press, 339–362.

Behie, A. M. and Pavelka, M. S. M. (2012) The role of minerals in food selection in a black howler monkey (Alouatta pigra) population in Belize following a major hurricane, *American journal of primatology* 74: 1054–63.

Bortolamiol, S., Cohen, M., Jiguet, F., Pennec, F., Seguya, A. and Krief, S. (2016) Chimpanzee non-avoidance of hyper-proximity to humans, *The Journal of Wildlife Management* 80: 924-934.

Brennan, E. J., Else, J. G. and Altmann, J. (1985) Ecology and behaviour of a pest primate: vervet monkeys in a tourist-lodge habitat, *African Journal of Ecology* 23: 35–44.

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T. and Humle, T. (2017) Activity and Habitat Use of Chimpanzees (Pan troglodytes verus) in the Anthropogenic Landscape of Bossou, Guinea, West Africa, *International Journal of Primatology*: doi: 10.1007/s10764-016-9947-4.

Bryson-Morrison, N., Matsuzawa, T. and Humle, T. (2016) Chimpanzees in an anthropogenic landscape: Examining food resources across habitat types at Bossou, Guinea, West Africa, *American Journal of Primatology* 78: 1237-1249.

Campbell-Smith, G., Campbell-Smith, M., Singleton, I. and Linkie, M. (2011) Raiders of the lost bark: Orangutan foraging strategies in a degraded landscape, *PloS one* 6: e20962.

Chapman, C. A. and Chapman, L. J. (1999) Forest Restoration in Abandoned Agricultural Land: a Case Study from East Africa, *Conservation Biology* 13: 1301–1311.

Chapman, C. A. and 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: 861–875.

Chivers, D. J. (1998) Measuring food intake in wild animals: primates', *Proceedings of the Nutrition Society*. Cambridge Univ Press 57: 321–332.

Chiyo, P. I., Cochrane, E. P., Naughton, L. and Basuta, G. I. (2005) Temporal patterns of crop raiding by elephants: a response to changes in forage quality or crop availability?, *African Journal of Ecology* 43: 48–55.

Conklin-Brittain, N.L., Knott, C.D. and Wrangham, R. . (2006) Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison, in Hohmann, G., Robbins, M.M. and Boesch, C. (eds.) *Feeding Ecology in*

Apes and Other Primates. Cambridge: Cambridge University Press: 445–472.

Conklin-Brittain, N. L., Dierenfeld, E. S., Wrangham, R. W., Norconk, M. and Silver, S. C. (1999) Chemical protein analysis: a comparison of Kjeldahl crude protein and total ninhydrin protein from wild, tropical vegetation, *Journal of chemical ecology* 25: 2601–2622.

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

Coogan, S. C. P. and Raubenheimer, D. (2016) Might macronutrient requirements influence grizzly bear–human conflict? Insights from nutritional geometry, *Ecosphere* 7: e01204.

Donati, G., Kesch, K., Ndremifidy, K., Schmidt, S. L., Ramanamanjato, J.-B., Borgognini-Tarli, S. M. and Ganzhorn, J. U. (2011) Better Few than Hungry: Flexible Feeding Ecology of Collared Lemurs Eulemur collaris in Littoral Forest Fragments, *PLoS ONE* 6: e19807.

Doran, D. (1997) Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees, *International Journal of Primatology* 18: 183–206.

Duvall, C. S. (2008) Human settlement ecology and chimpanzee habitat selection in Mali, *Landscape Ecology* 23: 699–716.

Felton, A. M., Felton, A., Lindenmayer, D. B. and Foley, W. J. (2009a) Nutritional goals of wild primates, *Functional Ecology* 23: 70–78.

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

Gabriel, D. N. (2013) Habitat use and activity patterns as an indication of fragment quality in a strepsirrhine primate, *International Journal of Primatology* 34: 388–406.

Ganzhorn, J. U. (1992) Leaf chemistry and the biomass of folivorous primates in tropical forests, *Oecologia,* 91: 540–547.

Ganzhorn, J. U. (1995) Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations, *Ecology* 76: 2084–2096.

Ganzhorn, J. U. (2002) Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics, *Oecologia* 131: 427–435.

Ghiglieri, M.P. (1984). *The Chimpanzees of Kibale Forest: A Field Study of Ecology and Social Structure.* New York: Columbia University Press.

Hill, C. M. (2000) Conflict of interest between people and baboons: crop raiding in Uganda, *International Journal of Primatology* 21: 299–315.

Hill, C. M. (2005) People, crops and primates: a conflict of interests, *Commensalism and* *conflict: The human-primate interface.*Norman, Oklahoma: American Society of Primatologists, 40–59.

Hockings, K. J. (2011) The Crop-Raiders of the Sacred Hill, in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The Chimpanzees of Bossou and Nimba*. London: Springer: 211–220.

Hockings, K. J., Anderson, J. R. and 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: 636–646.

Hockings, K. J. and McLennan, M. R. (2012) From forest to farm: Systematic review of cultivar feeding by chimpanzees–management implications for wildlife in anthropogenic landscapes, *PloS one* 7: e33391.

Hockings, K. and McLennan, M. (2016) Problematic Primate Behaviour in Agricultural Landscapes: Chimpanzees as “Pests” and “Predators, In Waller, M.T. (ed) *Ethnoprimatology*.Switzerland: Springer, 137-156.

Hohmann, G., Potts, K., N’Guessan, A., Fowler, A., Mundry, R., Ganzhorn, J. U. and Ortmann, S. (2010) Plant foods consumed by Pan: Exploring the variation of nutritional ecology across Africa, *American Journal of Physical Anthropology* 141: 476–485.

Humle, T; Koops, K; Cherif, P. (2011) Appendix B: Plant food list of Bossou chimpanzees including vernacular Manon name, as well as plant type and part consumed, in Matsuzawa, T; Humle, T; Sugiyama, Y. (ed.) *The Chimpanzees of Bossou and Nimba*. London: Springer, 406–411.

Humle, T. (2011) Location and Ecology, in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The Chimpanzees of Bossou and Nimba*. London: Springer, 13–21.

Humle, T. and Matsuzawa, T. (2004) Oil palm use by adjacent communities of chimpanzees at Bossou and Nimba Mountains, West Africa’, *International Journal of Primatology* 25: 551–581.

Irwin, M. T. (2008) Feeding Ecology of Propithecus diadema in Forest Fragments and Continuous Forest, *International Journal of Primatology* 29: 95–115.

Irwin, M. T., Raharison, J.-L., Raubenheimer, D. R., Chapman, C. A. and Rothman, J. M. (2015) The Nutritional Geometry of Resource Scarcity: Effects of Lean Seasons and Habitat Disturbance on Nutrient Intakes and Balancing in Wild Sifakas, *PLOS ONE* 10: e0128046.

Irwin, M. T., Raharison, J., Raubenheimer, D., Chapman, C. A. and Rothman, J. M. (2014) Nutritional correlates of the “lean season”: Effects of seasonality and frugivory on the nutritional ecology of diademed sifakas, *American Journal of Physical Anthropology,* 153: 78–91.

Janson, C.H and Chapman, C. (1999) Resources and primate community structure, in Fleagle, J.G; Janson, C. . and R. K. (ed.) *Primate Communities*. Cambridge: Cambridge University Press, 237–267.

Johnson, C. A., Raubenheimer, D., Chapman, C. A., Tombak, K. J., Reid, A. J. and Rothman, J. M. (2015) Macronutrient balancing affects patch departure by guerezas (*Colobus guereza*), *American Journal of Primatology*: doi:10.1002/ajp.22495.

Johnson, C. A., Raubenheimer, D., Rothman, J. M., Clarke, D. and Swedell, L. (2013) 30 Days in the Life: Daily Nutrient Balancing in a Wild Chacma Baboon, *PloS one* 8: e70383.

Kay, R. F., Madden, R. H., Van Schaik, C. and Higdon, D. (1997) Primate species richness is determined by plant productivity: Implications for conservation, *Proceedings of the National Academy of Sciences* 94: 13023–13027.

Key, C. and Ross, C. (1999) Sex differences in energy expenditure in non–human primates, *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266: 2479 LP-2485.

Knott, C. D. (1998) Changes in Orangutan Caloric Intake, Energy Balance, and Ketones in Response to Fluctuating Fruit Availability, *International Journal of Primatology* 19: 1061–1079.

Koch, F., Ganzhorn, J. U., Rothman, J. M., Chapman, C. A. and Fichtel, C. (2016) Sex and seasonal differences in diet and nutrient intake in Verreaux's sifakas (Propithecus verreauxi), *American Journal of Primatology*: doi: 10.1002/ajp.22595.

Koenig, A., Borries, C., Chalise, M. K. and Winkler, P. (1997) Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (Presbytis entellus), *Journal of zoology* 243: 215–235.

Lambert, J. E. and Rothman, J. M. (2015) Fallback Foods, Optimal Diets, and Nutritional Targets: Primate Responses to Varying Food Availability and Quality, *Annual Review of Anthropology* 44: 493–512.

Lee, R. J. (1997) *The impact of hunting and habitat disturbance on the population dynamics and behavioral ecology of the crested black macaque (Macaca nigra)*. PhD thesis, Eugene: University of Oregon.

Lodge, E., Ross, C., Ortmann, S. and MacLarnon, A. M. (2013) Influence of diet and stress on reproductive hormones in Nigerian olive baboons, *General and comparative endocrinology* 191: 146–154.

Matsumoto-Oda, A. and Hayashi, Y. (1999) Nutritional aspects of fruit choice by chimpanzees., *Folia primatologica* 70: 154–62.

Mckinney, T. (2011) The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced Capuchins (Cebus capucinus), *American Journal of Primatology* 73: 439–448.

McLennan, M. (2013) Diet and feeding ecology of chimpanzees (Pan troglodytes) in Bulindi, Uganda: foraging strategies at the forest–farm interface, *International Journal of Primatology* 34: 585-614.

McLennan, M. and Ganzhorn, J. (2017) Nutritional Characteristics of Wild and Cultivated

Foods for Chimpanzees (Pan troglodytes) in Agricultural Landscapes, *International Journal of Primatology*: doi:10.1007/s10764-016-9940-y.

McLennan, M. R. and Hockings, K. J. (2014) Wild chimpanzees show group differences in selection of agricultural crops, *Scientific reports* 4: 5956.

Ménard, N., Motsch, P., Delahaye, A., Saintvanne, A., Le Flohic, G., Dupé, S., Vallet, D., Qarro, M., Tattou, M. I. and Pierre, J. (2014) Effect of habitat quality on diet flexibility in Barbary macaques, *American Journal of Primatology* 76: 679–693.

Milton, K. (1999) Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us, *Nutrition* 15: 488–498.

Murray, C. M., Eberly, L. E. and Pusey, A. E. (2006) Foraging strategies as a function of season and rank among wild female chimpanzees (Pan troglodytes), *Behavioral Ecology* 17: 1020–1028.

N'guessan, A. K., Ortmann, S. and Boesch, C. (2009) Daily energy balance and protein gain among Pan troglodytes verus in the Taï National Park, Côte d'Ivoire, *International Journal of Primatology* 30: 481–496.

National Academy of Sciences (2005) *Dietary reference intakes for energy, carbohydrate, fiber, fat, fatty acids, cholesterol, protein, and amino acids.* Washington, DC: National Academies Press.

National Research Council (2003) *Nutrient requirements of nonhuman primates*. (2nd ed). Washington, DC: National Academies Press.

Osborn, F. V (2004) Seasonal variation of feeding patterns and food selection by crop-raiding elephants in Zimbabwe, *African Journal of Ecology* 42: 322–327.

Pandolfi, S.S. , van Schaik, C.P. and Pusey, A.E (2003) Sex differences in termite fishing among Gombe chimpanzees are due to socioecological factors, In de Waal, F.B.M. and Tyack, P.L. (eds) *Animal social complexity: intelligence, culture, and individualized societies,* Cambridge, MA: Harvard University Press, 414–418.

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

Pokempner, A. A. (2009) *Fission -fusion and foraging: Sex differences in the behavioral ecology of chimpanzees (Pan troglodytes schweinfurthii)*. PhD thesis, Stony Brook University.

Priston, N. E. C. and McLennan, M. R. (2013) Managing Humans, Managing Macaques: Human–Macaque Conflict in Asia and Africa, in *The Macaque Connection*. New York: Springer, 225–250.

Raubenheimer, D. (2011) Toward a quantitative nutritional ecology: the right-angled mixture triangle, *Ecological Monographs* 81: 407–427.

Raubenheimer, D., Machovsky-Capuska, G. E., Chapman, C. A. and Rothman, J. M. (2015)

Geometry of nutrition in field studies: an illustration using wild primates, *Oecologia* 177: 223–234.

Raubenheimer, D., Simpson, S. J. and Mayntz, D. (2009) Nutrition, ecology and nutritional ecology: toward an integrated framework, *Functional Ecology* 23: 4–16.

Remis, M. J. (2002) Food Preferences Among Captive Western Gorillas (Gorilla gorilla gorilla) and Chimpanzees (Pan troglodytes), *International Journal of Primatology* 23: 231–249.

Reynolds, V., Plumptre, A. J., Greenham, J. and Harborne, J. (1998) Condensed tannins and sugars in the diet of chimpanzees (Pan troglodytes schweinfurthii) in the Budongo Forest, Uganda, *Oecologia,* 115: 331–336.

Righini, N. (2017) Recent advances in primate nutritional ecology, *American Journal of Primatology*: *doi:* 10.1002/ajp.22634.

Riley, E. P. (2007) The human-macaque interface: Conservation implications of current and future overlap and conflict in Lore Lindu National Park, Sulawesi, Indonesia, *American Anthropologist* 109: 473–484.

Riley, E. (2008) Ranging patterns and habitat use of Sulawesi Tonkean macaques (Macaca tonkeana) in a human-modified habitat, *American Journal of Primatology* 70: 670-679.

Rode, K. D., Chapman, C. A., McDowell, L. R. and 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. and 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. and Pell, A. N. (2008a) Fiber-bound nitrogen in gorilla diets: implications for estimating dietary protein intake of primates, *American journal of primatology* 70: 690–4.

Rothman, J. M., Chapman, C. A. and 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. and Pell, A. N. (2008b) Nutritional quality of gorilla diets: consequences of age, sex, and season, *Oecologia* 155: 111–122.

Rothman, J. M., Plumptre, A. J., Dierenfeld, E. S. and Pell, A. N. (2007) Nutritional Composition of the Diet of the Gorilla(Gorilla Beringei): a Comparison Between Two Montane Habitats, *Journal of Tropical Ecology* 23: 673–682.

Rothman, J. M., Raubenheimer, D. and Chapman, C. A. (2011) Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein, *Biology Letters*: DOI: 10.1098/rsbl.2011.0321.

van Schaik, C.P and Pfannes, K. (2005) Tropical climates and phenology: a primate perspective, in Brockman, D.K and van Schaik, C. (ed.) *Seasonality in primates: studies of living and extinct human and non-human primates*. Cambridge: Cambridge

University Press, 23–55.

van Schaik, C. P., Terborgh, J. W. and Wright, S. J. (1993) The Phenology of Tropical Forests: Adaptive Significance and Consequences for Primary Consumers, *Annual Review of Ecology and Systematics* 24: 353–377.

Simpson, S. J. and Batley, R. (2003) Geometric analysis of macronutrient intake in humans: the power of protein?, *Appetite* 41: 123–140.

Simpson, S. J. and Raubenheimer. D. (2012) *The nature of nutrition: a unifying framework from animal adaptation to human obesity*. Princeton University Press.

Smith, R. J. and Jungers, W. L. (1997) Body mass in comparative primatology, *Journal of Human Evolution* 32: 523–559.

Spencer, R; Cross, R; Lumley, P. (2007) *Plant names: A guide to botanical nomenclature*. third edition. Melbourne: Royal Botanic Gardens.

Strum, S. C. (2010) The development of primate raiding: implications for management and conservation, *International Journal of Primatology* 31: 133–156.

Strum, S. S. and Latour, B. (1991) Redefining the Social Link From Baboons to Humans, *Primate Politics*: 73–85.

Sugiyama, Y. and Fujita, S. (2011) The Demography and Reproductive Parameters of Bossou Chimpanzees, in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The Chimpanzees of Bossou and Nimba*. London: Springer, 23–34.

Takemoto, H. (2002) *Feeding ecology of chimpanzees in Bossou, Guinea: coping with the seasonal fluctuation of food supply and micrometeorology in the tropical forest*, Unpublished PhD thesis, Kyoto University, Kyoto, Japan.

Takemoto, H. (2003) Phytochemical determination for leaf food choice by wild chimpanzees in Guinea, Bossou, *Journal of chemical ecology* 29: 2551–2573.

Terada, S., Nackoney, J., Sakamaki, T., Mulavwa, M. N., Yumoto, T. and Furuichi, T. (2015) Habitat use of bonobos (Pan paniscus) at Wamba: Selection of vegetation types for ranging, feeding, and night-sleeping, *American Journal of Primatology* 77: 701–713.

Tutin, C. E. G. (1999) Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon, *Primates* 40: 249–265.

Vogel, E. R., Alavi, S. E., Utami-Atmoko, S. S., van Noordwijk, M. A., Bransford, T. D., Erb, W. M., Zulfa, A., Sulistyo, F., Farida, W. R. and Rothman, J. M. (2016) Nutritional ecology of wild Bornean orangutans (Pongo pygmaeus wurmbii) in a peat swamp habitat: Effects of age, sex, and season, *American Journal of Primatology*: doi: 10.1002/ajp.22618.

Watts, D. P., Potts, K. B., Lwanga, J. S. and Mitani, J. C. (2012) Diet of chimpanzees (Pan troglodytes schweinfurthii) at Ngogo, Kibale National Park, Uganda, 1. Diet composition and diversity, *American journal of primatology* 74: 114–129.

Wong, S. N. P., Saj, T. L. and Sicotte, P. (2006) Comparison of habitat quality and diet of

Colobus vellerosus in forest fragments in Ghana, *Primates* 47: 365–373.

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: 689–697.

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

Wrangham, R. W., Conklin, N. L., Chapman, C. A., Hunt, K. D., Milton, K., Rogers, E., Whiten, A. and Barton, R. A. (1991) The Significance of Fibrous Foods for Kibale Forest Chimpanzees, *Philosophical Transactions of the Royal Society of London.Series B: Biological Sciences* 334: 171–178.

Wrangham, R. W. and Smuts, B. B. (1980) Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania, *Journal of reproduction and fertility* 28: 13–31.

Yamakoshi, G. (1998) Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use, *American Journal of Physical Anthropology* 106: 283–295.

Yamakoshi, G. and Sugiyama, Y. (1995) Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: A newly observed tool-using behavior, *Primates* 36: 489–500.

Chapter 6 GENERAL DISCUSSION

The aim of this thesis was to contribute to our understanding of the ecology of anthropogenic landscapes and the chimpanzees that reside within them. It has become increasingly recognised that in order to ensure the long-term survival of chimpanzees in the wild, and indeed many other wildlife species, we must understand their ability to adapt, both ecologically and behaviourally, to increasing pressures on their environment from human activities and presence (Hockings et al, 2015). By focusing my study on the chimpanzees at Bossou, I was able to take a step-wise approach whereby I began by describing empirically the floristic characteristics of the landscape, and then used these findings to examine habitat use for foraging and other behavioural activities within the context of risk perception from human presence and infrastructure such as roads and cultivated fields. Finally I investigated the nutritional dimensions of chimpanzee wild and cultivated food related decision making.

6.1 SUMMARY OF FINDINGS

Chapter 2 quantified the density, distribution and availability of chimpanzee plant food resources across all habitat types. Bossou is a highly heterogeneous landscape largely composed of regenerating forest with one of the lowest stem densities/ha reported for tropical forest areas inhabited by chimpanzees. The scarcity of large fruit bearing trees is offset by a high diversity of chimpanzee plant food resources dominated by species of the Moraceae family, as well as oil palm trees, terrestrial herbaceous vegetation, and cultivars, many of which produced food parts year round. Mature (or primary) forest and secondary forest harboured significantly higher densities and basal areas of plant food resources than other forested or highly disturbed habitat types. Overall, these results highlighted the importance of determining ecological characteristics across habitat types within an anthropogenic landscape as each available habitat type is unlikely to be equally important in terms of the spatial and temporal availability of resources.

Chapter 3 determined chimpanzee preferential use of habitat types (defined in Chapter 2) overall and across behavioural activities and examined the influence of anthropogenic risks on foraging behaviour. Two particularly important findings emerged from this chapter. The first of these was the chimpanzees' reliance, regardless of activity or season, on a small remnant patch of mature forest. A combination of thick tree cover, high densities of food species, and little to no human presence in this "sacred" area of forest appears to act like a "refuge" for the chimpanzees. The second important finding was the avoidance by chimpanzees to forage in non-cultivated habitat within 200 m of cultivated fields, preferring to forage > 200 m away. The results showed no effect of habitat type or season, suggesting that risks associated with likely human presence and potential negative interactions in cultivated fields were significantly influencing chimpanzee foraging behaviour in non-cultivated habitat. Prior to this study, the majority of research had examined the influence of human-induced risks within the context of cultivar-foraging and road crossing. Overall, my findings revealed chimpanzee reliance on different habitat types and the influence of human-induced pressures and risks on their behavioural activities and habitat use. Such information is important for the establishment of effective land-use management strategies for chimpanzees in anthropogenic landscapes.

Chapter 4 presented the macronutrient composition of important wild and cultivated chimpanzee foods, and compared these with recently published macronutrient compositions of chimpanzee foods in Bulindi, Uganda. My findings, along with those from Bulindi (McLennan & Ganzhorn, 2017), revealed that cultivars were higher in carbohydrates and lower in fibre than wild foods, thus providing empirical support for the widely accepted assumption that cultivars offer energetic benefits over most wild plant foods consumed by primates. This chapter also detailed, for the first time, the macronutrient composition of oil palm food parts (except flowers) consumed by chimpanzees and showed that these were nutritionally rich food sources high in protein, carbohydrates, lipids and/or fermentable fibre fractions (NDF). These findings provided nutritional support for the oil palm serving as a potentially critical resource for chimpanzees in anthropogenic landscapes across West Africa.

Chapter 5 used the macronutrient composition data described in Chapter 4 with behavioural information of food intakes to explore sex and seasonal differences in foraging and nutrient intake from wild and cultivated foods. Chimpanzees, and other primate species, within forest-agricultural mosaics frequently consume cultivars which negatively influences peaceful coexistence with local people. However, the nutritional drivers behind cultivar-foraging are poorly understood, and this is the first study to quantify primate wild and cultivated macronutrient and energy intakes within a forest-agricultural mosaic. Males and females showed no differences in diet composition and had strikingly similar food and macronutrient intakes, which they maintained across the year regardless of seasonal fruit availability. Cultivars, and most likely food parts from the oil palm, emerged as important sources of lipids and protein during the low fruit availability season. Nutritional geometry revealed that chimpanzee diets contained a consistent proportional intake of protein while carbohydrate and lipid intake varied. Furthermore, the chimpanzees were able to maintain a balanced intake of non-protein energy (NPE: carbohydrates, lipids and digestible fibre) to protein (AP) of 10:1 NPE:AP across the year. Overall, this chapter revealed that the chimpanzees experienced little seasonal fluctuations in diet quality and food intakes, suggesting that they have adapted their foraging strategies and habitat use in order to meet their nutritional requirements from the surrounding environment.

6.2 WIDER IMPLICATIONS AND FUTURE DIRECTIONS

6.2.1 Conserving chimpanzees in anthropogenic landscapes

It is estimated that by 2030 a mere 10% of African great ape habitat and 1% of Asian great ape habitat will remain free from human-related disturbances (Nelleman & Newton, 2002). Furthermore, to date as much as 80% of West African chimpanzees are found in anthropogenic landscapes outside formally protected areas (Kormos et al, 2003). There is little doubt that in order to conserve chimpanzees, and other primate species, we must understand their ability to respond to human activities and presence along with the capacity of disturbed environments to support viable populations in the long-term. Although parks and other designated protected areas rightly remain a key focus for conservation, ‘the time for delegating pristine ‘natural’ environments to be the sole solution for preserving great apes…..is long gone’ (Hockings et al, 2015, p. 221). Bossou offers an important case study for increasing current knowledge on chimpanzee ecology, behaviour and flexibility in response to human-induced change. Such information is critical for the development of sound land use management and conservation strategies and to this end the results of this thesis are important.

Chimpanzees are highly adaptable to environmental change and readily modify their behaviour in response to human-induced pressures (Hockings & Humle, 2009). However, my study indicated that the ability of chimpanzees to manage in disturbed landscapes is constrained by their need for access to mature forest or similar patches of natural habitat. Comparable findings were found for orangutans in landscapes dominated by oil palm plantations (Ancrenaz et al, 2015). Access to natural forest, even relatively small patches (mature forest in Bossou measures < 1 km^2), is evidently an important factor in sustaining great ape populations in anthropogenic landscapes. Small-scale traditional farming techniques, such as ‘slash and burn’, promote the persistence of forest-agricultural mosaics, and such landscapes can likely support chimpanzees if they are tolerated by local people. However, highly disturbed environments, such as areas of industrial agriculture, are often dominated by monoculture plantations with no, or limited access, to natural habitat (Humle, 2015). Expansion of industrial plantations, particularly those growing oil palm, have caused extensive habitat conversion to orangutan ranges in Southeast Asia (Wich et al, 2012). Industrial agriculture is also increasing in Africa and a recent report highlighted that current great ape distribution overlaps extensively with oil palm concessions or land suitable for future oil palm production (Wich et al, 2014). Plans for industrial plantations in chimpanzee ranges, and indeed those of other African great apes, must include setting aside areas of natural forest in order to sustain viable populations, as has been proposed for orangutans (Ancrenaz et al, 2015). Establishing the extent of chimpanzee reliance on patches of natural habitat across the anthropogenic continuum is therefore of paramount importance for future research and conservation of the species.

While orangutan research highlights the detrimental effects of large oil palm plantations, there is a growing body of evidence that suggests the survival of chimpanzee populations in degraded environments, particularly across West Africa, may actually be dependent on the presence of oil palms (Brncic et al, 2010). Indeed, such populations are known to rely heavily on oil palms for nesting (Leciak et al, 2005; Humle & Matsuzawa, 2004; Sousa et al, 2011) and food (Bessa et al, 2015; Brncic et al, 2010; Humle & Matsuzawa, 2004; Yamakoshi, 1998). Although considerable variation in oil palm use exists between chimpanzee communities in different habitats (Humle & Matsuzawa, 2004; McGrew, 1992), this study provides further support for the importance of oil palms for populations residing in anthropogenic landscapes. Oil palms were found in high densities across the majority of habitat types in Bossou (excluding mature forest) (Chapter 2), making them easily accessible for the chimpanzees. Most importantly however, this study demonstrated the potential nutritional advantages of oil palm food parts for chimpanzees (Chapters 4 and 5). Not only were oil palm food parts found to be rich in important macronutrients, they also likely contributed to the chimpanzee's ability to meet their nutrient requirements during the low fruit availability season. As a result, the chimpanzees were able to maintain their nutrient balance across the year and suffered none of the seasonal reductions in nutrient and/or energy intakes reported in other chimpanzee populations inhabiting more intact forests (Conklin-Brittain et al, 2006; N' guessan et al, 2009; Pokempner, 2009). These findings have clear implications for the importance of shared resources for chimpanzee survival that should help inform future research directions aimed at understanding the needs of people and chimpanzees for the development of locally appropriate management strategies.

Where chimpanzees are tolerated by local people, they can readily adapt to anthropogenic pressures on their environment and are known to display a variety of flexible behaviours that allow them to exploit human food sources and infrastructures, such as roads (Hockings et al, 2015). However, even when chimpanzees are afforded a degree of tolerance and not directly persecuted, living in close proximity to humans and sharing resources and space is not without real or perceived risks for both chimpanzees and people. Examples of such risks to people include economic and social costs incurred from crop losses, and fear for safety and well-being from potential or actual aggressive encounters and physical attacks (McLennan & Hockings, 2016). Risks to chimpanzees include negative interactions and retaliations from farmers when foraging on cultivars, disease transmission, and from vehicles during road-crossings (Hockings & Humle, 2009). Managing risks and risk perception resulting from human-chimpanzee interactions is one of the main conservation challenges within anthropogenic landscapes. Despite this, there is limited understanding of how human presence and pressures directly and indirectly impact on chimpanzees within anthropogenic landscapes, particularly for contexts other than cultivar-foraging and road crossing. The results of the present study provided evidence that likely human presence and highly contentious areas can indirectly impact on chimpanzee habitat use for important activities, such as resting and foraging on natural foods. These findings, along with increasing evidence that chimpanzees, and other primates, display signs of anxiety and stress in human-impacted environments (Carlitz et al, 2016; Hicks et al, 2012; Hockings, 2011; Hockings et al, 2006; Muyambi, 2005; Cyr & Romero, 2008; Wingfield & Romero, 2010) highlight that further research is urgently required to determine the influence of anthropogenic pressures on fundamental aspects of chimpanzee behaviour and well-being. Such information is necessary to help ensure species long-term viability and fitness within human-dominated environments.

6.2.2 The role of nutritional ecology in primate conservation

The fundamental aim of nutritional ecology is to ‘unravel the extensive web of nutritional links that directs animals in their interactions with their ecological and social environments’ (Raubenheimer et al, 2012, p. 1628). Thus, nutritional ecology can provide insights into the relationship between primate resource requirements, the ability of a habitat to meet these requirements, and the responses of primates when they are constrained from meeting their requirements (Raubenheimer et al, 2012). Seasonal food availability, high dietary diversity, and flexible feeding characterise the foraging ecology of chimpanzees and most other primate species (Lambert & Rothman, 2015). These traits challenge our ability to explain and predict primate responses and adaptability to human-induced disturbances on their environment.

However, recent applications of a nutritionally explicit analytical framework for determining nutritional requirements and food-related decision making in primates, suggest that this will become a powerful tool for applied conservation initiatives (Righini, 2017). The geometric framework for nutrition has been used to successfully inform conservation of other species, including supplementary feeding regimes to trigger breeding in the critically endangered Kakapo (*Strigops habroptila*) (Raubenheimer & Simpson, 2006). The ability of primate individuals to meet their nutritional requirements is a critical factor in enabling populations to persist in a given landscape. Understanding these nutritional requirements, and the ability of the surrounding environment to support them, would allow the development of species appropriate land-use management strategies aimed at protecting or regenerating plant foods necessary for achieving a balanced diet (Righini, 2017). For example, findings from a recent primate study that employed the geometric framework for nutrition led the authors to recommend that key abundant season foods should be the focus of conservation efforts for diademed sifakas (*Propithecus diadema*) in habitats affected by human disturbances (Irwin et al, 2015). My study demonstrated that chimpanzees within an anthropogenic environment can achieve a balanced nutrient intake by consuming a variety of wild and cultivated foods, with food parts from the oil palm emerging as particularly important during the fruit scarce season. However, further research is necessary to determine whether chimpanzees would be able to maintain a balanced diet without consuming cultivars, and to identify nutritionally important wild foods that could potentially act to replace or mitigate reliance on shared resources.

The propensity of chimpanzees, and many other primate species, to incorporate cultivars or other human-derived foods into their diet frequently causes negative interactions with people and can seriously impact on local economic and food security (Hill, 2005). As such, an important aspect of conservation initiatives within anthropogenic landscapes involves developing appropriate mitigation measures to deter and reduce foraging on anthropogenic foods. However, the implementation of effective management strategies is hampered by a lack of understanding of *why* primates choose to forage on human-derived foods as well as their nutritional dependence on these for their survival.

Several factors likely contribute to the extent to which primates incorporate cultivars or other shared resources into their diets (e.g. ecological and behavioural flexibility (Isaac & Cowlishaw, 2004), proximity of fields to forest boundary (Hill, 1997, 2000; Warren et al, 2007), and degree of risk involved in acquiring human food sources (Biquand et al, 1992; Hockings et al, 2009)). Nevertheless, knowledge of primate nutritional requirements is necessary for a more explicit understanding of the drivers behind foraging decisions within human-dominated environments. For example, recent advances in the nutritional ecology of brown bears (*Ursus arctos*) were used to develop a nutritionally explicit predictive framework aimed at informing the drivers behind the consumption of anthropogenic foods by bears (Coogan & Raubenheimer, 2016). This framework showed that bear macronutrient preferences were likely driving “nutrient-specific foraging behaviour” towards anthropogenic foods that allowed the bears to meet their macronutrient intake targets when the availability of natural foods constrained them from doing so (Coogan & Raubenheimer, 2016). Mountain gorilla (*Gorilla beringei*) populations in Virunga and Bwindi National Parks were found to regulate to a similar nutrient intake target despite consuming different wild plant foods (Raubenheimer et al, 2015), as did European badger (*Meles meles*) populations residing in different habitats (Kohl et al, 2015; Remonti et al, 2011). My study was able to provide important insights into chimpanzee macronutrient intake and balancing from wild and cultivated foods within an anthropogenic landscape. However, it is important to determine the extent to which diet selection and cultivar consumption is a result of active behavioural regulation of macronutrient intake, or if it is simply a consequence of the foods available within the environment (Raubenheimer et al, 2012). Particularly, as each of these scenarios would require fundamentally different land-use management and cultivar-foraging mitigation strategies. As such, a key focus for future research is to compare the macronutrient intake of the Bossou chimpanzees with populations experiencing varying degrees of human disturbances and environmental conditions, and with varying reliance on cultivated foods, to fully understand the role macronutrient regulation plays in cultivar foraging decisions.

6.3 CONSERVATION MANAGEMENT RECOMMENDATIONS

The findings of the present study highlight key areas that should be considered in conservation planning for chimpanzees within anthropogenic landscapes. The results of Chapter 2 and Chapter 3 are particularly relevant for land-use management aimed at restoring and/or maintaining areas within and around disturbed landscapes to ensure the long-term survival of viable chimpanzee populations. While the results of Chapter 4 and Chapter 5 have direct implications for chimpanzee reliance on shared resources that could be used to inform the development of cultivar-foraging mitigation strategies. Chapter 4 and Chapter 5 also highlight the need for conservation initiatives to consider the ability of anthropogenic landscapes to meet chimpanzee dietary requirements within a nutritionally explicit framework. The following recommendations are specifically aimed at the conservation management of chimpanzees but may be applicable to other primate species residing in human-dominated environments. For information on current conservation action plans for West African chimpanzees see Kormos et al (2003). For detailed discussion on the impacts of industrial agriculture for ape species across Africa and Asia see Humle (2015). For general recommendations for the management of negative interactions between great apes and people see Hockings & Humle (2009).

It is evident from the results discussed in Chapter 2 that the ecological characteristics of an anthropogenic landscape must be examined across all available habitat types in order to fully determine the habitats and/or specific areas where important chimpanzee resources are found. At the local scale, land-use management planning should include spatial and temporal assessments of chimpanzee resources across the entire matrix of habitat types found within an anthropogenic landscape in order to establish key areas to protect and/or regenerate. Similarly, characterising the ecology of human-dominated environments for chimpanzees across the anthropogenic continuum, along with the land-use practises and economic, social and cultural beliefs of local people, would provide a clearer picture of what defines such landscapes as well as their ability to support viable chimpanzee populations in the long-term. Thus, the results of local-scale ecological assessments should also be used at the regional scale in order to identify key traits of anthropogenic landscapes necessary for sustaining chimpanzee populations and to allow for more informed use of conservation resources.

The findings presented in Chapter 3 on chimpanzee habitat use and risk perception suggest that access to areas of natural habitat, where an abundance of wild resources is coupled with limited human pressures and presence, are necessary for chimpanzee survival within human-dominated environments. Such refuges are likely to be particularly important in highly degraded landscapes, such as areas of industrial agriculture, as has been found for orangutans residing in oil palm plantations (Ancrenaz et al, 2015). Consequently, it is imperative that conservation projects work with stakeholders to ensure future plans for industrial plantations in chimpanzee ranges include designating and protecting areas of natural habitat where important chimpanzee food and nesting resources remain, or can be restored, and where human disturbances and presence are minimised. Such refuge habitats could also potentially act to reduce chimpanzee reliance on agricultural areas, minimising the risk of negative interactions between chimpanzees and people.

Nevertheless, the results of Chapter 4 and Chapter 5 provide nutritional support for the mounting evidence of chimpanzee reliance on oil palm resources within human-dominated environments across West Africa, which must be considered in future plans for oil palm plantations within chimpanzee ranges. Tolerance towards chimpanzees foraging on oil palms differs between sites depending on the economic, social and cultural beliefs of local people (Humle & Matsuzawa, 2004). However, the economic value of commercially grown oil palm in industrial plantations means that foraging on oil palm parts by chimpanzees is likely to lead to high levels of negative interactions with plantation owners (Humle, 2015). As such, chimpanzee reliance on oil palm resources must be assessed in order to fully evaluate the impact of planned oil palm plantations for resident chimpanzee populations. Ideally, strategic land-use planning should be used to avoid large-scale development in known chimpanzee ranges in order to limit the negative impacts of industrial plantations on chimpanzee populations (Humle, 2015). However, if chimpanzee ranges are designated for oil palm concessions, it is essential that the needs of resident chimpanzee populations are included in management plans. For example, education of plantation workers on chimpanzees and how to react when encountering them is necessary for limiting negative interactions and disease transmission. Management plans must also include measures to increase tolerance towards chimpanzee use of oil palms and plantation areas, particularly if access to oil palms is deemed necessary for the survival of resident chimpanzee populations. Furthermore, given that poaching of apes for meat and the pet trade is known to increase in areas of industrial agriculture (Humle, 2015), it is important that retaliatory killings and hunting of chimpanzees is prevented to protect the long-term survival of populations.

Similarly, conservation initiatives need to assess the extent to which shared resources are necessary for the survival of chimpanzees in anthropogenic landscapes. Many chimpanzee populations, and indeed other primate species, in forest-agricultural mosaics rely heavily on crops to supplement their diets. My research shows that crops are an easily digestible high energy food source compared to most wild foods (Chapter 4; McLennan & Ganzhorn, 2017). Furthermore, the Bossou chimpanzees were able to maintain a balanced nutrient intake across seasons by consuming a variety of wild and cultivated foods (Chapter 5). These results provide evidence for the importance of cultivated foods to the diet, and highlight that crops may be integral in allowing chimpanzees to meet their nutritional requirements within disturbed environments. However, chimpanzee use of cultivars and other shared resources is rarely tolerated by farmers and can incur considerable costs for both chimpanzees and people (Hockings & Humle, 2009). As such, it is important that land-use management plans balance cultivar-foraging mitigation strategies with ensuring that chimpanzee populations can continue to meet their nutritional needs from the surrounding environment. Preserving abandoned cultivated species in regenerating habitat and/or using these species for forest enrichment should be considered. Particularly, cultivars that provide chimpanzees with fruit during the fruit scarce season and/or food parts that are highly preferred, such as mango, orange, banana and oil palm (Chapter 3 and Chapter 5). This would not only serve to provide chimpanzees with easily assessable foods that may be necessary for meeting their dietary requirements but could also alleviate the need for chimpanzees to use cultivated fields and plantations. For example, at Bossou mango trees are commonly found in regenerating habitat, including fallow areas and secondary forest (Bryson-Morrison et al, 2016; Hockings et al, 2009), and the chimpanzees feed extensively from these naturalised trees when in fruit and rarely forage from mango trees growing in agricultural areas (Chapter 5; Hockings et al, 2009).

Furthermore, my results suggest that cultivar-foraging mitigation strategies are more likely to be effective if they are developed within a nutritionally explicit framework (Chapter 5; Hill, 2017). Foraging decisions are based on a balance between meeting dietary needs and avoiding risks (Hill, 2016). As such, determining the ability of chimpanzees to meet their nutritional requirements from the surrounding environment is fundamental for unravelling the drivers behind their food related decision making within anthropogenic landscapes (Chapter 5). For example, chimpanzees will be more likely to seek out cultivars and forage in riskier environments, such as areas of high human presence and pressures, if crop consumption is driven by a need to meet specific nutrient requirements. In such scenarios, mitigation techniques aimed at increasing the perceived risks of foraging in agricultural areas or the relocation of crops further from the forest edge, are unlikely to be effective. On the other hand, if foraging decisions are driven more by the availability and/or accessibility of crops within the environment, then the aforementioned mitigation strategies may be effective, particularly if alternative wild foods are available that can fulfil similar dietary needs. As such, conservation projects should work with nutritional ecologists in order to develop more informed cultivar-foraging mitigation and land-use management strategies based on the ability of the surrounding environment to meet chimpanzee nutritional requirements and the drivers behind their decisions to forage on cultivars and other shared resources.

6.4 LESSONS LEARNED AND FINAL REMARKS

Chapter 2 concentrated specifically on determining the availability of chimpanzee food resources across habitat types. Surveys therefore included tree species measuring ≥10cm diameter at breast height (DBH), as this is the widely accepted minimum size that trees generally produce fruits and other reproductive parts consumed by primates (Chapman et al, 1994). However, future work in Bossou, and other degraded environments, should aim to sample all stems, including saplings and stems measuring <10cm DBH, as this would provide invaluable insights into the regenerating capacities of different types of disturbed and forested habitat as well as being more representative of all plant stages that chimpanzees may exploit in their environment. Similarly, mapping all forested and highly disturbed habitat types within the surrounding environment using a handheld GPS would allow for a more detailed examination of landscape changes over time as well as revealing how such changes can influence chimpanzee habitat use and ranging patterns. Such information would be useful for land-use management aimed at conserving or regenerating particular areas or habitats for chimpanzees.

The present study focused on empirically describing the ecology of the landscape for chimpanzees (Chapter 2) in order to provide much needed information necessary for comparing between chimpanzee populations to evaluate the suitability of anthropogenic environments as viable long-term habitat. Furthermore, the results presented in Chapter 3 showed that chimpanzee habitat use within anthropogenic landscapes is influenced not only by the availability of important resources, but also by likely human presence and infrastructure. These findings make it difficult to generalise on the suitability of degraded environments for chimpanzees at different sites. As even if the overall ecology of the landscapes are similar, there is likely to be differences in both human land-use practises and the availability of resources within particular habitat types. This is highlighted in the differing use of riverine forest fragments by chimpanzees at Bossou and Bulindi, Uganda. Bossou chimpanzees generally avoided riverine forest areas, characterised by lower food availability and higher human presence than other forested habitat types (Chapters 2 and 3), while Bulindi chimpanzees rely heavily on food-dense riverine forest fragments (McLennan & Plumptre, 2012). These findings emphasise that future studies should include measures of resource availability and distribution and human land-use practises across all habitat types, as the availability of a particular habitat does not necessarily indicate use by chimpanzees. This is particularly significant for informing projects aimed at maintaining or regenerating habitat deemed to be important for conserving chimpanzees within degraded landscapes.

One of the biggest challenges of working with chimpanzees in anthropogenic landscapes is ensuring a balance between ethical and scientific integrity. For example, researchers are restricted to observing the Bossou chimpanzees for no more than 6 hours per day to minimise disturbance, over-habituation to human presence, and to reduce the risks of disease transmission. Similarly, it important that researchers exercise caution when chimpanzees enter cultivated fields to feed on crops so that their presence does not exacerbate an already sensitive situation. Maintaining good ethical practice is of upmost importance which often requires that compromises be made in research design and data collection procedures. During the present study, collecting the appropriate data for examining the nutritional goals of the chimpanzees was particularly logistically challenging. For example, it is recommended, when possible, to conduct continuous focal observations of the same individual over the course of an entire day (Felton et al, 2009a) as nutrient regulation likely occurs over this time period (de Castro, 2000; Johnson et al, 2013; Robbins et al, 2007). Average daily nutrient intake, as used in the present study and by others constrained by ethical and/or practical difficulties (e.g. Rothman et al, 2008), may underestimate the relative contribution of some macronutrients by not recording all foods consumed in a day (Felton et al, 2009a). Further challenges were faced in ensuring an adequate number of wild and cultivated food samples were collected that represented the bulk of the chimpanzee diet. Firstly, in order to maintain good ethical practise and relations with local villagers, it was necessary to buy crops grown in cultivated fields, such as corn and pineapple, from the village market or obtain these from fields tended by local field assistants. Secondly, the fruits from different fig species were combined as the required sample sizes necessary for conducting nutritional analyses on each species individually could not be collected (approximately 30 g of dry weight). Lastly, it was necessary to use previously reported macronutrient concentrations for leaves eaten by the Bossou chimpanzees in order to ensure enough time and resources were available to analyse an adequate number of wild and cultivated fruit and pith samples. These compromises may have influenced the results of the macronutrient composition of these foods, given that nutrient content can vary over temporal and spatial scales both between and within species (Rothman et al, 2012). Nevertheless, the results presented in this thesis are in line with other reports of the dietary composition of chimpanzees (e.g. Conklin-Brittain et al, 1998; Pokempner, 2009) and nutrient balancing in primates (Felton et al, 2009b; Irwin et al, 2015; Johnston et al, 2013; Johnston et al. 2015; Rothman et al, 2011; Simpson & Raubenheimer, 2012). Despite the challenges posed by anthropogenic landscapes, more research is essential on chimpanzee populations across the anthropogenic continuum. Given that the chimpanzees at Bossou are the only habituated population residing within a long-term field site characterised by high levels of human disturbances, they are uniquely placed for continuing to yield important insights into chimpanzee behaviour, ecology, and nutrition within anthropogenic landscapes.

This study was conducted primarily from the chimpanzee perspective and another critical dimension that would require further investigation is the human perspective of coexistence within anthropogenic landscapes. Human influences on chimpanzee ecology and behaviour were evident throughout this thesis from the resources and habitat types available within the landscape, to chimpanzee use/avoidance of particular habitats for specific activities, and finally in their seasonal foraging strategies and dietary nutrient intakes from wild and cultivated foods. However, the ecologies and behaviours of chimpanzees and humans are inevitably interconnected when they live in close proximity (Fuentes & Hockings, 2010), and it is equally important to understand the cultural, economic, and socioecological perspectives of the people that share space and resources with chimpanzees (Humle & Hill, 2016). Particularly as conservation and management efforts are more likely to succeed if they include strategies for economic, cultural and/or social security for local people along with strategies for protecting chimpanzee populations and their habitats (Lee, 2010). Effective conservation informed by research from both perspectives is required if we are to secure a future of sustainable coexistence for people and chimpanzees.

6.5 REFERENCES

Ancrenaz, M., Oram, F., Ambu, L., Lackman, I., Ahmad, E., Elahan, H., Kler, H., Abram, N.K. and Meijaard, E. (2015). Of Pongo, palms and perceptions: a multidisciplinary assessment of Bornean orang-utans Pongo pygmaeus in an oil palm context, *Oryx* 49: 465-472.

Bessa, J., Sousa, C. and Hockings, K. J. (2015) Feeding ecology of chimpanzees (Pan troglodytes verus) inhabiting a forest-mangrove-savanna-agricultural matrix at Caiquene-Cadique, Cantanhez National Park, Guinea-Bissau, *American Journal of Primatology* 77: 651–665.

Biquand, S., Biquand-Guyot, V., Boug, A. and Gautier, J.P. (1992). The distribution of Papio hamadryas in Saudi Arabia: Ecological correlates and human influence, *International Journal of Primatology* 13: 223-243.

Brncic, T., Amarasekaran, B. and McKenna, A. (2010). Sierra Leone national chimpanzee census. *Tacugama Chimpanzee Sanctuary, Freetown, Sierra Leone.*

Chapman, C.A., Wrangham, R. and Chapman, L.J. (1994). Indices of habitat-wide fruit abundance in tropical forest, *Biotropica* 26: 160-171.

Coogan, S. C. P. and Raubenheimer, D. (2016) Might macronutrient requirements influence grizzly bear–human conflict? Insights from nutritional geometry, *Ecosphere* 7: e01204. 10.1002/ecs2.1204.

Conklin-Brittain, N.L., Knott, C.D. and Wrangham, R.(2006). Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison, in Hohmann, G., Robbins, M.M. and Boesch, C. (eds.) *Feeding Ecology in Apes and Other Primates*. Cambridge: Cambridge University Press: 445–472.

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

Cyr, N., & Romero, L. (2008). Fecal glucocorticoid metabolites of experimentally stressed captive and free-living starlings: implications for conservation research, *General Comparative Endocrinology* 158, 20-28.

de Castro, J.M. (2000) Macronutrient selection in free-feeding humans: evidence for long-term regulation. In Berthoud, H,R. and R.J. Seeley, R.J. (eds) *Neural Control of Macronutrient Selection*, Boca Raton: CRC Press, 43–51.

Felton, A. M., Felton, A., Lindenmayer, D. B. and Foley, W. J. (2009a) Nutritional goals of wild primates, *Functional Ecology* 23: 70–78.

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

Fuentes, A. and Hockings, K. J. (2010) The ethnoprimatological approach in primatology, *American Journal of Primatology*, 72: 841–847.

Hicks, T., Roessingh, P. and Menken, S. (2012). Reactions of Bili-Uele chimpanzees to humans in relation to their distance from roads and villages, *American journal of primatology* 74: 721-733.

Hill, C. M. (1997) Crop-raiding by wild vertebrates: The farmer’s perspective in an agricultural community in western Uganda, *International Journal of Pest Management*, 43: 77–84.

Hill, C. M. (2000) Conflict of interest between people and baboons: crop raiding in Uganda, *International Journal of Primatology* 21: 299-315.

Hill, C. M. (2005). People, crops and primates: a conflict of interests, *Commensalism and conflict: The human-primate* i*nterface. Norman, Oklahoma: American Society of Primatologists*: 40-59.

Hill, C. M. (2017) Primate crop feeding behavior, crop protection and conservation, *International Journal of Primatology* 38: 385-400.

Hill, R. A. (2016). Nonhuman primate approaches to landscapes. In: B. David, & J. Thomas (Eds.) *Handbook of Landscape Archaeology.* (pp. 95-101). New York: Routledge.

Hockings, K.J. (2011). The Crop-Raiders of the Sacred Hill. In: Matsuzawa, T., Humle, T. and Sugiyama, Y. eds. *The Chimpanzees of Bossou and Nimba*. London: Springer, 211–220.

Hockings, K., Anderson, J. and Matsuzawa, T. (2006). Road crossing in chimpanzees: a risky business, *Current Biology* 16: 668-670.

Hockings, K.J., Anderson, J.R. and 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: 636–646.

Hockings., K.J. and. Humle, T. (2009). *Best Practice Guidelines for the Prevention and Mitigation of Conflict between Humans and Great Apes.* Gland, Switzerland: IUCN/SSC Primate Specialist Group.

Hockings, K. and McLennan, M. (2016) Problematic Primate Behaviour in Agricultural Landscapes: Chimpanzees as “Pests” and “Predators, In Waller, M.T. (ed) *Ethnoprimatology: Primate conservation in the 21st century*. Switzerland: Springer, 137-156.

Hockings, K.J., McLennan, M.R., Carvalho, S., Ancrenaz, M., Bobe, R., Byrne, R.W., Dunbar, R.I., Matsuzawa, T., McGrew, W.C., Williamson, E.A. and Wilson, M.L. (2015). Apes in the Anthropocene: flexibility and survival, *Trends in Ecology & Evolution* 30: 215-222.

Humle, T. (2015). Impacts of industrial agriculture on ape ecology. *State of the apes: Industrial agriculture and ape conservation*, Cambridge University Press.

Humle, T. and Hill, C. (2016). People-primate interactions: Implications for primate conservation, in Wich, S.A. and Marshall, A.J (eds) *An Introduction to Primate Conservation.* Oxford: Oxford University Press, 219-240.

Humle, T. and Matsuzawa, T. (2004) Oil Palm Use by Adjacent Communities of Chimpanzees at Bossou and Nimba Mountains, West Africa, *International Journal of Primatology* 25: 551–581.

Irwin, M. T., Raharison, J.-L., Raubenheimer, D. R., Chapman, C. A. and Rothman, J. M. (2015) The Nutritional Geometry of Resource Scarcity: Effects of Lean Seasons and Habitat Disturbance on Nutrient Intakes and Balancing in Wild Sifakas, *PLOS ONE* 10: e0128046.

Isaac, N.J.B. and Cowlishaw, G. (2004) How species respond to multiple extinction threats, *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271: 1135–1141.

Johnson, C. A., Raubenheimer, D., Chapman, C. A., Tombak, K. J., Reid, A. J. and Rothman, J. M. (2015) Macronutrient balancing affects patch departure by guerezas (*Colobus guereza*), *American Journal of Primatology*: doi:10.1002/ajp.22495.

Johnson, C. A., Raubenheimer, D., Rothman, J. M., Clarke, D. and Swedell, L. (2013) 30 Days in the Life: Daily Nutrient Balancing in a Wild Chacma Baboon, *PloS one* 8: e70383.

Kohl, K.D., Coogan, S.C. P. and Raubenheimer. D. (2015). Do wild carnivores forage for prey or nutrients? *BioEssays* 37:701–709.

Kormos, R., Boesch, C., Bakarr, M.I. and Butynski, T.M. (2003). *West African chimpanzees: status survey and conservation action plan.* IUCN/SSC Primate Specialist Group. Gland, Switzerland and Cambridge, UK: IUCN.

Lambert, J. E. and Rothman, J. M. (2015) Fallback Foods, Optimal Diets, and Nutritional Targets: Primate Responses to Varying Food Availability and Quality, *Annual Review of Anthropology* 44: 493–512.

Leciak, E., Hladik, A. and Hladik, C.M. (2005). The oil palm (Elaeis guineensis) and the cores of high biodiversity in gallery forests of Guinea in relation to human and chimpanzees commensalism, *Revue D Ecologie-La Terre Et La Vie*: 179-184.

Lee, P. C. (2010) Sharing Space: Can ethnoprimatology contribute to the survival of nonhuman primates in human-dominated globalized landscapes?, *American Journal of Primatology* 72: 925–931.

McLennan, M. and Ganzhorn, J. (2017). Nutritional Characteristics of Wild and Cultivated Foods for Chimpanzees (Pan troglodytes) in Agricultural Landscapes, *International Journal of Primatology*: doi: 10.1007/s10764-016-9940-y.

McLennan, M.R., and Plumptre, A.J. (2012). Protected apes, unprotected forest: composition, structure and diversity of riverine forest fragments and their conservation value in Uganda, *Tropical Conservation Science* 5 : 79-103.

Muyambi, F. (2005). The impact of tourism on the behaviour of mountain gorillas. *Gorilla Journal* 30: 14-15.

Nelleman, C. and Newton, A. (2002) *Great Apes — The Road Ahead. An Analysis of Great*

Ape Habitat, using GLOBIO Methodology, United Nations Environment Programme.

N’guessan, A. K., Ortmann, S. and Boesch, C. (2009) Daily energy balance and protein gain among Pan troglodytes verus in the Taï National Park, Côte d’Ivoire, *International Journal of Primatology* 30: 481–496.

Pokempner, A. A. (2009) *Fission -fusion and foraging: Sex differences in the behavioral ecology of chimpanzees (Pan troglodytes schweinfurthii)*.PhD thesis, Stony Brook University.

Raubenheimer, D., Machovsky-Capuska, G. E., Chapman, C. A. and Rothman, J. M. (2015) Geometry of nutrition in field studies: an illustration using wild primates, *Oecologia* 177: 223–234.

Raubenheimer, D. and Simpson, S. J. (2006) The challenge of supplementary feeding: can geometric analysis help save the kakapo? *Notornis* 53, 100–111.

Raubenheimer, D., Simpson, S. J. and Tait, A. H. (2012) Match and mismatch: conservation physiology, nutritional ecology and the timescales of biological adaptation, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367: 1628–1646.

Remonti, L., Balestrieri, A. and Prigioni. C. (2011). Percentage of protein, lipids, and carbohydrates in the diet of badger (*Meles meles*) populations across Europe. *Ecological Research* 26: 487–495.

Righini, N. (2017) Recent advances in primate nutritional ecology, *American Journal of Primatology*: *doi:* 10.1002/ajp.22634.

Robbins, C.T., Fortin, J.K., Rode, K.D., Farley, S.D., Shipley, L.A. and Felicetti, L.A. (2007) Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore, *Oikos* 116: 1675–1682.

Rothman, J. M., Chapman, C. A. and 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. and Pell, A. N. (2008) Nutritional quality of gorilla diets: consequences of age, sex, and season, *Oecologia* 155: 111–122.

Rothman, J. M., Raubenheimer, D. and Chapman, C. A. (2011) Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein, *Biology Letters*: DOI: 10.1098/rsbl.2011.0321.

Simpson, S. J. and Raubenheimer. D. (2012) *The nature of nutrition: a unifying framework from animal adaptation to human obesity*. Princeton University Press.

Sousa, J., Barata, A. V, Sousa, C., Casanova, C. C. N. and Vicente, L. (2011) Chimpanzee oil-palm use in southern Cantanhez National Park, Guinea-Bissau, *American Journal of Primatology*, 73: 485–497.

Warren, Y., Buba, B. and Ross, C. (2007) Patterns of crop-raiding by wild and domestic animals near Gashaka Gumti National Park, Nigeria, *International Journal of Pest Management* 53: 207–216.

Wich, S.A., Garcia-Ulloa, J., Kuhl, H.S., Humle, T. and Lee, J.S.H. (2014). Will oil palm's homecoming spell doom for Africa's great apes? *Current Biology* 24: 1659–1663.

Wingfield, J., & Romero, L. (2010). Adrenocortical responses to stress and their modulation in free-living vertebrates. *Comprehensive Physiology, Supplement 23: Handbook of Physiology, the Endocrine System, Coping with the Environment: Neural and Endocrine Mechanisms*: 211-234.