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INFLUENCE OF FRUIT SEASONALITY ON MACRONUTRIENT AND ENERGY INTAKE AND ITS SIGNIFICANCE ON REPRODUCTION IN FEMALE CHIMPANZEES (*PAN TROGLODYTES*)

Female chimpanzee in estrous feeding on Ficus mucuso fruits

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DEDICATION

To my family

Thank you for your love and support

DECLARATION

I hereby declare that the work described is my own work and has never been submitted to Makerere University or any other institution for any award.

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ACRONYMS

THV: Terrestrial herbaceous vegetation

TNC: Total non-structural carbohydrates

WSC: Water soluble carbohydrates

AP: Available protein

NPE: Non protein energy

NDF: Neutral detergent fibre

ADF: Acid detergent fibre

GF: Geometry framework of nutrition

DBH: Diameter at breast height

FAI: Fruit availability index

ADCP: Acid detergent insoluble crude protein

ABSTRACT

Human population increases and an expanding agricultural frontier are driving tropical deforestation. As a result some of the indigenous tree species which serve as primate foods are likely to become rare or even extinct from the wild. A better understanding of the nutritional composition of different primate foods and how primate species cope with the changes in diet quality due to fluctuating food resources is critical for conservation efforts. Previous studies indicated that Kibale chimpanzees prefer high-quality drupe fruits and the timing of reproductive events i.e estrous, conceptions and births is often associated with availability of drupes. It has thus been commonly assumed that consumption of drupe fruits leads to increased energy intake which favours reproduction in female chimpanzees. Against this background I focused on the female chimpanzees (*Pan troglodytes schweinfurthii*) of Kanyawara community in Kibale National Park, and: 1) examined whether dietary variation relates to macronutrient and energy intake variation; 2) applied the principles of nutritional geometry to examine the nutritional strategy of female chimpanzees; and 3) examined whether macronutrient intake variation relates to the timing of reproductive events in female chimpanzees. Fruit seasonality resulted into variations in macronutrient intake while energy intake was relatively stable. Female chimpanzees switched their diet and adjusted their behavior in order to maximize intake of high-quality nutrients, minimize foraging costs and acquire a nutritionally balanced diet. Similar to frugivorous spider monkeys (*Ateles* sp.) and humans, female chimpanzees tightly regulated protein intake while maximizing carbohydrate intake. The results also indicated that there was no predictable seasonality in the timing of reproductive events or in macronutrient or energy intake. While the patterns of timing of reproductive events were not consistent with the patterns in the intake of high-quality macronutrients, there was a positive relationship between energy intake and estrous and births. Additionally the findings suggest that minimum temperature has an effect on the estrous and conceptions. Since increase in minimum temperature negatively affects fruiting in tropical forests, there is a likelihood that female chimpanzees are using minimum temperature as a cue for predicting fruit availability. The increased consumption of carbohydrates and reduction of foraging costs during drupe months might allow female chimpanzees to reach a positive energy balance thereby resuming cycling when drupes are abundant. This study, supports the increasing recognition of nutrient balancing as a foraging strategy used by female chimpanzees and the relevancy of using feeding rates to estimate intake in wild primates. Furthermore, the study provides insights on the relevancy of the different food types in chimpanzee habitats and this information can be used to better manage chimpanzee ecosystems and captive chimpanzee populations.

GLOSSARY OF TERMS

Fallback foods are foods of relatively poor nutritional quality and high abundance that are eaten when preferred foods are unavailable. For chimpanzees these foods are mainly fig fruits or terrestrial herbaceous vegetation which includes young leaves, pith, seeds, flowers and woody plant parts.

Feeding bout length is the total amount of time that the focal individual fed on a food item in a feeding patch uninterrupted (without stopping to groom, rest or indulge in any other activity) for more than five minutes.

Feeding patch is as an aggregation of food items that allowed uninterrupted feeding or foraging movements by individuals or parties. Generally, this was a single tree or large sapling, but it also included multiple adjacent stems of terrestrial vegetation and, for species growing in dense groves (e.g., *Uvariopsis congensis* or *Teclea nobilis*), multiple adjacent trees when their crowns overlapped sufficiently to allow direct tree-to-tree travel.

Foraging behavior includes all the methods by which an organism acquires and utilizes sources of energy and nutrients. This includes the location and consumption of resources, as well as their retrieval and storage, within the context of the larger community.

Foraging strategy includes all the behaviors and decisions made by the animal to acquire food which will help it achieve its intake target.

Nutritional strategy includes a set of behaviours and decisions that show how the animal balances its nutrient intake.

Reproductive ecology is the study of relationships among an animal's procreative decisions, fecundity, fertility and the biotic and abiotic conditions in their environment.

Aseasonal breeders are those animals whose infant births are not limited or concentrated to a particular season.

Phenology is the study of periodic plant life cycle events and how these are influenced by seasonal and interannual variations in biotic (e.g. pollination, predation) and abiotic factors (e.g. climate, irradiance, elevation).

High-quality diets are those that are comprised of foods that are rich in easily digestible energy (lipids and simple sugars) and protein.

Low-quality diets are comprised of foods that are poor in easily digestible energy and protein but rich in dietary fibre.

Intake target is a point in the nutrient space which represents a combination of nutrients that an animal needs to consume in order to reach its optimal state (its nutritional optimum). This intake target (nutrient requirements) is not static but changes with time.

Rule of compromise is a nutritional decision made by the animal when the foods available in its environment are nutritionally imbalanced. The animal is normally forced to eat too little of some nutrients and/or too much of others.

CHAPTER ONE: GENERAL INTRODUCTION

1.1 Background

Animals require energy to maintain life, stimulate tissue maintenance, growth and reproduction and this energy is obtained through diet. In most mammals the main substrates of energy include carbohydrates, proteins, and lipids. Nutrient intake is affected by the type of foods available (Kinzey & Norconk, 1990; Milton, 2006)and the availability of preferred foods in time and space (Knott, 1998; Masi et al., 2015; Rothman, Dierenfeld, Hintz, & Pell, 2008). Regardless of the type of foods available, the acquisition of macronutrients is influenced by the morphology and behavior of the animal in question (Lambert, 1998; National Research Council, 2003). Nutritional intake may also be affected by other intrinsic factors such as age, sex, reproductive state, or social factors such as rank and resource competition (National Research Council, 2003; Oftedal, 1991). The differential and combined effect of each of these factors influences diet and contributes to a large amount of inter-species and inter-individual variation in energetics, and ultimately, reproductive performance (e.g., baboons: Muruthi, Altmann, & Altmann, 1991).

The procurement and utilization of macronutrients from the environment by different organisms is examined through nutritional ecology (Cork & Foley, 1991; Raubenheimer, Simpson, & Mayntz, 2009). Nutritional ecology aims to understand the relationships between animal habitat use, food choice, diet composition and nutrition. Most nutritional ecology studies focus heavily on relationships between animal habitat use and diet composition (Brockman & van Schaik, 2005). Few studies have endeavored to assess how fluctuations in fruit seasonality relate to macronutrient and energy intake and the implications on the consumer. Recent advances in nutritional ecology appreciate that nutrition is multidimensional and complex and that behavioral responses in animals are geared towards balancing and regulating the intake of multiple nutrients simultaneously (Raubenheimer, Machovsky-Capuska, Chapman, & Rothman, 2015). The implications of variations in foraging responses and nutrient intake on the consumers' reproductive behavior, growth and other physiological aspects can be understood through nutritional ecology. Nutritional ecology studies are therefore important for addressing questions related to food choice, life history and reproductive success of individuals or primate communities.

Food in its various forms is the only source of energy for animals. Regardless of whether an animal is largely frugivorous, folivorous or omnivorous, individuals make choices on what to include in their diet in order to acquire a full set of nutrients required by most mammals (Oftedal,

1991). These choices are influenced by the type of food available, i.e. nutritional, chemical and structural qualities or due to ecological availability of the food (Lambert, 2011; Lambert, Chapman, Wrangham, & Conklin-Brittain, 2004; Milton, 1999). The choices made influence the individual's nutritional state and ultimately its health and reproductive fitness (Altmann, 1998).

Coupled with food choices, mammals modify their behavior in terms of time spent searching for food, the rate of food intake, or the compounds to avoid in order to maximize energy intake and minimize constraints of energy intake. Such foraging strategies affect their energy balance from which female mammals may choose whether to resume cycling or delay reproduction depending on their energetic condition (Ellison, Panter-Brick, Lipson, & O'Rourke, 1993; Knott, 2001, 2005). Reproduction in female mammals is energetically costly due to the high energy demands of gestation and lactation (Gittleman & Thompson, 1988; Wade & Schneider, 1992). Therefore, to minimize the high costs of reproduction, female mammals either time their reproductive seasons to coincide with the periods of high-quality food abundance (income breeders, such as in Hanuman langurs (*Presbytis entellus)* (Koenig, Borries, Chalise, & Winkler, 1997), and capuchins (*Cebus capucinus*) (Carnegie, Fedigan, & Melin, 2011) or invest in their energetic condition and initiate breeding once they have reached positive energy balance (such as apes: (Brockman & van Schaik, 2005; Knott, 2005). In female mammals, energy balance plays a significant role in that it influences ovulation (Ellison & Valeggia, 2003; Knott, 2001), and thus provides an important clue to understanding the relationship between the feeding strategy and reproductive success of females.

1.2 Drivers of food selection in primates

Four major theories have been advanced to explain what drives food selection in different primate species in the face of fluctuating food availability: (i) energy maximization (Schoener, 1971); (ii) nitrogen/protein maximization (Mattson, 1980; Milton, 1979); (iii) avoidance and/or regulation of plant secondary metabolites and fibre (Freeland & Janzen, 1974); and (iv) nutrient balancing (Raubenheimer & Simpson, 2004; Robbins et al., 2007). The first three theories are based on the premise that food choice in primates is geared towards maximization or minimization of a single nutrient, which is a unidimensional approach (optimal foraging theory).

However, given the complexity of primate diets coupled with the complexity of consumers' responses to changes in the diets, it is difficult to understand what drives food choice of different primate species using a unidimensional approach. Therefore, through recent advances in nutritional ecology primatologists have adopted a multidimensional approach (nutrient balancing mode) to explain the food choices made by primates in space and time. The geometric

framework of nutrition (GF) is one such multidimensional approach which seeks to understand the interactive effects of nutrients on animal food choices. Using the GF two or more variables such as food components are represented and the amount of ingested nutrients which form a geometric space within which nutritional targets and outcomes can be quantified.

Through the GF, scientists have been able to better understand the drivers of food choice for various animals (insects: Behmer, Raubenheimer, & Simpson, 2001; Jensen et al., 2012; fish: Raubenheimer, Zemke-White, Phillips, & Clements, 2005; birds: Köhler, Raubenheimer, & Nicolson, 2012; humans: Simpson, Batley, & Raubenheimer, 2003; primates: Felton et al., 2009; Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2015; Rothman, Raubenheimer, & Chapman, 2011). In general, these studies show that, when suitable food combinations are available, animals select a diet that provides a specifically targeted amount and balance of macronutrients (especially protein, lipids and carbohydrates), termed as "an intake target," and that the selected blend optimizes outcomes associated with fitness, for example growth and fecundity (e.g. Jensen et al., 2012; Simpson, Sibly, Lee, Behmer, & Raubenheimer, 2004). In many ecological circumstances, however, combinations of foods that enable animals to achieve their intake target are not available. In such cases, the animal is forced into a trade-off between over-eating some and/or under-eating other nutrients (Raubenheimer et al., 2009). The nutritional regulatory strategy that the animal adopts to deal with this trade-off is termed a "rule of compromise."

The GF has so far been applied to a few primate species to determine their intake targets and rule of compromise. For example, it was revealed that frugivorous spider monkeys (*Ateles chamek*) prioritize protein (Felton, Felton, Raubenheimer, et al., 2009; Felton, Felton, Wood, et al., 2009) while folivorous mountain gorillas (*Gorilla beringei*) prioritize non-protein energy (NPE) (Rothman et al., 2011). On the other hand folivorous diademed sifakas (*Propithecus diadema*) did not maximize or prioritize any particular nutrient (Irwin et al., 2015). Information from these studies reveal that food choice is not always driven by energy content in frugivorous primates or by protein content in folivorous primates as commonly assumed. Since female chimpanzees and spider monkeys are both frugivorous and have comparable responses to fruit-scarce seasons, it was hypothesized that chimpanzees would have a similar nutritional strategy like that of spider monkeys.

Frugivorous chimpanzees and spider monkeys share a lot in common in that they both have fission-fusion dynamics and adjust their social structure depending on food conditions (Asensio, Aureli, Schaffner, & Korstjens, 2008; Chapman, 1988; Wrangham et al., 1996). They are both

considered as ripe fruit specialists because they spend >70% of their foraging time consuming ripe fruit and figs account for the highest percentage of ripe fruit intake (Basabose, 2004; Chapman, 1988; Conklin-Brittain, Wrangham, & Hunt, 1998; Uwimbabazi et al., 2019; Wallace, 2005). Both chimpanzees and spider monkeys select large volumes of fruit that are rich in lipids and carbohydrates (Conklin-Brittain, et al., 1998; Felton, Felton, Wood, et al., 2009). While chimpanzees often subsist on young leaves, flowers and other herbaceous vegetation irrespective of the fruit-season (Uwimbabazi et al., 2019; Watts, Potts, Lwanga, & Mitani, 2012b), spider monkeys temporarily switch to young leaves, flowers or unripe fruit when ripe fruit is scarce (Felton, Felton, Wood, & Lindenmayer, 2008; Wallace, 2005). Chimpanzees and spider monkeys tend to respond similarly to fruit-scarce periods, such as feeding in smaller parties (Asensio et al., 2008; Basabose, 2004; Doran, 1997; Shimooka, 2003), increasing their dietary breadth and spending more time feeding on fallback foods (Uwimbabazi et al., 2019; Wallace, 2005; Watts, Potts, Lwanga, & Mitani, 2012a). Ripe figs are important fallback foods for both chimpanzees and spider monkeys (Conklin-Brittain & Wrangham, 1994; Felton et al., 2008; Wrangham et al., 1993).

To this end, this study used GF to determine the intake target and rule of compromise of female chimpanzees. The information gleaned from geometric analyses is likely to provide important implications for the field of primate nutritional ecology as well as for forest management, primate conservation and evolution theory.

1.3 Nutrition and reproduction

The relevance of nutrition to reproduction has been demonstrated in species from every mammalian order including primates (Wade, Schneider, & Li, 1996). Large amounts of energy are required for successful pregnancy and lactation (Gittleman & Thompson, 1988). Intake of particular nutrients, especially protein and energy balance is known to affect female reproductive success and fitness such as in vervet monkeys (*Chlorocebus pygerythrus*) (Lee, 1987), savannah baboons (*Papio cynocephalus*) (Altmann & Alberts, 2005; Altmann, 1998, 2006) and chimpanzees (Emery Thompson, 2013; Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007). For example, in Hanuman langurs (*Presbytis entellus*), females were likely to conceive if their nutritional status was high (Koenig et al., 1997). Accordingly, reproduction in most primates is said to be positively associated with positive energy balance (Emery Thompson, 2013; Knott, 2001, 2005).

The energetic costs of reproduction are mainly high in female mammals due to the high energy demands of both gestation and lactation (e.g., red deer: Clutton-Brock, Albon, & Guinness,

1989). Estimations of energy requirements show that there is a 20-30% increase in calories consumed by female mammals during gestation and a 66% -188% increase during lactation (Clutton-Brock et al., 1989; Gittleman & Thompson, 1988). Therefore, it's no wonder that reproductive events in most primates are associated with their diet quality (review by Brockman & van Schaik (2005). Reproductive hormones are influenced by the nutritional state and, thus, the onset of the ovarian cycle, and the probability of conception partly depends on nutrition (Bercovitch & Strum, 1993). Therefore, in order to understand the patterns in reproductive events observed in most primate species, it is important to explore the quality and quantity of nutrients provided by the different food types available in time and space.

1.4 Chimpanzee ecology

Chimpanzees (*Pan troglodytes schweinfurthii*) are mainly found in varying types of African tropical forests including lowland and submontane tropical forests, forest galleries as well as savannah woodlands (Gombe: Goodall, 1986; Kibale: Ghiglieri, 1984; Mahale: Nishida, 1990; Budongo: Reynolds, 2005; Kahuzi-Biega: Basabose, 2002; Bulindi: McLennan, 2013; Bwindi: Stanford & Nkurunungi, 2003; Kibale: Wrangham et al., 1996).

As social animals, chimpanzees live in fusion-fission systems whereby temporary subgroupings called parties come together and separate throughout the day. These parties vary in size, in relation to the abundance and distribution of the food supply and the presence of estrous females (who serve as a magnet for males (Goodall, 1986). The flexibility of fusion-fission societies enables chimpanzees to abate competition for food and other resources such as nesting sites.

The diet of chimpanzees is comprised of a wide variety of food items including several plant and animal items. Their ability to utilise food items from different vertical strata (high, mid, low canopy and ground level) with different phenological patterns allows them to occupy a broad range of habitats. Their dietary composition is closely related to the habitat and varies from one community to the next. For example, the diet of Ngogo and Kanyawara chimpanzee communities which are found in the same forest but 10 km apart is found to be importantly different as a result of differences in plant composition (Potts, 2011). The dietary composition of chimpanzees also varies over short and long time periods, even within the same habitat, due to variation in production of foods such as fruits and young leaves (Basabose, 2002; Doran, 1997; Tutin, Ham, White, & Harrison, 1997). Despite the differences in diet composition, chimpanzees in all habitat types are found to be ripe fruit specialists (Newton-Fisher, 1999; Stanford & Nkurunungi, 2003; Tutin et al., 1991; Watts et al., 2012a; Wrangham et al., 1996).

Due to the temporal and spatial variations in food availability, the proportion of fruit and other food items is found to vary (Harrison & Marshall, 2011; Watts et al., 2012b; Wrangham et al., 1996). This variation has implications for the nutritional state, behavioral and reproductive ecology of chimpanzees. Consequently, chimpanzees adjust their activity patterns depending on type of foods available seasonally and individual nutrient requirements (Tutin et al., 1997; Wrangham et al., 1996). Furthermore, evidence from previous shows that fluctuations in quantity and quality of foods affect nutrient intake in chimpanzees (Conklin-Brittain, et al., 1998; Wrangham, Conklin-Brittain, & Hunt, 1998). Relatedly, the nutrient content of different food items is partly attributed to their positioning of different food items along the vertical strata (Houle, Conklin-Brittain, & Wrangham, 2014). For example, upper-crown sites produce higher density and quality of food than lower-crown sites of the same tree (Houle et al., 2014).

As is the case for most primates, the reproduction in chimpanzees is largely influenced by diet quality (Anderson, Nordheim, & Boesch, 2006; Emery Thompson & Wrangham, 2008; Wallis, 1995). Although, chimpanzees are aseasonal breeders, giving birth all year round, evidence from previous studies seems to suggest that some of the reproductive events are constrained by diet quality. Evidence from different chimpanzee communities shows that increased rates of conceptions and maximal swellings are associated with availability of preferred high-quality foods (Anderson et al., 2006; Emery Thompson & Wrangham, 2008; Janette Wallis, 1995). These findings suggest that reproduction in female chimpanzees might be influenced by energy or macronutrient intake. This suggestion is explored in this study.

1.4.1 Why is it important to study the nutritional ecology of chimpanzees

The global chimpanzee population has significantly reduced from 1 million to 300,000 chimpanzees in the past 20 to 30 years and they continue to be threatened by habitat destruction and poaching (Plumptre et al., 2016).

In Uganda, an estimated population of about 5000 chimpanzees live in forest habitats, mostly in protected areas (Plumptre, Cox, & Mugume, 2003). The chimpanzee population in Uganda, as in many parts of Africa, is threatened by anthropogenic disturbances such as forest fragmentation, habitat loss and forest degradation (McLennan, 2008; Plumptre et al., 2003). Even in protected sites, illegal activities including agricultural encroachment, illegal timber harvesting and hunting pose a major threat to chimpanzees (Plumptre et al., 2016). Accordingly, the increased rate of deforestation in Uganda (the highest in East Africa; 1.9% per annum), may result not only in habitat loss but also in the loss of important plant species that provide vital nutrients for the survival of chimpanzees, thus affecting their health, reproduction and viability (Obua, Agea, &

Ogwal, 2010; Plumptre, 2002). Hence, as much as chimpanzees need forests to survive, forests need chimpanzees. Given this mutual relationship, it is important to understand the interactions between chimpanzees and trees in terms of the foods and nutrients that trees provide. This will inform the conservation and management of wild chimpanzees better.

1.5 Problem statement

In order to understand how primates choose and acquire food to satisfy their nutritional requirements it is important to use proper methods to estimate food and nutrient intake. Most studies have used time spent feeding to estimate food and/or energy intake. Such studies assume that the intake rate and processing time for all foods is the same. In practice however, food items vary in weight, in the speed they are eaten, and in how much energy or nutrients they contain (Nakagawa, 2008, 2009; Schülke, Chalise, & Koenig, 2006). Thus, time spent feeding underestimates the weight of fruit consumed, and overestimates the weight of foliage consumed (Aristizabal, Rothman, García-Fería, & Serio-Silva, 2017; Chivers, 1998; Kurland & Gaulin, 1987).

While there have been attempts to estimate nutrient intake using feeding rates for Kanyawara chimpanzees, previous studies did not categorise feeding rates according to sex (Conklin-Brittain, Knott, & Wrangham, 2006; Wrangham et al., 1993), yet feeding rate is known to be dependent on body mass in addition to other physiology and social factors (Nakagawa, 2008). A few studies that have related diet and reproduction used time spent feeding to estimate food intake and diet quality (Emery Thompson et al., 2007; Emery Thompson & Wrangham, 2008). Yet time spent feeding is said to overestimate intake for foods which take longer to be digested and underestimate intake of foods which are digested faster (Nakagawa, 2009). Hence, the food intake estimates in these studies may be incomplete and inconclusive. Furthermore, despite the fact that diet-quality has been associated with rates of reproductive events at Kanyawara (Emery Thompson & Wrangham, 2008) and other chimpanzee sites such as Gombe (Pusey, 1997; Wallis, 1997) and Tai (Anderson et al., 2006), no attempts have been made to estimate if indeed energy or macronutrient intake as a result of high-quality diets is responsible for the rates of reproductive events observed. Additionally, much as it is noted that that chimpanzees adjust their foraging behavior and switch diets during drupe-scarce periods, the rationale behind these adjustments has not been explored as is the case for other primates such as spider monkeys, gorillas, guerezas and sifakas (Felton, Felton, Raubenheimer, et al., 2009; Felton, Felton, Wood, et al., 2009; Irwin et al., 2015; Johnson et al., 2017; Rothman et al., 2011).

1.6 Objectives

1.6.1 General objective

This study sought to understand how female chimpanzees nutritionally cope with fluctuations in food resources and how this relates to the timing of reproductive events in the Kanyawara community of Kibale National Park in Uganda.

1.6.2 Specific objectives and hypotheses

Objective 1: To examine the effect of fruit-seasonality on macronutrient and metabolisable energy intake by female chimpanzees.

Hypothesis

> H_0: Daily macronutrient and energy intake by female chimpanzees is the same across fruit-seasons.

Objective 2: To determine the nutritional strategy used by female chimpanzees to regulate energy and macronutrient intake using a multidimensional approach (GFN).

Hypothesis

> H_0: The nutritional strategy of female chimpanzees is similar to that of frugivorous spider monkeys due to their similarity in feeding behavior and responses to fruit-scarce periods.

Objective 3: To determine whether variations in energy and macronutrient intake were associated with the timing of maximal sexual-swellings, conceptions and births in female chimpanzees.

> H_0: The frequency of reproductive events is not associated with variations in energy and macronutrient intake.

1.7 Justification

A deeper understanding of a primate's nutrition and the related consequences is vital for effective conservation of wild populations. The population of chimpanzees in the wild has declined from 1 million to about 300,000 individuals (Plumptre et al., 2016). This decline is largely attributed to habitat degradation and loss which is associated with decline in food resources. Food is one of the most important biotic factors limiting population size, hence an understanding of the direct and causal relationships among food resources availability, diet and nutrition is important for conservation of primates in-situ and ex-situ.

In order to understand how fruit-seasonality impacts nutrient intake, it is important to use a weight based approach to estimate intake since different food items have different feeding rates. Relatedly, using continuous focal follows instead of scan observations is a better approach to determine daily intakes of individual animals (Gilby, Pokempner, & Wrangham, 2010). In this study, the relationship between fruit-availability, diet and nutrient intake is explored using nutritional geometry as has been used for other primate species (gorillas: Rothman, Raubenheimer, & Chapman, 2011; sifakas: Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2015; colobus monkeys: Johnson et al., 2017; and blue monkeys: Takahashi, Rothman, Raubenheimer, & Cords, 2019). This information adds to a growing literature using geometric analyses to describe the foraging strategy of different primate species. This study provides insights on how female chimpanzees cope with nutritional shortages arising from fluctuation of fruit resources and how this relates to their reproductive strategy. The findings of this study can be used by conservation managers on how to manage chimpanzees in less disturbed and degraded forest ecosystems as well as managing chimpanzees in captivity.

1.8 Conceptual framework

An overview of the functional linkages among food availability, food acquisition and energy intake and the implications for the reproductive ecology of female chimpanzees is displayed in Figure 1.1.

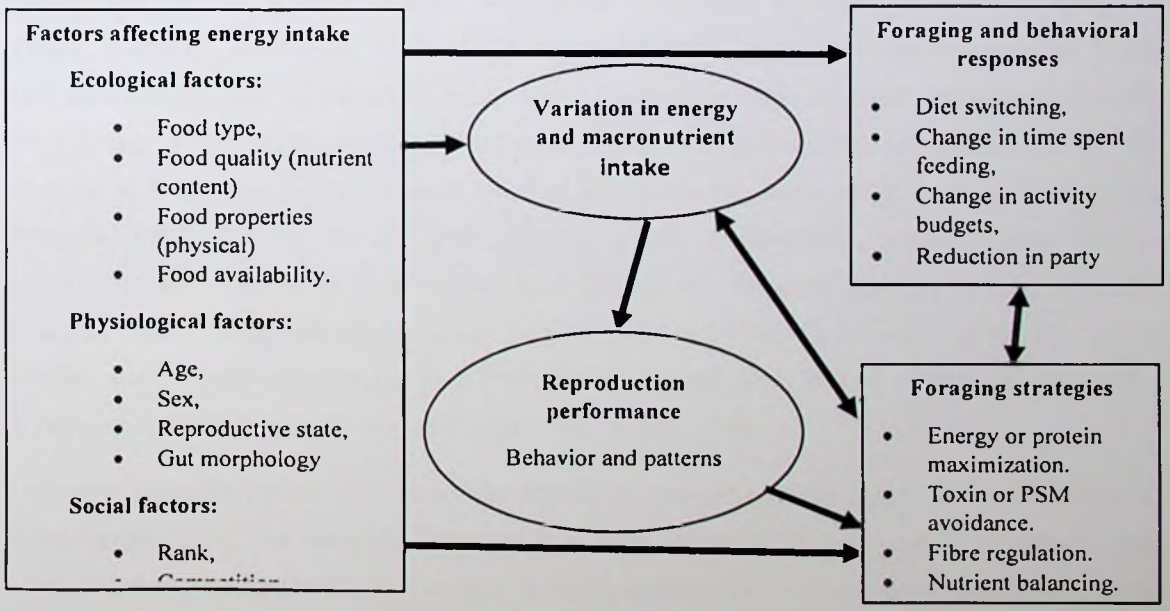

Figure 1-1: Conceptual framework showing the associations among factors that influence energy intake, and foraging responses and strategies and reproductive performance of female primates.

Given the chance, primates and all other animals are expected to consume an optimal diet, but they are often constrained by ecological conditions. Chimpanzee habitats are comprised of different food items including ripe fruit, young leaves and pith, whose nutrient makeup varies and might change depending on the development stage (Conklin-Brittain, et al., 1998; Wrangham et al., 1998). The distribution and availability of these foods varies spatially and temporally (Anderson, Nordheim, Boesch, Moermond, & Marchant, 2002; Furuichi, Hashimoto, & Tashiro, 2001; Tutin & Fernandez, 1993; Yamagiwa & Basabose, 2006). Therefore, chimpanzees have to make daily decisions in order to acquire the right nutrients in sufficient amounts from the complex diet, these decisions entail their foraging strategy. Besides optimizing or regulating or balancing of nutrients, the foraging strategy is also informed by behavioral changes as the food environment changes.

The foraging strategy of any animal is often influenced by different factors which may be extrinsic or intrinsic. Extrinsic factors include ecological factors such as food availability, food type, food quality (chemical and mechanical properties); and social factors such as rank and competition for food resources. Intrinsic factors are mainly physiological such as age, sex and reproductive state which drive the individual's nutrient requirements.

Variations in food availability follow the diverse phenological patterns among plant individuals, species and communities (Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999; van Schaik, Terborgh, & Wright, 1993). Physical and chemical characteristics of available foods; such as hardness, size and shape (which influence handling time of food), nutritional content, gross energy, digestibility of the food (content of digestibility reducing substances, e.g. simple phenols, hydrolysable and condensed tannins) also form the basis of food choice (Kinzey & Norconk, 1990; Lambert et al., 2004; Milton, 1999). Furthermore, social factors such as competition and rank have been shown to influence the foraging strategy in primates. For example, high ranking individuals in any primate group are likely to consume or increase intake of high-quality foods compared to their low-ranking counterparts (Janson, 1988; Johnson, Malik, & Berman, 1991; Murray, Eberly, & Pusey, 2006; Vogel, 2005).

Relatedly, primates adjust their behavior in order to compensate for a poor nutrition diet or to avoid competition. For example, chimpanzees may adjust their party sizes to reduce food competition especially during fruit-scarce periods, increase or decrease time spent feeding and travelling, switch to keystone resources and fall back foods (e.g. figs and foliage) and increase in diet composition (Doran, 1997; Moscovice et al., 2007; Newton-Fisher, Reynolds, & Plumptre, 2000; Tutin et al., 1997).

Ultimately, adjustments of behavior and foraging strategy are meant to help the animal meet their "intake target" and the outcomes are associated with fitness, such as reproductive performance (Emery Thompson, 2013; Knott, Emery Thompson, Stumpf, & McIntyre, 2010; Potts, 2013).

1.9 Thesis structure

This thesis has seven chapters.

Chapter One is the general introduction which introduces the concept of nutritional ecology in primates and chimpanzee ecology. The chapter also presents the research problem, objectives, justification and the conceptual framework.

Chapter Two presents an overview of the establishment of this study by reviewing the empirical and theoretical literature.

Chapter Three introduces the study area, study subjects and general methods used in this research.

In Chapter Four data on feeding rates, nutrient content and time spent feeding on different chimpanzee foods is used to compute daily food, macronutrient and energy intake. From the phenology data, fruit availability index for each month was computed and the months were categorized as either drupe or fig-months. It was hypothesized that fruit-seasonality would lead to changes in diet-quality which would in turn lead to variations in macronutrient and energy intake.

In Chapter Five nutritional geometry framework (GF) is used to determine the nutritional strategy of female chimpanzees. The nutritional strategy of female chimpanzees was predicted to be protein prioritization just like that of spider monkeys which are frugivorous and behave similarly to female chimpanzees when fruit is scarce.

Chapter Six builds uses a long term data set to ascertain if there are patterns in macronutrient and energy intake and if these relate to the timing of reproductive events in female chimpanzees. Circular statistics was used to determine if reproductive events are distributed in a predictable manner. In this chapter, it was hypothesized that energy intake would be positively related to the timing of reproductive events since previous studies have shown that reproductive events are concentrated in periods when preferred ripe fruit are abundant.

Chapter Seven presents the general discussion and conclusion of results from Chapters Four, Five and Six in the light of previous studies. Also included in this chapter is a brief description of implications of the results, lessons learnt from the study and recommendations drawn from this study.

Manuscript based on Chapters Four has been published in the African Journal of Ecology and while that based on Chapter Five is yet to be submitted to the American Journal of Primatology.

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CHAPTER TWO: LITERATURE REVIEW

2.1 Nutritional ecology in primates

Nutritional ecology explains how individuals choose, acquire, and process food to satisfy their nutritional requirements in an ecological and evolutionary context. Intake of particular macro and micronutrients, especially protein and energy balance, is known to affect infant and juvenile growth patterns and female reproductive success and fitness (Altmann, 1998; Emery Thompson, 2013; Lee, 1987; Vogel et al., 2012). Hence nutritional ecology is relevant not only to feeding and behavioral ecology studies but also to primate ontogeny and life history studies (Leigh, 1994).

In order to fully address the questions related to feeding ecology and social behavior, it is important to understand the foraging strategies of the primate in question. A primates' foraging strategy may be influenced by different factors ranging from chemical, social, physiological and ecological factors. This section presents a review of existing literature on these factors and relates this knowledge to the current study.

2.1.1 Chemical and mechanical properties of food

Primate foods are complex in that they contain a mixture of organic and inorganic compounds (Milton, 1984; Oftedal, 1991). Furthermore, some foods may contain traces of toxic elements or may be difficult to digest, thereby causing consumers to avoid or denature them (Glander, 1982; Norconk, Wright, Conklin-Brittain, & Vinyard, 2009). Mechanical properties of foods such as hardness, size and shape also present a challenge to foragers in that they affect ingestion, mastication and digestion of the food items in question (Norconk et al., 2009). A food's nutritional content, gross energy, antifeedant content (digestibility reducing substances, such as simple phenols, hydrolysable and condensed tannins) or mechanical properties influence energy intake.

Nutrient content of plants varies between the different plant parts and the growth stage of the plant parts (Milton, 1999). For example, young leaves are known to be rich in protein and moderate in fibre, whereas fruits are rich in easily digestible sugars and moderate in fibre content (Milton, 1999). On the other hand, mature leaves have high levels of fiber compared to that found in young leaves and fruit. Often times, primates select foods based on the concentrations of extractable protein or easily digestible sugars or concentration of fibers or both. For example, leaf selection in lemur species was influenced by high concentrations of extractable protein and low concentrations of fibre (Ganzhorn, 1992). Relatedly fruit selection in chimpanzees is said to be influenced by high concentrations of easily digestible sugars (Wrangham & Waterman, 1983).

Furthermore, flowering plants possess defensive plant chemicals also known as plant secondary metabolites (PSMs) which protect them against herbivory (Glander, 1982; McKey, Waterman, Mbi, Gartlan, & Struhsaker, 1978). There are various PSMs and these have the ability to reduce digestibility of a given food and are often avoided by herbivores. Hydrolysable and condensed tannins can bind with protein thereby reducing digestibility and the nutritional quality of the food in question (Feeny, 1970). Nonetheless, some primate species have specialized guts or have evolved strategies to cope with the PSMs. For example, the golden bamboo lemur is able to tolerate high amounts of cyanide from their bamboo diet which would be lethal to humans (Glander, Wright, Seigler, Randrianasolo, & Randrianasolo, 1989). Relatedly, some studies have shown that there is a tradeoff between toxicity and the therapeutic value of PSMs (Forbey et al., 2009). Hence, animals may exploit some foods with high levels of chemical defenses due to the fact that the PSMs may contain active ingredients which mitigate the costs of infection by parasites, enhance reproduction, moderate thermoregulation, and increase alertness. Therefore, although PSMs may acutely or chronically toxic to herbivores, they cannot be completely avoided (due to their ubiquity and complexity). So, herbivores, may consume small amounts of a variety of plants or may ingest smaller, more frequent meals and thereby minimize the dose of SMs in any single meal (McLean & Duncan, 2006; Sorensen, Heward, & Dearing, 2005; Wiggins, McArthur, McLean, & Boyle, 2003).

Mechanical properties such as food toughness, size and shape also affect food choice and eventually energy intake. Previous studies show that mechanical properties place a significant load on the masticatory apparatus of the animal and may influence feeding rate of some food items (Coiner-Collier et al., 2016; Wright et al., 2008; Yamashita, Vinyard, & Tan, 2009). For example, very high fibre levels reduce digestibility and limit intake affecting bite size and chew rate, all important factors in the complex functional response of animals to variable diets (Searle & Shipley, 2008). Therefore, it is not surprising that many animals prefer low-fibre diets when they are available, and finding plants of different qualities allows animals to manage their fibre intake. Additionally, research has shown that the size of food item may influence the amount of dry matter ingested in a given time. For instance, in one minute of feeding on large size, ripe mangoes (*Mangifera indica*), red howler monkeys ingested as much food (dry mass) as when feeding on compound leaves of *Pithecellobium tortum* for 7.5 mins (Oftedal, 1991).

2.1.2 Physiological factors

Variation in energy and nutrient intake may be caused by changes in nutrient requirement as a result of body size, gut morphology, age and sex or reproductive state (Altmann, 1998; Koenig, Borries, Chalise, & Winkler, 1997; Rothman, Dierenfeld, Hintz, & Pell, 2008).

2.1.2.1 Body size, brain size and gut morphology

Body size and diet are correlated, as a consequence of the negative allometry of metabolic rate. The larger the body size, the lower the basal metabolic rate (BMR) and consequently the lower the nutrient quality (Clutton-Brock & Harvey, 1977; Gaulin, 1979). Generally, large bodied primates are expected to have higher energetic requirements and thereby eat more food than smaller primates. Due their low BMR, large animals need less energy per unit weight than smaller ones. This means that larger primates such as gorillas (adult weight 83-278 kgs) can consume lower-quality foods than smaller primates such as chimpanzees (adult weight 34-50 kgs) which mainly subsist on high-quality foods such as ripe fruits (Rothman et al., 2008; Watts, Potts, Lwanga, & Mitani, 2012).

Linked to body size is the brain and gut size. The larger the animal, the larger the absolute brain size (cranial volume in cm^3) but not necessarily the relative brain size (brain size to body size ratio). While larger brain (in terms of absolute brain size and absolute neuron number) is associated with the level of intelligence or cognition (Herculano-Houzel, 2009), large brains are energetically expensive to maintain. For example, the larger brains of humans (2.5 to 3 times higher than primates) require ~20-25% of energy for brain metabolism (Burini & Leonard, 2018). On the other hand, non-human primates expend a relatively small proportion of their energy budget on brain metabolism (8-10 %) (Burini & Leonard, 2018). Nonetheless, among mammals, primates are notable for having relatively large brains. The large brain size in primates is attributed to cognitive and social strategies (Dunbar, 2007; Dunbar, 1992) or on the demands of obtaining various dietary components (Milton, 1999). Diet quality has long been suspected to play a role in brain size evolution, in that species which largely subsist on ripe fruit or animal matter often have larger brains than those whose diets require more digestive processing (e.g. folivores have comparatively smaller brains than frugivores) (Clutton-Brock & Harvey, 2009).

Furthermore, the relatively large gastrointestinal tract in some primates means that there is slow passage rate and more retention time of food and thereby providing for more nutrient absorption (Demment, 1983). Large primates with large digestive tracts are expected to be more efficient at digesting low-quality fibrous foods compared to small sized animals with smaller guts

(Demment & Van Soest, 1985; Van Soest, 1994). Hence the diet of some large primates such as gorillas consists of high proportion of foliage foods because their longer larger intestines and colon allows for longer passage rates to absorb nutrients from leaves, which are generally more difficult to digest than fruits (Milton, 1984). There are some exceptions to this general rule (body and gut size rule), such as is the case in large sized chimpanzees (weight: 34-50 kgs) which subsist largely on fruits rather than on leaves compared to small sized cercopithecines (weight: 3-10.5 kgs) (Conklin-Brittain, Wrangham, & Hunt, 1998; Wrangham, Conklin-Brittain, & Hunt, 1998).

Additionally, most primate species have gut modifications that facilitate the efficient digestion of certain foods (Chivers & Hladik, 1980). For instance, some small bodied primates such as the colobine monkeys mainly subsist on a leafy diet because they have sacculated stomachs that provide opportunities for microbial action to break down leaves (National Research Council, 2003). Although chimpanzees have large digestive tract compared to colobine monkeys, they lack the gut modifications that facilitate the efficient digestion of fibrous foods. Hence the proportion of leaf in chimpanzee diets is lower than that in colobine diets.

2.1.2.2 Age, Sex and Reproductive state

Juveniles have higher BMR due to their small size and thus have greater nutritional needs per unit of body mass than non-lactating, non-pregnant adult females and male adults. Hence juveniles may mainly subsist on high-quality diets which are rich in digestible energy and protein necessary to sustain growth and development of body organs. For example, in rhesus monkeys, it was reported that younger females consumed more dry matter than older females thereby ingesting larger quantities of high-quality foods (R. L. Johnson, Malik, & Berman, 1991). In mountain gorillas, it was reported that juveniles consumed more dry matter to ingest more protein than silverbacks (Rothman et al., 2008). Similarly, juvenile Japanese macaques (*Macaca fuscata*) have been noted to consume more animal matter compared to the adult males (Hanya, 2003).

In most primate species, females have higher-quality diets than the males of their species (Altmann, 1991; Muruthi, Altmann, & Altmann, 1991; Serio-Silva, Hernandez-Salazar, & Rico-Gray, 1999; Strier, 2000). This relationship stems from the body size-diet relationship (discussed in section 2.1.2.1) in sexually dimorphic species, and from the high energetic costs associated with reproduction in female mammals. Although large bodied males have higher maintenance requirements on an absolute basis than adult females, the high energetic demands of pregnancy

and lactation can outweigh the reproductive costs of adult males (Gittleman & Thompson, 1988; Oftedal & Hudson, 1985).

Dietary sex differences have been studied for some primate species. For example, in mountain gorillas, it was reported that adult females and males ate diets with similar nutrient concentrations, however adult reproductive females consumed more dry matter per day to ingest more nutrients (Rothman et al., 2008). Also, energy intake by lactating females was higher than that for juveniles or silverbacks in western gorillas (Masi et al., 2015). In orangutans, adult females had higher intakes of energy, TNC, and protein than adult males (Vogel et al., 2017). In sifakas, lactating females ingested more dry matter and as a result ingested more energy, crude protein, fat and non-structural carbohydrates than the adult males (Koch, Ganzhorn, Rothman, Chapman, & Fichtel, 2017). For chimpanzees, it is reported that females spend more time feeding compared to males but they do not ingest more dry matter than males (Chemurot, Isabirye-Basuta, & Sande, 2012).

In regards to the reproductive states, previous studies show differences in feeding behavior and food intake among lactating, pregnant and non-cycling females. Pregnancy and lactation increase a female's energy cost by up to 25 and 50% respectively and increase her protein and mineral requirements (Dunbar & Dunbar, 1988; Lee, 1989). For instance, in baboons, pregnant and lactating females spent more time feeding and had higher daily energy and protein intake than when they were sexually cycling (Muruthi et al., 1991). This partly explains why females and males of the same species may differ in time spent feeding, the type of food eaten and the proportions of different foods eaten (Boinski, 1988; Chemurot et al., 2012; Gautier-Hion, 1980; Harrison, 1983; Rothman et al., 2008). The effect of reproductive state on food and /or energy intake has not been given fair attention in chimpanzees. However, evidence from one study shows that pregnant females more meat (probably more protein) than lactating or cycling females (O'Malley et al., 2016). In order to minimize effect of the reproductive state on intake, only one group of reproductive state was considered in this study: lactating female chimpanzees.

2.1.3 Social factors

Social factors such as competition and rank have been shown to influence food choice and intake rates in primates, thereby influencing the foraging strategy and fitness. High ranking individuals in any primate group are likely to consume or increase intake of high-quality foods compared to their low ranking counterparts (Janson, 1988; Johnson et al., 1991; Murray, Eberly, & Pusey, 2006; Vogel, 2005). For example, female green monkeys (lower ranking than males) fed on young leaves even though fruits and flowers were abundant, partly because they were avoiding

competition with the males which are high ranking and therefore occupied the best feeding spots in the trees (Harrison, 1983). Similarly, in rhesus monkeys, high ranking females spent more time feeding compared to their low ranking counterparts (Johnson et al., 1991).

In female chimpanzees, female dominance interactions are rare and the occurrence of aggressive interactions or ritualized displays does not have a meaningful impact on the social or feeding behaviour of females (Goodall, 1986). Therefore, there is a likelihood that social factors will have less or no effect on food intake by female chimpanzees.

2.1.4 Food availability

Variation in macronutrient intake for tropical primates is largely attributed to vagaries in the phenological patterns of tropical trees (chimpanzees: Conklin-Brittain, Wrangham, & Hunt, 1998; Moscovice et al., 2007;; sifakas: Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2014; orangutans: Knott, 1998; western gorillas: Masi et al., 2015; mountain gorillas: Rothman, Dierenfeld, Hintz, & Pell, 2008). The marked spatiotemporal variation in fruit supplies results in fruit scarcity periods in tropical forests and this implies that frugivores face potential energetic deficits, that ultimately drive important responses in their ecology and physiology (Dietz, Baker, & Miglioretti, 1994; Knott, 1998; Vogel et al., 2012; Wallace, 2005). Previous studies show that during the fruit-scarce season, there is reduction in nutrient intake as primates increase consumption of fall back foods of low nutrient quality (Conklin-Brittain et al., 1998; Irwin et al., 2014; Isabirye-Basuta, 1988; Knott, 1998; Rothman et al., 2008).

Long-term phenology studies reveal that most tropical forest communities display seasonal variation of three phenophases, i.e., new leaves, flowers and fruits which form the bulk of most primate foods (Chapman et al., 2005; Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999; van Schaik & Pfannes, 2005; van Schaik, Terborgh, & Wright, 1993). Variation in these phenophases has been attributed to both biotic (e.g. seasonal abundance of pollinators, avoidance of predation or herbivory) and abiotic factors (irradiance, temperature and rainfall) (Rathcke & Lacey, 1985; van Schaik et al., 1993). Whereas biotic processes may favour the strength of phenological convergences, climatic (abiotic) factors always determine the timing of phenophases (van Schaik et al., 1993). The effect of fluctuating irradiance, temperature and rainfall on phenology of tropical plants has been well documented (review by van Schaik & Pfannes, 2005).

In tropical lowland forests such as KNP where there are no marked changes in temperature and rainfall, phenological patterns are diverse and the environmental cues influencing the patterns are not clear. Nonetheless, evidence from long-term studies shows that minimum temperature and

irradiance is related to fruiting and flowering respectively (Chapman et al., 1999; Tutin & Fernandez, 1993). Synchronisation of flowering and fruiting has been observed, even in areas like KNP with two rainy seasons where water stress is said to be reduced (Chapman et al., 2005, 1999). Despite this synchronization, high annual variability in fruiting or flowering among species has been reported. Furthermore, although flowering and leafing seem to be largely determined by climatic variables, the same is not true for fruiting peaks. For example, at Kanyawara, fruiting patterns of different species differ and are very irregular for some tree species despite the regular flowering patterns (Chapman et al., 1999). Additionally, existing evidence suggests that the fruiting changes observed at community level may be due to climate change and the responses to this climate change are complex and vary among species (Chapman et al., 2005). The different fruiting periodicities have implications for the foraging strategies and eventually the reproductive behavior of primary consumers such as chimpanzees, but these have not been fully explored.

2.1.5 Implication of food characteristics and animals' social and physiological dimensions on feeding rate

Scientists are continually emphasizing the value for nutrition studies to incorporate feeding rates to estimate energy intake because food items vary in weight, in the speed they are eaten, and in how much energy or nutrients they contain (Nakagawa, 2008, 2009; Rothman, Chapman, & Van Soest, 2012; Schülke, Chalise, & Koenig, 2006; Stammati, Sabbatini, & Visalberghi, 2008). Previous studies show that assessments based only on time spent feeding tend to underestimate the weight of fruit consumed, and overestimate the weight of foliage consumed (Aristizabal, Rothman, García-Fería, & Serio-Silva, 2017; Chivers, 1998; Kurland & Gaulin, 1987). Feeding rate may be termed as: harvesting rate (Barton & Whiten, 1994a), feeding speed (Koenig et al., 1997) or speed of dry weight intake (Nakagawa, 1997). In this study feeding rate is defined as the rate of the dry mass of food ingested per unit of time (Schülke et al., 2006; Stammati et al., 2008; Zinner, 1999). Feeding rate in herbivores is affected by various factors as discussed below.

Arguably, different plant food items have different physical (shape, size or hardness) and chemical characteristics (e.g. fibre or toxicity level) which might impact on their feeding speed (see section 2.1.1).

The physiology (age, sex, reproductive state) of the animal may also affect its feeding rate. For example, in Japanese macaques, juveniles' feeding speed was slower than that of adults (Hanya, 2003; Jaman & Huffman, 2011). The extent of age difference in feeding speed varies with the

food type: the difference is likely to be large for fibrous foods, but small for fruits or seeds (Hanya, 2003).

Additionally, some studies show that feeding rates for some food types differ between sexes, whereby males consume foods faster than females (Nakayama, Matsuoka, & Watanuki, 1999). Relatedly, studies have revealed that lactating females in some primate species take in significantly more energy and food items per hour while feeding than pregnant and cycling females; but they did not spend more time eating than other females did, and they did not differ in the composition of their diet (McCabe & Fedigan, 2007).

Relatedly, body size which is linked animal morphology characteristics (e.g. jaw length, molar size, mouth volume) that are related to the ability to ingest and process food have an impact on feeding rates (Shipley, Gross, Spalinger, Hobbs, & Wunder, 1994). Body size accounts for 34% to 40% of the variance in average feeding rate (Nakagawa, 2008).

Also, social aspects such as rank and group size may also have an impact on feeding rates (Janson, 1985; Wilmers & Stahler, 2002). For example, in brown capuchin monkey (*Cebus apella*) and white-faced capuchin monkeys (*Cebus capucinus*), an individual's feeding rate for a given food species was affected by its rank and the number of agonistic interactions within the feeding tree (Janson, 1985; Vogel, 2005).

Other factors that affect feeding rate include the spatial and temporal availability of the foods (Barton & Whiten, 1994; Nakagawa, 1990a, 1990b) and satiation levels of individual animals (Dougherty, Cornelius, Bradley, & Lauriault, 1989). A combination of all these factors may impact the feeding rate of an animal at any given time and the feeding rate may change depending on the condition of the food and the animal. This has a bearing on the overall food intake of an animal, therefore, it is important for nutrition studies to include feeding rate for different food items in the equations for estimation of food intake.

2.2 Response of frugivorous primates to fluctuations in fruit availability

Primate species have evolved different foraging strategies to combat the nutritional deficits in the fruit scarce seasons (Clink, Dillis, Feilen, Beaudrot, & Marshall, 2017; Doran, 1997; Koch et al., 2017; Masi et al., 2015; Murray et al., 2006; Wallace, 2005). Frugivorous primates respond to fruit scarcity by adjusting their behaviours, such as reduction in party size, increase or decrease in time spent feeding and travelling, switch to keystone resources and fall back foods (e.g. figs and foliage) and increase in dietary breadth (Chapman, White, & Wrangham, 1994; Clink et al.,

2017; Conklin-Brittain et al., 1998; Doran, 1997; Moscovice et al., 2007; Newton-Fisher, Reynolds, & Plumptre, 2000; Wrangham et al., 1998).

During the fruit scarce periods, many smaller new world frugivorous primates subsist on high-quality but very scarce foods such as insects, gums and nectar. For example, *Saguinus imperator* and *S. fuscicollis* feed on nectar and *Callimico goeldii* feed on exudates during the fruit scarce seasons (Porter, Garber, & Nacimento, 2009; Terborgh, 1986). On the other hand, some large frugivorous primates subsist on leaves and other nutritionally poor foods e.g. *Pan troglodytes, Cercopithecus nictitans* and *Cercocebus albigena* (Tutin, Ham, White, & Harrison, 1997). In some cases, frugivorous primates may switch to a different fruit type rather than entirely feeding on foliage during fruit scarce periods as is the case with Sulawesi crested black macaque, common squirrel monkeys and chimpanzees (Felton, Felton, Wood, et al., 2009; Furuichi, Hashimoto, & Tashiro, 2001; O'Brien & Kinnaird, 1997; Terborgh, 1986; Tutin et al., 1997).

Foraging responses also tend to be sex-specific in some primate species (squirrel monkeys: Boinski, 1988; orangutans: Knott, 1998; Verreaux's sifakas: Koch *et al.*, 2017; White-Faced Capuchins: Rose, 1994; Mountain gorillas: Rothman *et al.*, 2008; Chimpanzees: Uehara, 1986; Wrangham and Smuts, 1980; Bornean orangutans: Vogel *et al.*, 2017). The variance in availability of food can have different impacts for males and females, due to differences in energy requirements between sexes.

Behavioral adjustments have been reported in some of the female primates as a response to reduction in food resources. Based on foraging models and evidence from different primate species, some female primates may consume lower-quality diets, increase foraging time and diet breadth during food scarce seasons (Clutton-Brock & Harvey, 1977; Wrangham et al., 1991). In most cases, females spend more time feeding than do adult males, but this pattern is not consistent for all primate species (Rose, 1994; Waser, 1977). In pygmy chimpanzees, females increased time spent feeding and reduced their travel times during the fruit scarce seasons (N'guessan, Ortmann, & Boesch, 2009). In some *Cercopithecus* monkeys and white-faced capuchins, females avoid competition with males when preferred foods are scarce by exploiting low-quality foods, or foraging on foods which require less handling (Gautier-Hion, 1980; Harrison, 1983; Rose, 1994).

Linked to sex is the rank effect in most sexually dimorphic species. The effect of rank on foraging strategies has been evidenced in female chimpanzees (Murray et al., 2006; O'Malley et al., 2016; Pusey, 1997). It is reported that high ranking female chimpanzees tend to consume greater quantities of high-quality diet (e.g. meat) compared to their subordinate counterparts; and

that low ranking females may feed less efficiently especially during fruit scarce seasons (Murray et al., 2006; O'Malley et al., 2016). Additionally, low ranking females compensate for reduced food access by adopting different strategies to those exhibited when food is scarce, such as spending more time feeding (Murray et al., 2006).

Evidence from the few sex-specific chimpanzee studies reveal that during the fruit scarce season, females broaden their diet, increase foraging effort but not ingest more dry matter than the males and they maintain a high-quality diet despite the season (Murray et al., 2006). Additionally, females tend to avoid competition for limited food resources in the food scarce seasons by feeding alone or with their dependent offspring (Wrangham et al., 1996). However, the responses of female chimpanzees in terms of macronutrient and energy intake and the implications on their reproductive behavior remains unclear.

2.3 Nutritional strategies

The ultimate reason why animals feed is to provision themselves with nutrients that will maximize fitness, subject to the physical, physiological and ecological constraints associated with finding, ingesting and processing foods. But, given the complexity of herbivore diets, the consumption of nutritionally imbalanced foods is sometimes inevitable, forcing trade-offs between eating too much of nutrients present in the foods in relative excess against too little of those in deficit. Therefore, primates have to make food choices which will help them attain a nutritionally balanced diet. The decision on what food to eat, when to eat the food and how much food to eat may further be driven by the nutrient needs and the nutrient composition of the available foods (Simpson & Raubenheimer, 2011). The nutrient requirements are not fixed but change as an animal grows or as its physiology changes. Equally, the nutrient content of foods changes with time, for instance, as plants develop or their growth condition changes.

Therefore, making food choices in primates is a daunting task because as animals try to access an optimal diet, they have to match uncertain changing nutrient availability to changing and sometimes uncertain requirements. Equally, this presents a difficult task to primatologists who try to understand the decisions made by animals when choosing different food types and the amounts to include in their diet. Thus, the mechanisms used by foragers to obtain a nutritionally balanced diet remain unclear for most primate species, including chimpanzees.

Nonetheless, four major schools of thought in nutritional ecology have been fronted to explain the nutritional strategy of different primate species, each of which proposes that diet selection subserves a different primary nutritional goal: single currency models which include energy maximization (Schoener, 1971), nitrogen maximisation (Byrne, Whiten, Henzi, & McCulloch,

1993), avoidance of plant secondary metabolites and regulation of dietary fibre (Freeland & Janzen, 1974; Milton, 1979), and multidimensional models such as nutrient balancing (Raubenheimer, Machovsky-Capuska, Chapman, & Rothman, 2015; Robbins et al., 2007).

2.3.1 Optimal foraging models

Single currency models use a unidimensional approach to decipher food choices in animals and these are based on optimal foraging theory (OFT) (Pulliam, 1974; Pyke, Pulliam, & Charnov, 1977). According to OFT the animal's foraging strategy is either maximization of energy or protein or minimization of antifeedants or toxins given the constraints of foraging such as search time or handling time. In this case, the animal adjusts it behavior to ensure that the constraints are minimized while the currency (energy or protein) is maximized. The optimization criteria has been used to describe food choices in some primate species. For instance in baboons, it was noted that patch residency was longer in patches with higher biomass and high-quality foods and higher biomass patches with high-quality foods were preferred and this led to maximization of energy intake (Barton and Whiten, 1994). Equally, a number of studies have related the foraging/nutritional strategies of primates to OFT, although they have not tested it. For instance primatologists tend to generally assume that high-quality diet of frugivorous primates equates to high energy intake, thereby fitting into the energy maximization model (Lambert & Rothman, 2015; Leighton, 1993).

Furthermore, in order to access an optimal diet, animals tend to avoid or regulate toxins or any other antifeedants. Avoidance of plant secondary metabolites and regulation of fibre intake as a food selection criterion has been explored in different primate species (Fashing, Dierenfeld, & Mowry, 2007; Ganzhorn, 1992; McKey et al., 1978; Oates, 1977; Rogers, Maisels, Williamson, Fernandez, & Tutin, 1990; Wrangham & Waterman, 1981). Plant secondary metabolites (PSMs) have evolved to protect plants against herbivory and these chemical defenses affect different animals in different ways (Freeland & Janzen, 1974). PSMs can have toxic effects on the animal's physiology or influence digestion or even lead to death if consumed in high amounts (McLean, 1970). Yet, animals may select plants with high toxic levels for their pharmaceutical value (McLean & Duncan, 2006). Fibre primarily includes cellulose, hemicellulose and lignin (Cork & Foley, 1991). Animals are limited by the extent to which they can digest fibre owing to different gut modifications and/or specialisations such as presence of gut-microorganisms that facilitate efficient digestion of fibre (Cork & Foley, 1991).

While concentrations of energy or protein or PSMs may influence some primates' overall food selection, each chemical component may not satisfactorily explain the species' relative

preference for different food items. For example, although chimpanzees are assumed to be energy maximisers due to the fact that they mainly consume a high-quality diet, they do not necessarily avoid foods with high condensed tannin content (Reynolds, Plumptre, Greenham, & Harborne, 1998). Hence, the optimization models are limited in that they consider one nutrient at a time and are not able to show the interactions between nutrients or how the animal responds to other nutrients in the diet. As such, there is growing evidence that many animals attempt to regulate intake of multiple nutrients independently instead of optimizing a single nutrient. Therefore, in order to fully understand what governs food choice in primate species such as chimpanzees with complex diet, there is need to apply a multidimensional approach such as the nutrient balancing model. Through the multidimensional approaches, earlier conclusions about their foraging strategies of some species were disputed. For example, spider monkeys were thought to be energy maximisers because of: (i) their preference for ripe fruits (Dew, 2005), (ii) their short retention times (Milton, 1981) and (iii) their large territories and fluid structure (Strier, 1992). But recent research using the GFN shows that the nutritional goal of spider monkeys is to ingest a set amount of protein rather than maximizing energy intake (Felton, Felton, Raubenheimer, et al., 2009; Felton, Felton, Wood, et al., 2009).

2.3.2 Multidimensional models

Modern theories argue that no single currency drives the nutritional strategy of animals, but instead animals may use several optimization strategies such as energy or protein:fiber maximization, nutrient balancing, and plant secondary metabolites avoidance or fibre regulation (Righini, 2017). It is evident that food choice in primates (and other animals) is influenced by the need to ingest necessary nutrients and minimize the constraints imposed by food availability and digestion inhibitors such as PSMs and dietary fibre. In combination, these factors can lead to mixed diets whereby the most energetically profitable food is not eaten exclusively even when it is abundant.

2.3.2.1 Geometric Framework of nutrition

The geometric framework of nutrition (GFN) is a multidimensional approach which examines patterns of macro and micronutrient intake in multidimensional space, offers an instructive model to understand the interactive effects of nutrients on animal food choices (Raubenheimer, Simpson, & Mayntz, 2009; Simpson & Raubenheimer, 2011). It considers more than one nutrient simultaneously, each represented by its own axis and focusses on interactions among the various nutrients. These multidimensional models enable one to view the effect of multiple nutrients such as dietary lipids, carbohydrates and protein on feeding behavior (Figure 2.1). The

nutrient axes constructed represent a nutrient space. The point where the axes meet in a nutrient space is called an intake target.

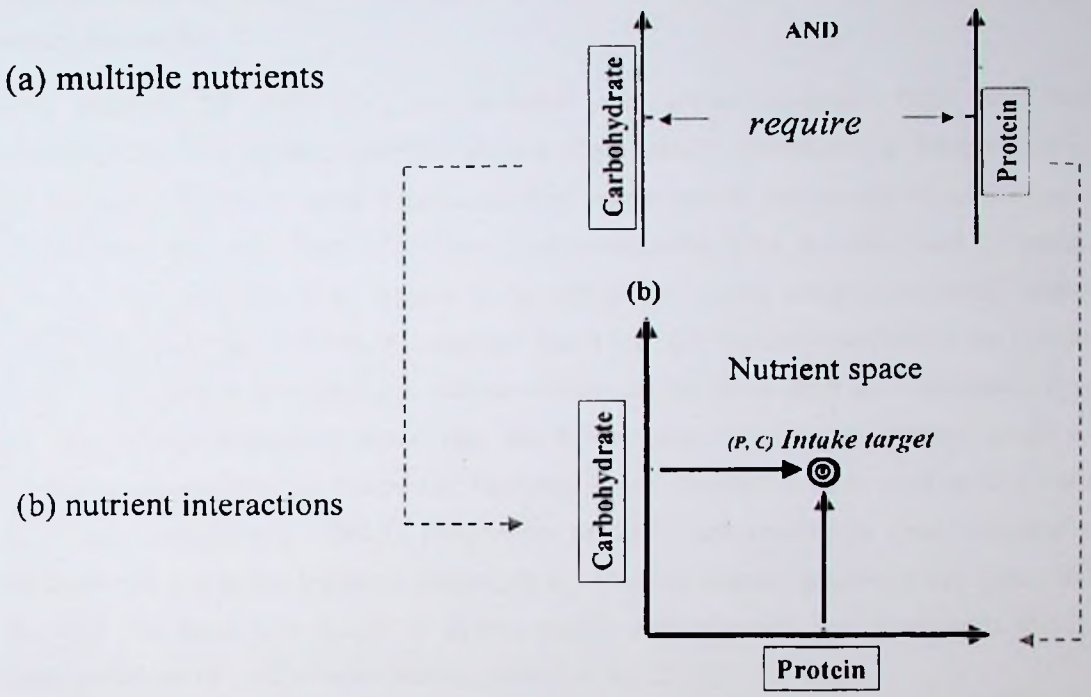

Figure 2-1: (a) Two or more nutrient axes that might be represented in a geometric model; (b) The axes are combined in a nutrient space to form a single point called the intake target.

In reality however, the combination of foods that enable animals to achieve their intake target are not available. Hence the animal is forced to combine nutritionally imbalanced foods in order to reach its intake target. In such cases, the animal is placed into a predicament in which it is forced to accept too little of some nutrients or too much of others, this trade-off is referred to as the rule of compromise.

By using the GFN, primatologists have unraveled the rule of compromise used by some primates such as spider monkeys (Felton *et al.*, 2009a, 2009b), diademed sifakas (Irwin *et al.*, 2015), guereza (Johnson *et al.*, 2017) and mountain gorillas (Rothman *et al.*, 2011). For example, frugivorous spider monkeys maintain a relatively stable protein intake throughout the year, while varying non-protein energy according to the availability of fruits and leaves in the environment (Felton *et al.*, 2009a). On the other hand, for folivorous mountain gorillas, it was revealed that the intake of non-protein energy was relatively constant throughout the year while protein intake varied according to the availability of leaves and fruits in the environment (Rothman et al., 2011). Although these two examples show different patterns of nutrient regulation, both studies

suggested that primates regulate nutrient intake in order to balance protein, lipid and carbohydrate consumption, and they appear to do this on a daily basis. Similarly, in this study, the GFN was used to unravel the nutritional strategies used by chimpanzees in the face of fluctuating diet quality.

Different methods of GFN (i.e. amount-based and proportion-based GF) have been demonstrated. The GFN defines important aspects of an animal's nutrition (e.g. food or nutrient requirements) in a Cartesian space where each food component is represented by a dimension. This enables the combined effects of different food components to be quantified and the various levels of animal response (e.g. intake) to be integrated in the multidimensional context (Raubenheimer et al., 2015, 2009). For amount based GF, the factors described in the nutrient space are represented as amounts (e.g. nutrient content of the food, such as in Rothman *et al.* (2011), whereas for proportion based GF, the factors described in the nutrient space are represented as proportions (e.g. balance of nutrients X and Y within a food, such as in Irwin *et al.* (2015) and Johnson *et al.* (2013). Proportions based GF are commonly used compared to amount based GF due to the logistical challenges of obtaining amount based nutrient intake data and the fact that there is a dearth of studies which used absolute intake amounts thereby minimizing chances of comparisons (Raubenheimer et al., 2015).

2.4 Reproduction seasonality in primates

Reproductive events of most wild primates are dictated by food availability patterns, (especially preferred foods) in their environment. Natural selection is expected to favour reproductive strategies that time births or weaning periods to the optimal period of energy availability, thus maximizing survival for the mother and the weanling (Carnegie, Fedigan, & Melin, 2011). As such, when an animal does not have enough energy resources for immediate survival needs such as maintaining body temperature, metabolism and foraging, it will defer or arrest reproduction (Bronson, 1986, 1995; Emery Thompson, 2013; Potts, 2013).

A complete reproductive cycle of ovulation, conception, pregnancy, and lactation is one of the most energetically expensive activities that a female mammal can undertake (Gittleman & Thompson, 1988; Wade & Schneider, 1992). Although pregnancy is less affected by energy availability, both lactational performance and maternal behaviors are highly responsive to the energy supply. It is reported that the amount of energy required (calories consumed) by female mammals increases 20%–30% during gestation and 66%–188% during lactation (Gittleman & Thompson, 1988). Existing evidence suggests that female reproductive hormones respond to nutrient intake, energy expenditure and energy balance (Ellison, Panter-Brick, Lipson, &

O'Rourke, 1993). Food scarcity/negative energy balance leads to decrease in gonadotropin releasing hormone and luteinising hormone pulsatility, thereby suppressing both ovulation and estrous behavior (Wade & Schneider, 1992). Therefore, most mammals would rather time their reproductive cycle to coincide with resource abundance thereby ensuring survival of the offspring and mother (Bronson, 1995; Wade & Schneider, 1992).

The environmental factors that influence reproduction in mammals include food availability, a variety of social cues and four aspects of an animal's physical environment: day length, temperature, humidity and rainfall. Among these, food/nutrition is considered as the most fundamental factor because all facets of an animal's well-being ultimately depend on it. Some environmental factors do not directly affect the actual ability of an animal to reproduce, but are cues to help the animal to prepare itself metabolically for a breeding season. The cues that trigger the onset of the breeding or conception season may not be accurate indicators of ecological conditions during the subsequent birth season, lactation or weaning periods (Crockett & Rudran, 1987a, 1987b). Hence most primates exhibit flexibility in timing of their reproduction to nutritional and social cues (Lindburg, 1987).

The degree of reproductive seasonality in primates and other animals is said to be a direct consequence of the strength of seasonal variation in ecological variables such as food and rainfall (Crockett and Rudran, 1987a; Janson and Verdolin, 2005). Many studies have shown that fluctuation in food abundance affects the timing of female fecundity and reproduction in non-human primates (Brockman and van Schaik, 2005). The timing of reproductive events in primates varies greatly across species; certain species exhibit very concentrated birthing seasons (e.g. most primate species in the temperate regions), while others give birth throughout the year (Lindburg, 1987). To this end two breeding models have been proposed to explain the reproductive strategy of different primate species, i.e. income breeders and capital breeders.

2.4.1 Reproduction theories

The income-vs-capital breeding model has recently been used to characterise reproductive patterns in non-human primates (Carnegie et al., 2011; Janson & Verdolin, 2005). An income breeder is described as one that uses exogenous cues (e.g., photoperiod, rainfall) to initiate reproductive events. An income breeder adjusts its food intake concurrently with breeding, without reliance on food stores. This is common in environments where environmental cues can reliably indicate when changes in food or climate will occur (Janson & Verdolin, 2005).

This breeding strategy is mainly used by primate species with short life spans and which time their births to occur during the mean peak of food abundance implying that initiation of reproduction is dependent on the current food conditions. For example, in vervet monkeys, the first three months of the infant's life which is the time of high lactational burden coincide with high dietary quality seasons (Lee, 1987). Many lemurs have two to three week long breeding seasons which coincide with the food abundant seasons (Kappeler, 1996).

In contrast, a capital breeder is one that acquires its resources in advance and stores them endogenously or exogenously until they are needed to supply aspects of offspring production (Brockman & van Schaik, 2005). This strategy is mainly used by animals inhabiting less predictable environments, where species may not be able to anticipate when and where food may be abundant (Janson & Verdolin, 2005). Hence, for such primate species greater variation in the timing of reproductive events is accordingly expected (Brockman & van Schaik, 2005). This is the case in primate species such as apes with long life spans and gestation periods that exceed the annual cycle of resources within their habitat (e.g. orangutans: Wich et al., 2004; chimpanzees: Brockman and van Schaik, 2005; and humans: Seidman, Ever-Hadani, & Gale, 1989).

For capital breeders, the females have to acquire a certain energy threshold before they can initiate reproduction (Emery Thompson, 2013; Potts, 2013). This they do by storing nutrients and only breeding once they reach high enough stores for successful reproduction. Most capital breeders are species with long gestation periods. The capital breeding strategy favours them because the favourable conditions that may initiate breeding and favour conception may not always be reliable indicators of future conditions during the time of birth, lactation or weaning (Janson & Verdolin, 2005).

2.4.2 Reproductive strategies

Primate females have several adaptations through which they compensate for and meet the energetic demands of reproduction ((Dufour & Sauther, 2002). The most common strategy employed by primates to offset the high costs of reproduction is increasing energy intake through consumption of high-quality foods or spending more time feeding and ingesting more food. For example, in Hanuman langurs, it is reported that pregnant and lactating females spent more time feeding than the non-cycling females, thereby consuming more energy (Koenig et al., 1997). In squirrel monkeys, females consume higher quality foods when they are cycling (Boinski, 1988). Female primates may also reduce energy expenditure by reducing physical activities or foraging costs, e.g. lactating green monkeys tend to be less active (Harrison, 1983).

Capital breeders may also metabolize fat stores which causes them to loose weight during lactation (McFarland, 1997). This strategy is contrary to that used by income breeders, whereby daily energy intake almost entirely dictates successful lactation. Nonetheless, some primate species, particularly apes, are thought to use a mixed strategy because it has been noted that they can increase caloric intake as well as increase adipose deposition from which they can draw energy reserves to initiate reproduction (Knott, 2001, 2005; Knott, Emery Thompson, Stumpf, & McIntyre, 2010).

Chimpanzees have longer reproductive cycles than the annual cycles of resources within their habitat. This coupled with the unpredictability of preferred food resources makes it difficult for chimpanzees to time their births to coincide with maximal food abundance. Female chimpanzees are said to use risk-averse reproductive strategy wherein reproductive investment is allocated in accordance with maternal condition (Emery Thompson, 2013). As such female chimpanzees are most likely to conceive if they maintain a positive energy balance, whereby they can divert energy from somatic maintenance to reproduction (Emery Thompson, 2013; Knott, 2001). Hence the high rates of conceptions and maximal swellings in female chimpanzees reported during fruit abundant seasons seem to suggest high energy intake and positive energy balance (Anderson, Nordheim, & Boesch, 2006; Emery Thompson & Wrangham, 2008; Wallis, 1995). On the other hand the likelihood of their conceiving during a fruit-scarce season is low because female chimpanzees are then energetically stressed (Emery Thompson, Muller, Kahlenberg, & Wrangham, 2010). Despite the suggestions that energy intake and balance is associated with conceptions and maximal swellings in female chimpanzees, the relationship between energy intake and reproductive events has been inferred from the relationship of various measures of reproductive performance with the amount of time spent eating fruits, rather than energy intake itself (Anderson et al., 2006; Emery Thompson & Wrangham, 2008; Wallis, 1995). Thus, this study seeks to explore the relationship between energy intake and seasonality in reproductive events (maximal-swellings, conceptions and births).

2.5 The case of female chimpanzees

Wild chimpanzee communities are multi-male, multi-female and are characterized by a male dominance hierarchy in which philopatric males form the stable core of the community and defend a group territory (Goodall, 1986).

As in most sexually dimorphic animals, male chimpanzees are bigger in body size than the females and also show distinct sex differences in behavior. These include differences in feeding and ranging patterns (Hashimoto & Furuichi, 2015; Wrangham & Smuts, 1980), such that

females typically range and feed in small overlapping core areas (Chapman & Wrangham, 1993; Murray, Mane, & Pusey, 2007) while males range more broadly throughout the territory. Additional sex differences in foraging include a male-bias towards hunting of vertebrate prey (Gilby, Eberly, Pintea, & Pusey, 2006). In East African chimpanzees, there are distinct sex differences in sociality, such that adult females are significantly less gregarious than adult males, spending much of their time accompanied only by their dependent offspring (Gombe: (Murray et al., 2007), Kanyawara: (Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007; Wrangham et al., 1996)). As such, male-male dyads have stronger association indices than female-female dyads (Gilby & Wrangham, 2008). Male chimpanzees also participate in more direct physical aggression than females, both within communities during competition for dominance status and between communities during cooperative territorial defense (Muller & Mitani, 2005; Wilson & Wrangham, 2003).

Evidence from previous studies suggests that males and females exhibit differences in feeding behavior, for example males range further than females in search for food (Wrangham & Smuts, 1980), yet males spend less time feeding compared to females (Chemurot et al., 2012; Van Lawick-Goodall, 1968). In addition females tend to consume a greater proportion of higher-quality diet than males (Van Lawick-Goodall, 1968). Hence male and females have different foraging strategies.

The responses of males and females to food scarcity periods give an insight on their foraging strategies. Apparently when food is scarce the behaviour of individuals is directed to maximising feeding efficiency but when food is abundant males may forego maximisation of feeding efficiency for the sake of increased reproductive effort. On the other hand, females maximise feeding efficiency when food is abundant. Females attempt to forage so as to maximize net energy intake, while males sacrifice an optimal foraging strategy for the sake of reproductive competition (Wrangham & Smuts, 1980).

Furthermore, as discussed in section 2.1.2.2 above, even among females, the feeding behavior may vary according to age or reproductive state of the individual as is the case in gorillas and macaques (Hanya, 2003; Rothman et al., 2008).

Linked to variations in feeding behavior and diet, are the sex differences in reproductive strategies. Female chimpanzees generally carry the bulk of reproductive costs, they gestate for relatively long periods of time and provide the majority of parental care for dependent offspring (Emery Thompson, 2013; Murray, Lonsdorf, Eberly, & Pusey, 2009). As such their reproductive

success is limited by their ability to turn food resources into offspring, while male reproductive success depends more on their access to mates.

Therefore, this study focused on adult female chimpanzees of reproductive age (>11 years old; because females in the wild start reproducing at 13-15 years (Emery Thompson, 2013; Pusey & Schroepfer-Walker, 2013) in order to control for the behavior and social differences in sex and age.

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CHAPTER THREE: GENERAL METHODS

3.1 Study Area

This research was conducted at Kanyawara, in Kibale National Park (KNP). KNP (776 km^2) is located in southwestern Uganda (0°13' to 0°41'N and 30°19' to 30°32'E) near the foothills of the Rwenzori Mountains (Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999) (Figure 3.1). Kanyawara study site is bordered by Sebitoli in the north and Ngogo in the south where other habituated chimpanzee communities are hosted (Figure 3.1). Kanyawara is located at an elevation of 1500 m and consist of a series of moderately undulating valleys with an average slope of 8.7° (Chapman & Wrangham, 1993).

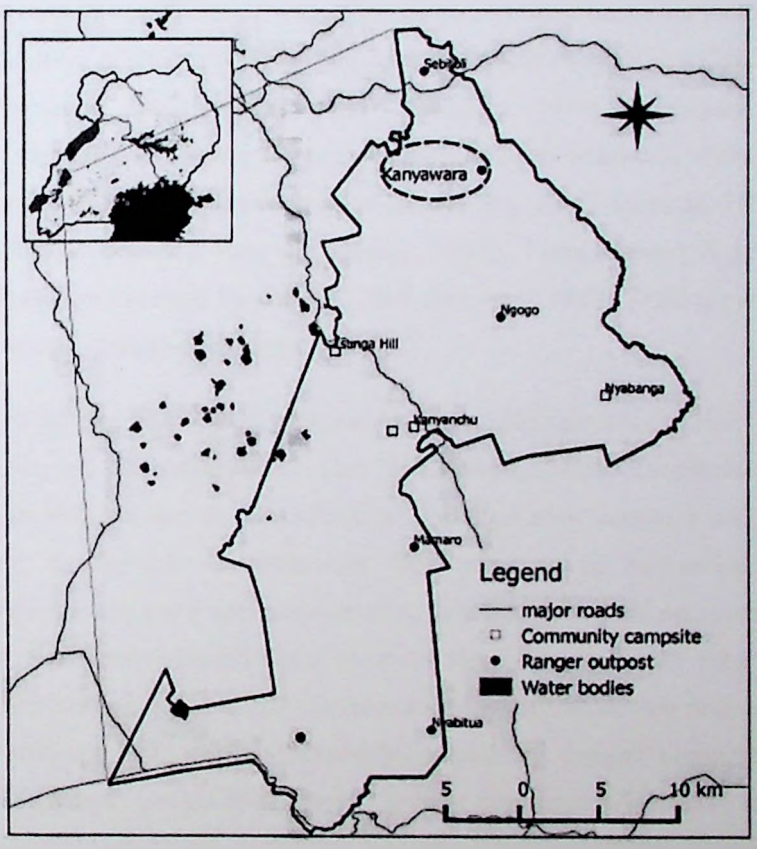

Figure 3-1: Map showing location of study site (Kanyawara) within Kibale National Park in Uganda.

3.1.1 History of management of KNP

The Kibale forest received the protected status of a National Park in 1993. Prior to this date, the area had been a Forest Reserve (gazetted in 1932) with the stated goal of providing a sustained production of hardwood timber (Osmaston, 1959). A planned polycyclic felling cycle of 70 years was initiated, and it was recommended that the logging open the canopy by approximately 50 percent through the harvest of trees over 1.52 m in girth (Kingston, 1967). Twenty-seven hardwood species were recommended for harvesting.

At Kanyawara there are unlogged areas and areas that have been harvested to various intensities. Compartment K-30 (300 ha) which is considered as a primary forest was not commercially logged although, prior to 1970, a few large stems (0.03-0.04 trees/ha) were removed by pitsawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Skorupa, 1988). Compartment K-14 (390 ha) was lightly and selectively harvested between May and December 1969 (averaging 14 m^3/ha or approximately 5.1 stems/ ha). Twenty-three tree species were removed, with only 9 species contributing 94 percent of the total timber harvest (Kasenene, 1987; Skorupa, 1988). Harvesting was not evenly distributed in this area (Struhsaker, 1997). Compartment K-15 (360 ha) was heavily and selectively cut between September 1968 and April 1969. Total harvest averaged 21 m^3/ha or approximately 7.4 stems/ha (Skorupa, 1988).

Evidence from previous studies suggests primates including chimpanzees utilize both logged and non-logged compartments (Chapman, Struhsaker, & Lambert, 2005). Nonetheless, the longterm effects of logging are still evident via the differences in vegetation structure and fauna diversity in the logged and non-logged compartments. For instance, in comparison to unlogged compartments, selectively logged compartments in Kibale National Park on average have higher light levels, different structure characterized by lower stem density, lower total basal area and lower above-ground biomass, and a distinct taxonomic composition driven primarily by changes in the relative abundance of species. Conversely, selectively logged compartments are like unlogged plots in functional composition, having similar community-weighted mean values for wood density, maximum height and maximum diameter (Osazuwa-Peters, Chapman, & Zanne, 2015). Relatedly, longterm studies show that vegetation, primate and avian recovery in logged sites is generally slow (Chapman & Chapman, 1997; Chapman, Struhsaker, et al., 2005; Dranzoa, 1998). The low primate diversity in logged compartments (K15) is attributed to low food availability (Swift, 2012).

3.1.2 Climatic variables

Kanyawara experiences a bimodal rainfall pattern with the first wet season (less severe) in March and April and the second wet season September to November. There are two dry periods, i.e. May to August and December to February. The mean annual rainfall distributed between two distinct wet and dry seasons is 1,749 mm; mean daily minimum and maximum temperatures are 14.9 and 20.2°C, respectively (1990–2001; (Chapman, Chapman, et al., 2005). Despite these bimodal trends, there is great year-to-year variation in the magnitude, onset, and duration of wet and dry seasons. The variation in the onset of rains and rainfall distribution has implications for the phenology patterns of tree species in the forest (Chapman et al., 1999).

3.1.3 Vegetation and animals in KNP

Kibale forest is a moist evergreen forest which transitions between lowland rain forest and montane forest (Struhsaker, Lwanga, & Kasenene, 1996). The park comprises a mosaic of vegetation formations: 58% mature forest, 15% grassland, 6% woodland, 2% lakes and wetlands and 19% colonizing forest regenerating in areas used in the past for agriculture; (Chapman & Lambert, 2000; Struhsaker et al., 1996).

The vegetation in KNP varies at different sites corresponding to the elevational gradient from north to south (Struhsaker, 1997). The northern sites, Sebatoli and Kanyawara are classified as *Parinari* forest, distinguished on photo aspect maps by large spreading crowns of *Parinari excelsa* (Kingston, 1967). The major subdominant at Sebitoli is *Carapa grandiflora*. At Kanyawara the major subdominants include *Aningeria altissima*, *Olea welwitschii*, *Newtonia buchananii*, and *Chrysophyllum gorungosanum* (Struhsaker, 1997). These assemblages are thought to represent climax forests between 1,370 m and 1,525 m (Osmaston, 1959). Ngogo, at 1350 m, has some features of lower elevation forest. *P. excelsa* is still present, but the forest is very mixed with *Chrysophyllum spp.* and *Celtis spp.* being common (Struhsaker, 1997).

Kibale National Park is home to 115 mammal species out of which 14 are small mammals, 327 bird species, 56 reptile species and 33 amphibian reptile species (Kasenene, 1980; Plumptre et al., 2007). Some of the fauna in KNP include threatened and near threatened species such as *Loxodonta africana* (elephants), *Panthera pardus* (leopard), *Pan troglodytes* (chimpanzee) and *Procolobus rufomitratus tephrosceles* (red colobus monkeys). The park boasts of a rich and abundant primate community; 13 nonhuman primates which account for 67% of Uganda's primate species. Six of the diurnal primates have been subjects of extensive research: red colobus, black-and-white colobus (*Colobus guereza*), red-tailed monkeys (*Cercopithecus*

ascanius), blue monkeys (*C. mitis*), mangabeys (*Lophocebus albigena*), and chimpanzees (Struhsaker, 1997).

3.1.4 Fruiting phenology at Kanyawara

Long term studies have shown that the proportion of fruiting trees at Kanyawara is influenced by minimum temperature in the previous dry season (Chapman, Chapman, et al., 2005). A recent analysis on long term phenological patterns reveals that temporal variability as well as interannual variation in fruit availability at Kanyawara is very high (Chapman, Chapman, et al., 2005). Although some species at Kanyawara exhibit regular fruiting patterns, the trends are not consistent every year. For example, despite the synchronous fruiting and fairly regular fruiting pattern in *Uvariopsis congensis* in June or July, there has been years when this species did not fruit (Chapman, Chapman, et al., 2005). The high temporal variability in fruit availability implies that there is no predictable seasonal fruiting pattern at Kanyawara. Nonetheless, the community level fruit peak period is said to occur when the first wet season of the year is ending and the dry season is beginning and the fruit scarce season is said to be between January and March (Chapman et al., 1999).

Variation in fruit production at Kanyawara has also been attributed to logging. Previous studies show that fruit production in unlogged compartments (K-30) was higher than in logged compartments (K-14 and K-15). In the logged sites, fruit production is reported to be more in the heavily logged sites (K-15) than in the slightly logged sites (K-14) (Chapman & Chapman, 1997). But density of *Ficus* fruiting trees was reported to be more in the slightly logged compartments (K-14) followed by the unlogged sites (K-30) and much less in the heavily logged sites (K-15, 12, 13, 17). Compartments K-30 and K-14 are considered as higher-quality areas for frugivorous primates in terms of food quality compared to compartments K-15, 12, 13, 17 which lie in the north of Kanyawara (Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007).

3.2 Study subjects

The Kanyawara chimpanzee community ranges in the northwestern sector of KNP (Figure 3.1) and it has been continuously studied since 1987 (Isabirye-Basuta, 1988; Wrangham et al., 1991). The chimpanzees were habituated to the presence of researchers without provisioning. Kanyawara chimpanzees mainly utilize compartments K14, 15 and 30 an indication that they utilize both logged and unlogged compartments (Emery Thompson et al., 2007).

Kanyawara chimpanzees preferentially consume drupe fruits when available (Wrangham et al., 1996), and three particularly preferred species (*Mimusops bagshawei, Pseudospondias*

microcarpa, and Uvariopsis congensis) show strong relationships to reproductive timing (Emery Thompson et al., 2007; Emery Thompson & Wrangham, 2008), although they are sporadically available (Wrangham et al., 1996).

At the time of this study (January 2014 to June 2015), the Kanyawara chimpanzee community comprised 47 to 51 chimpanzees of which 17 were adult females. Most of the females were fully habituated to human presence, however, three of the 17 females were still shy to human presence and could not be observed for longer time periods. Additionally, during the study period, most of the adult females were nursing infants, and as such the common reproductive state was lactating females. Hence, only fourteen lactating females were considered for this study.

Table 3.1: Demographic attributes of the female chimpanzees considered in this study

Female ID	Age	Mean observation hrs/mo	Parity[a]
AL	32	10.37	Multi
MU	53.7	11.06	Multi
LN	17	10.61	Primi
ML	17	11.31	Primi
NP	14	11.34	Nulli (September 2014)
OT	16	11.33	Multi
OU	35	11.24	Multi
PO	14	11.19	Nulli (September 2014)
QT	22	11.45	Primi (November 2014)
RD	18	11.24	Nulli (October 2014)
TG	34	11.36	Multi
UM	33	11.93	Multi
WA	23	11.56	Multi

Female ID	Age	Mean observation hrs/mo	Parity[a]
WL	22	11.45	Primi (January 2015)

[a]Indicates whether the female was observed while nulliparous, primiparous or multiparous; dates are indicated if females switched categories during the study period.

3.3 Ethical note

This research complied with all regulations of the Uganda National Council for Science and Technology and Uganda Wildlife Authority.

3.4 General methodology

The aim of this section is to give an overview of the methodologies used to collect data during this study. To avoid repetition, a detailed explanation of the methods for data collection for each objective are included in Chapters Four, Five and Six. Field data was collected continuously between January 2014 and June 2015, a total of 18 months. Laboratory analyses were conducted between September 2015 and May 2016.

3.4.1 Chimpanzee behavioral data collection

All behavioral data were collected using a combination of check sheet and notebook and pencil. A pair of binoculars (magnification 10 x 42), a stop watch and a wrist watch were used during feeding observations.

Behavioral data were collected on study subjects for 18 mo using continuous focal observations on focal individuals which were selected daily (Altmann, 1974). Ideally, each focal observation (or "follow") started at dawn when the focal individual left her nest and ended at dusk when she entered her sleeping nest. However, sometimes the focal individual had already left the nest before dawn, or was lost before she entered her night nest at dusk. Due to the large home ranges and variable sub-group composition of chimpanzees, it was difficult to predetermine a focal individual, hence these were located and chosen opportunistically. A rotating scheme was used to ensure that each female individual was sampled for a similar amount of time during the study period. Therefore, for each month, every focal individual was sampled for atleast one day. On average, during the study period each individual was observed for 15±1 days as a focal and for each day an individual was observed for ~11 hours (Table 3.1).

During each focal sample, the following data was collected for all feeding bouts: the group size, feeding bout length (the start and end time of feeding on a particular food item to the nearest minute), the plant species, part ingested and its developmental stage (e.g. ripe or unripe fruit,

young or mature leaf). When possible (if the animal was in good visibility), the number of discrete food units (individual items e.g. one fruit, a strip of leaves or bunch of flowers) consumed per minute were recorded. The size of discrete food units was determined according to how chimpanzees processed the food item before ingesting it. For example, if the female chimpanzees picked one strip of young leaves at a time, the number of young leaves on each leaflet was estimated and used that as the unit. For pith and bark, the length of the stem picked by the individual chimpanzee at a time was estimated. For instance, if on average, a chimpanzee spent 2 minutes feeding on 50 cm stem of *Aframomum angustifolium* K.Schum, the discrete food unit was estimated as 25 cm (50/2) per minute. In order to determine the average number of discrete food units ingested per food item, records were taken at every five-minute interval throughout the feeding bout, or when observation conditions allowed. A total of 4314 records of discrete units ingested per minute were taken totaling to 648 hours. A total of 1699 feeding bouts were recorded ranging from 5 feeding bouts on mature leaves to 619 feeding bouts on ripe fruit which was the common food type. Feeding was defined as reaching for, picking, handling, or chewing a food item as well as short intervals (<5 sec) of searching (defined as searching for the next food item).

3.4.2 Food sample collection and processing

Samples of all the plant foods eaten during focal follows were collected in air tight bags on the same day or within the same week from the exact plant eaten by chimpanzees or from adjacent plants of the same species. Food samples were processed in a way that mimicked chimpanzee actions. For example, if the chimpanzee peeled the fruit or stem or spat out the seed before eating the fruit, the collected sample was also peeled and seeds removed before weighing it. The samples were weighed using a portable balance to yield the "wet unit weight". At least 30 wet unit weights for each food item were recorded to assess the mean and variance of the mass (Rothman, Chapman, & Van Soest, 2012). Wet unit weight measurements were taken at the end of the day (or within 24hrs) before the same sample was dried at ~40°C using a Nesco plant dehydrator to constant weight. This temperature was chosen to inhibit enzymatic activity and prevent chemical and physical changes, while preserving the sample's nutritional attributes (Rothman et al., 2012). Dried samples were then weighed to obtain the dry unit weight.

The dried samples were ground using a Wiley mill fitted with a 1 mm screen to obtain uniform particle size. Ground samples were analysed in the nutritional ecology laboratory at Harvard University, Anthropology Department and/or the nutritional ecology laboratory at Hunter College of the City University of New York.

In this study, I only considered plant foods because they form the bulk of chimpanzee diet. Much as chimpanzees occasionally consume vertebrates and invertebrates, and much as these provide more protein, they paradoxically comprise a smaller portion of their diet, at most 7.5% (Hohmann, 2009). Previous studies have revealed that the percentage of meat in the diet of chimpanzees, particularly females is very low (Gilby et al., 2017; Hohmann, 2009). The low proportion of meat in chimpanzee diet is attributed to the fact that hunting is energy demanding and vertebrates are patchily distributed (McGrew, 2014). Also, evidence shows that female chimpanzees have low hunting rates compared to males even when they encounter prey as often as the males (Gilby et al., 2017). Relatedly, due to their risk-averse foraging strategy coupled with the high energetic costs of lactation, females tend to forego meat for other accessible protein-rich plant foods (Brockman & van Schaik, 2005; Gilby et al., 2017; Hohmann, 2009). Besides, primates in habitats like Kanyawara where protein-rich plant sources are easily accessible do not need to consume a substantial amount of meat to obtain sufficient protein (Hohmann, 2009; Uwimbabazi et al., 2019). Primate diets which contain atleast 7-11% of protein can sustain the primate's bodily functions (McGrew, 2014; Wasserman & Chapman, 2003). In fact, recent evidence suggests that meat eating in Kanyawara chimpanzees is attributed to sodium acquisition since Kanyawara soils and foods are poor in sodium (Venable et al., in review.). Therefore, since the contribution of meat to daily calorie intake is small, it is not likely to influence macronutrient regulation patterns significantly.

3.4.3 Measuring fruit availability

Phenological data was collected monthly for 18 months (January 2014-June 2015) to describe annual patterns of food availability. This data was collected from 207 trees representing 19 tree species. These trees were located along permanently marked phenology transects (each 200 x 10 m = 0.2 ha). Five phenophases were considered i.e. young leaves, mature leaves, flowers, ripe fruits, unripe fruits and these were estimated using visual counts, on a 5-point scale (0=0%, 1=1-25% of the crown are, 2=25-50% of the crown area, 3=50-75% of the crown area, 4=>75-100% of the crown area) (Chapman et al., 1992). Estimates of fruit abundance were based on the number of trees in the phenology sample with non-zero scales (Wrangham, Conklin-Brittain, & Hunt, 1998). The proportion of trees in fruit for each species per month was determined as the number of trees of that species which had ripe fruit divided by the total number of trees of the species observed with ripe fruit for each month. We calculated the monthly fruit abundance index (FAIm) as:

where Pkm denotes the proportion of the number of trees in fruit for species k in month m (Wrangham et al., 1998).

Since some of the fruit tree species which are included in the phenology sample were not eaten by chimpanzees during the study period, FAIm was calculated using only tree species whose ripe fruits were eaten at least once during the study period.

For each month the dominant fruiting tree species was identified based on which species in the phenology sample had the largest FAI. From this, the fig-months or drupe-months were identified depending on whether the abundant fruiting tree species in a given month was a *Ficus* species or non-*Ficus* (drupe) species respectively.

3.4.4 Laboratory analyses

Laboratory analyses were conducted at the nutritional ecology laboratories at Harvard University, Anthropology Department and Hunter College of the City University of New York. Multiple samples of the same foods were pooled to account for intraspecific variation and were analysed in duplicate for carbohydrates (including digestible fibre), protein and lipids the following the conventional methods as in Conklin-Brittain et al. (1998) and Rothman et al. (2012). The assays run are discussed in detail below:

First, the organic matter of each sample was determined, because all nutrient values were expressed as a percentage of organic matter (OM) instead of dry matter (DM). DM includes ash, yet ash (total inorganic minerals) does not contribute energy to a food.

Dry matter, total ash and organic matter

Field dried-milled samples were dried in an oven at 105°C for 8 hours and weighed them hot to estimate the dry matter correction coefficient. Total ash was estimated by burning the dry matter sample at 502°C for 8h and then weighing it at 100°C.

Organic matter correction coefficient of the sample was calculated as:

[redacted]

Available protein

Near-infrared reflectance spectroscopy (NIRS) using a Foss XDS Rapid Content Analyzer was used to estimate concentrations of total nitrogen (N), and crude protein (CP) was calculated by multiplying nitrogen by 6.25 (Rothman, Chapman, & Pell, 2008). Available protein (AP) (not bound by lignin in the plant cell wall) was estimated by subtracting acid detergent insoluble

crude protein (ADCP) from CP. The ADCP values for Kibale foods were obtained from Conklin-Brittain *et al.* (1999).

Lipid

Lipid content was estimated using petroleum ether extraction for four days at room temperature (Conklin-Brittain and Wrangham, 1994). Petroleum ether was added to weighed plant samples (dried and milled) in an Erlenmeyer flask with an air tight glass stopper under a fume hood. The jars containing the sample and ether were left in the fume hood for four days. After four days, the petroleum ether was poured into pre-weighed beakers through a glass funnel under the fume hood. The beakers with the filtrates were then left in the fume hood to allow the filtrates to evaporate overnight. After all the solvent had evaporated, the glass beakers were placed into the oven at 60°C for a minimum of 8 hours. After which, the beaker with the lipid residue were hot weighed. To account for all the non-lipid non-nutritive components extracted by the procedure (e.g., waxy substances, cutin, essential oils), one was subtracted from the percentage of ether extract (Rothman et al., 2012).

Water-soluble carbohydrates

Water soluble sugars (WSC) were first extracted with water, followed by phenol/sulfuric acid colorimetric assay with a sucrose standard.

A mixture of water and pre-weighed plant sample was boiled and filtered. Distilled water was then added to a sample of the extract. Along these a sucrose standard (contained sucrose solution) and a reagent blank (contained distilled water) was prepared. Phenol and concentrated sulphuric acid were then added to the above solutions under a fume hood. The mixtures were then placed into a Spectronic 20D+ spectrophotometer for one hour and read at 490 nm wavelength.

Fiber fractions

Neutral detergent fiber (NDF with α-amylase), acid detergent fiber (ADF), and acid detergent lignin (ADL) were estimated through sequential analysis using an A200 fiber analyzer (ANKOM, Macedon, NY). Hemicellulose (HC) was estimated as the difference between NDF and ADF. Cellulose (Cs) was estimated as the difference between ADF and lignin.

Total non-structural carbohydrates (TNC)

Total nonstructural carbohydrates (TNC) was estimated by subtracting NDF, lipid, AP, and ash from 100%.

3.4.5 Food and nutrient intake calculations

First, the wet weight ingested per minute for each food item was computed as the product of its wet unit weight and the corresponding average number of discrete food units eaten per minute. Feeding rate was calculated as:

Feeding rate for each food item= wet weight ingested per minute * dry to wet weight(wet unit weight *100)

Daily amount of dry food ingested (g/day) was calculated as:

$$\text{dry mass} = \sum (ti * \lambda i)$$

where ti=time spent feeding on food item i per day (mins); λi= average feeding rate for item i (g/min).

Daily nutrient intake (g/day) was calculated as the product of daily amount of dry food ingested per food item and its corresponding mean nutrient content.

The metabolisable energy (MEH) content per food item was computed using the equation below, following Conklin-Brittain, *et al.* (2006):

$$MEH(kcal\ per\ 100g\ OM) = (4 * \%TNC) + (4 * \%AP) + (9 * \%lipids) - (1.65 * \%NDF)$$

Energy intake rate per food item per minute: average feeding rate (g/ min) * energy content (Kcal/g).

Daily energy intake (Kcal/day) was calculated as:

$$\text{Daily energy intake } (ME) = \sum (g_i * MEH_i)$$

where g_i=amount of dry food of food item i ingested per day (grams); MEH_i= the energy content of food item i (Kcal/g).

For each day, the percent grams of fig ripe fruits, drupe ripe fruits or terrestrial herbaceous vegetation (THV: young leaves, pith or flowers) consumed was calculated. From this, the food type with the largest percent was determined and days were classified either as figs (fig-days), drupes (drupe-days) or THV (THV-days).

3.4.6 Geometric framework of nutrition

The geometric framework of nutrition (GF) is a multivariate approach which examines patterns of macro and micronutrient intake in multidimensional space, offers an instructive model to understand the interactive effects of nutrients on animal food choices(Raubenheimer, Simpson,

& Mayntz, 2009). The GF uses a nutrient mixing model feeding strategy which argues that individual food choices are based on the regulation of multiple nutrients in response to the consumers' changing nutrient needs (Simpson, Sibly, Lee, Behmer, & Raubenheimer, 2004). Using the GF two or more variables such as food components are represented and the amount of ingested nutrients which form a geometric space within which nutritional targets and outcomes can be quantified. The GF helps understand the relationship between nutrition and ecology by disentangling the discrete and interactive roles of different food components.

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CHAPTER FOUR: INFLUENCE OF FRUIT AVAILABILITY ON MACRONUTRIENT AND ENERGY INTAKE BY FEMALE CHIMPANZEES

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ABSTRACT

Daily energy intake of adult female mammals is influenced by environmental conditions and physiological requirements, including reproduction. The effects of fruit availability on macronutrient and metabolisable energy intake by adult female chimpanzees (*Pan troglodytes schweinfurthii*) of the Kanyawara community in Kibale National Park, Uganda were examined from January 2014 through June 2015. Drupe fruits were abundant for four months, whereas the other fourteen months were dominated by fig fruits. The mean daily intake of food (dry matter) and metabolisable energy, did not differ between drupe-months and fig-months. However, foraging costs were higher during fig-months, as indicated by a 20% increase in feeding time. Furthermore, during drupe-months female chimpanzees ingested more water-soluble carbohydrates and lipids, and less available protein and neutral detergent fibre. Although metabolisable energy intake did not differ consistently between drupe-months and fig-months, they consumed more on days when ripe fruit dominated the diet than when leaves and pithy stems dominated the diet. The findings suggest that differences in diet quality between drupes and figs can have important effects on frugivore foraging, and that they influence net energy gain more by their effects on macronutrient composition or foraging cost than by their direct impact on energy intake.

Keywords: Macronutrient intake, feeding rates, drupes, fig fruits, female chimpanzees, monthly variation.

4.1 Introduction

As frugivorous primates, chimpanzee (*Pan troglodytes*) foraging success is constrained by fruit availability (Newton-Fisher, 1999; Tutin *et al.*, 1991). Evidence of seasonal fluctuations in fruit availability affecting diet and nutrient composition has been documented for many ape species, including chimpanzees, orangutans (*Pongo pygmaeus*), western gorillas (*Gorilla gorilla*), western chimpanzees (*Pan troglodytes verus*), and mountain gorillas (*Gorilla beringei*) (Conklin-Brittain, Knott, & Wrangham, 2006; Knott, 1998; Masi *et al.*, 2015; N'guessan, Ortmann, & Boesch, 2009; Rothman, Dierenfeld, Hintz, & Pell, 2008). During months of highest fruit production, orangutans increased their intake of calories by feeding on a diet dominated by fruit (Knott, 1998). Furthermore, during fruit-scarce seasons, frugivorous primates can adjust their behavior by feeding in smaller groups (reducing inter-individual competition), by increasing or reducing their foraging time, travel time or diet breadth, and by incorporating lower-quality foods (Doran, 1997; Felton, Felton, Wood, & Lindenmayer, 2008; Harrison, Morrogh-Bernard, & Chivers, 2010; Hemingway & Bynum, 2005; Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2014; Lambert & Rothman, 2015; Masi, Cipolletta, & Robbins, 2009; Tutin, Ham, White, & Harrison, 1997; Wright et al., 2015).

Two distinct periods of fruit production, drupe-fruit (or non-fig) and fig-fruit seasons (hereafter referred to as drupe-months and fig-months respectively), have been documented at Kanyawara, Kibale National Park, Uganda (Emery Thompson & Wrangham, 2008; Gilby & Wrangham, 2007; Wrangham et al., 1996). Previous studies show that Kanyawara chimpanzees (*Pan troglodytes schweinfurthii*) exhibit a range of behavioral and physiological modifications during periods of drupe-fruit scarcity (fig-months) (Conklin-Brittain, et al., 2006; Emery Thompson & Wrangham, 2008; Gilby & Wrangham, 2007; Wrangham et al., 1996). During fig-months, Kanyawara chimpanzees feed in smaller groups and increase their dietary breadth (Wrangham et al., 1996). Another behavioral response associated with drupe-months is increased hunting rates (Gilby & Wrangham, 2007). Furthermore, availability of drupes has been associated with positive energy balance among male chimpanzees in Kanyawara (Emery Thompson, Muller, Wrangham, Lwanga, & Potts, 2009).

Figs (*Ficus spp.*) have a high fibre content and are lower-quality fruits compared to drupaceous fruits, which tend to be richer in soluble sugars (Conklin-Brittain & Wrangham, 1994; Wrangham et al., 1993). Despite this lower quality, figs are major fallback foods because they are abundant and available year-round, allowing the proportion of figs in the diet to increase

when drupes are scarce (Marshall & Wrangham, 2007; Wrangham et al., 1991; 1996). Hence, it has been reported that Kanyawara chimpanzees, like gibbons (*Hylobates albibarbis*), spider monkeys (*Ateles chamek*) and orangutans, prefer drupes when they are available (Clink, Dillis, Feilen, Beaudrot, & Marshall, 2017; Felton, Felton, Wood, & Lindenmayer, 2008; Leighton, 1993; Wrangham et al., 1996). Previous studies of Kanyawara chimpanzees revealed that during drupe-months, there was increased intake of non-structural carbohydrates, and reduced intake of fiber (Conklin-Brittain, Wrangham, & Hunt, 1998; Wrangham, Conklin-Brittain, & Hunt, 1998). By contrast, during fig-months there was an increase in dietary breadth, foraging time and a reduction in group size, suggesting that chimpanzees may experience seasonal nutritional shortfalls when drupe fruits are scarce (Wrangham et al., 1996).

Despite the availability of fig fruits throughout the year, it appears that seasonal variation in drupe fruit availability significantly affects reproductive success of female chimpanzees. At Kanyawara, increased consumption of drupe-fruits has been correlated with high conception rates and elevated ovarian hormone production as well as lower cortisol levels in lactating females (Emery Thompson & Wrangham, 2008; Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007; Emery Thompson, Muller, Kahlenberg, & Wrangham, 2010). This chapter examines how the foraging behavior of female chimpanzees varies in relation to drupe fruit abundance, to evaluate the proposition that their reproduction is limited by the availability of drupe fruits.

Optimal foraging theory argues that chimpanzees should maximise the long-term rate of energy intake by choosing foods rich in digestible energy (Lambert & Rothman, 2015; Pyke, Pulliam, & Charnov, 1977). It was thus predicted that during the drupe-months, the diet should comprise mostly drupe fruits and female chimpanzees should spend less time feeding since drupe fruits are rich in non-structural carbohydrates. To test these predictions: (1) the feeding rates, energy intake rates and macronutrient content of the foods eaten by female chimpanzees were determined; and (2) differences in feeding behavior and diet between months when fruit availability and diets were dominated by either drupe fruits or fig-fruits were examined. Comparisons include the daily time spent feeding and total amount of food eaten, as well as intake rates of ripe fruit, terrestrial herbaceous vegetation i.e. pith and leaves, figs, drupes, metabolizable energy and macronutrients.

4.2 Methods

4.2.1 Study site and subjects

Female chimpanzees of the Kanyawara community, in Kibale National Park (KNP) were observed by MU from January 2014 to June 2015. KNP (776 km^2) is located in southwestern Uganda (0°13' to 0°41'N and 30°19' to 30°32'E) near the foothills of the Rwenzori Mountains (Chapman, Chapman, Kaufman, & Zanne, 1999). The Kanyawara chimpanzee community ranges in the northwestern sector of KNP and has been studied since 1983 (Isabirye-Basuta, 1987; Wrangham et al., 1991). At the time of this study, the Kanyawara chimpanzee community comprised 47 to 51 chimpanzees of which 17 were adult females. Fourteen multiparous female chimpanzees who were fully habituated were selected as study subjects. Estimated ages at the start of the study were between 13.3 and 54.9 years.

4.2.2 Collection of behavioral and feeding data

Behavioral data were collected using continuous focal observations (Altmann, 1974). Ideally, each focal observation (or "follow") started at dawn when the focal individual left her nest and ended at dusk when she made her sleeping nest. However, sometimes the focal individual had already left the nest before dawn, or was lost before she entered her night nest at dusk. Due to the large home ranges and variable sub-group composition of chimpanzees, it was difficult to predetermine the location of a focal individual, hence focal females were located and chosen opportunistically. As far as possible, focal females were selected based on a rotating scheme to ensure that all animals were sampled for a similar amount of time. In each month, focal observations were conducted for a mean of 14±2 days, with each individual sampled as a focal for at least one day per month. On average, each individual was subjected to 15±1 days of focal observations. Additionally, for each focal sample, the foraging group size (the number of individual chimpanzees in the same feeding patch with the focal individual) was recorded.

During each focal sample, the following data was collected for all feeding bouts: the start and end time of feeding on a particular food item to the nearest minute, the plant species, part ingested and its developmental stage (e.g. ripe or unripe fruit, young or mature leaf). When possible, the number of discrete food units (individual items e.g. one fruit, a strip of leaves or bunch of flowers) consumed per minute was recorded (Rothman et al., 2008). The size of discrete food units was determined according to how chimpanzees processed the food item before ingesting it. For example, if the female chimpanzees picked one strip of young leaves at a time, the number of young leaves on each leaflet was estimated and used as the unit. For pith and bark, the length of the pith or bark picked by the individual chimpanzee was estimated. For instance, if on average, a chimpanzee spent 2 min feeding on 50 cm pith of *Aframomum*

angustifolium K.Schum, the discrete food unit was estimated as 25 cm (50/2) per min. To determine the average number of discrete food units ingested per food item, records were noted at five-minute intervals throughout the feeding bout, or when observation conditions allowed. A total of 4314 records of discrete units ingested per minute were taken totaling 648 hrs of observations. A total of 1699 feeding bouts were recorded ranging from 5 feeding bouts on mature leaves to 619 feeding bouts on ripe fruit, which was the common food type. Feeding was defined as reaching for, picking, handling, or chewing a food item as well as short intervals (<5 sec) of searching (defined as searching for the next food item).

4.2.3 Food sample collection and processing

Samples of all the foods eaten during focal follows were collected in air tight bags on the same day or within the same week from the exact plant eaten by chimpanzees or from adjacent plants of the same species. Food samples were processed in a way that mimicked chimpanzee actions. For example, if the chimpanzee peeled the fruit and spat out the seed before eating the fruit, seeds were removed from the collected sample before weighing it. The samples were weighed using a portable balance to yield the "wet unit weight". At least 30 wet unit weights for each food item were taken at the end of the day (or within 24 hrs) before the same sample was dried to constant weight at ~40°C using a Nesco plant dehydrator (Rothman, Chapman, & Van Soest, 2012). This temperature was chosen to inhibit enzymatic activity and prevent chemical and physical changes, while preserving the sample's nutritional attributes (Rothman et al., 2012). Dried samples were then weighed to obtain the dry unit weight.

The dried samples were ground using a Wiley mill fitted with a 1 mm screen to obtain uniform particle size. Ground samples were analysed in the nutritional ecology laboratory at Harvard University, Anthropology Department and/or the nutritional ecology laboratory at Hunter College of the City University of New York.

4.2.4 Measuring fruit availability

To describe annual patterns of food availability, phenological data was collected monthly for 18 months (January 2014-June 2015) from 207 trees representing 19 tree species. These trees were located along permanently marked phenology transects (each 200 x 10 m = 0.2 ha) (Wrangham et al., 1998). Each phytophase was estimated using visual counts, i.e. young leaves, mature leaves, flowers, ripe fruits, unripe fruits on a 5-point scale (0=0%, 1=1-25% of the crown are, 2=25-50% of the crown area, 3=50-75% of the crown area, 4=>75-100% of the crown area) (Chapman et al., 1992). Phytophases for all trees > 10 cm DBH within the plot were recorded. Estimates of fruit abundance were based on the number of trees in the phenology sample with

non-zero scores (Wrangham et al., 1998). The proportion of trees in fruit for each species per month was determined as the number of trees of that species that had ripe fruit divided by the total number of trees of the species observed with ripe fruit for each month. The monthly fruit availability index (FAI_m) was calculated according to the equation below as in (Wrangham et al., 1998):

$$FAI_m = \sum P_{km}$$

where P_{km} denotes the proportion of the number of trees in fruit for species k in month m.

Some of the fruit tree species that were included in the phenology sample were not eaten by chimpanzees during the study period, accordingly FAI was calculated using tree species whose ripe fruits were eaten at least once during each month.

For each month the dominant fruiting tree species was determined based on which species in the phenology sample had the largest FAI.

4.2.5 Laboratory analyses

Multiple samples of the same foods were pooled to account for intraspecific variation and were analysed in duplicate. Near-infrared reflectance spectroscopy (NIRS) using a Foss XDS Rapid Content Analyzer was used to estimate concentrations of total nitrogen; and crude protein (CP) was calculated by multiplying total nitrogen by 6.25 (Rothman, Chapman, Hansen, Cherney, & Pell, 2009). Available protein (AP) (not bound by lignin in the plant cell wall) was estimated by subtracting acid detergent insoluble crude protein (ADCP) from CP. ADCP values for Kibale foods estimated by (Conklin-Brittain, Dierenfeld, Wrangham, Norconk, & Silver, 1999) were used. For the rest of the macronutrients, traditional standardized methods were used following (Conklin-Brittain et al., 1998). Lipid content was measured using petroleum ether extraction for 4 days at room temperature (Conklin-Brittain & Wrangham, 1994). Water-soluble carbohydrates (WSC) were estimated using a modified phenol/sulfuric acid colorimetric assay with a sucrose standard (Strickland & Parsons, 1972). Neutral detergent fiber (NDF with α-amylase), acid detergent fiber (ADF), and acid detergent lignin (ADL) were measured through sequential analysis using an A200 fiber analyzer (ANKOM, Macedon, NY) (Goering & Van Soest, 1970; Van Soest, Robertson, & Lewis, 1991). Hemicellulose (HC) was estimated as the difference between NDF and ADF. Cellulose (Cs) was estimated as the difference between ADF and lignin. Total nonstructural carbohydrates (TNC) was estimated by subtracting NDF, lipid, AP, and ash from 100%.

The method used by Conklin-Brittain et al. (2006) was adopted to determine dry matter, total ash, and organic matter. Nutrient values were expressed as a percentage of organic matter (OM) instead of dry matter (DM).

A dry-matter correction coefficient (g 105°C DM/g field dried sample) was calculated by drying the field-dried samples in an oven at 105°C for 8 h and weighing them hot. Total ash (g ash/g field-dried sample) was measured by ashing (burning) the same DM sub-sample at 502°C for 8h and then weighing it at 100°C. Organic matter correction coefficient of the sample was calculated as:

OM correction coefficient (g OM/g field-dried sample) = (1 - total ash) x DM correction coefficient.

These DM and OM correction coefficients were applied to the field-dried DM value to determine the grams of OM in the fresh food:

g OM/ g fresh food = field DM coefficient x final DM correction coefficient x OM correction coefficient.

4.2.6 Food and nutrient intake calculations

First, the wet weight ingested per minute for each food item was computed as the product of its wet unit weight and the corresponding average number of discrete food units eaten per minute.

Feeding rate defined as the dry weight ingested per minute (e.g. Rothman et al., 2008; Schülke, Chalise, & Koenig, 2006) was calculated as:

> Feeding rate for each food item= wet weight ingested per minute * (dry unit weight÷wet unit weight *100).

Daily amount of dry food ingested (g/day) was calculated as: dry mass = $\sum (t_i * \lambda_i)$; where t_i=time spent feeding on food item i per day (mins); λ_i= average feeding rate for item i (g/min).

Daily nutrient intake (g/day) was calculated as the product of daily amount of dry food ingested per food item and its corresponding mean nutrient content.

The metabolisable energy (ME) content per food item was computed using the equation below, following Conklin-Brittain, et al. (2006):

$$ME\ (kcal\ per\ 100g\ OM) = (4 * \%TNC) + (4 * \%AP) + (9 * \%lipids) + (1.6 * \%NDF)$$

Energy intake rate per food item per minute: average feeding rate (g/ min) * energy content (Kcal/g).

Daily energy intake (Kcal/day) was calculated as: $\sum(g_i * e_i)$; where g_i=amount of dry food of food item i ingested per day (grams); e_i= the energy content of food item i (Kcal/g).

For each day, the percent grams of fig ripe fruits, drupe ripe fruits or terrestrial herbaceous vegetation (THV: young leaves, pith or flowers) consumed was computed. From this, the dominant food type for each day was determined as the food type with the largest percent either as figs (fig-days), drupes (drupe-days) or THV (THV-days).

4.2.7 Statistical analysis

To examine the differences among food types in feeding and energy intake rates, Kruskal-Wallis (H) tests and Dunn's post-hoc tests for pairwise comparisons ($\alpha = 0.05$) were used. These tests were chosen because of the small sample sizes for some of the food types and the fact that the dependent variables did not conform to normality and homoscedasticity assumptions. To test the differences in macronutrient content among the different food types, one-way ANOVA with Welch's test was used because the data violated the assumption for equal variances. Games-Howell's post-hoc tests were used for pairwise comparisons. Linear mixed effect models were used to analyse if: 1) daily time spent feeding, grams of food ingested, macronutrient and energy intake (response variables) could be predicted by the type of fruit-month (fixed factor), and 2) daily grams of food ingested, macronutrient and energy intake (response variables) could be predicted by the dominant food type (fixed factor). A further predictor variable included in the model was foraging group size, since competition is associated with larger groups and can affect food intake (Janson, 1985; Janson, 1988). All models included the identity of the individuals as a random factor. The models were fitted by REML (Restricted Maximum Likelihood criterion) using the lmer package. The analyses were run in in SPSS version 20.0 software and R version 3.5.1.

4.3 Results

For analysis, only focal follows with a minimum of 10 hrs of observation were considered because the average total time spent observing the female chimpanzees daily was 11 hrs (SEM=0.6 hrs, range 9.6 to 12.5 hrs). Hence from a total of 210 focal follows, only 141 complete focal follows representing 1597 observation hours from January 2014 to June 2015 were used in the analysis. There were 93 complete focal observations during fig-months and 48 during drupe-months. Focal females fed on 90 different plant parts from 61 plant species.

4.3.1 Diet quality based on intake rates and nutrient content

Feeding rate (dry weight ingested per min) and energy intake (Kcal per min) varied across food types (Table 4.1). Both feeding rate and energy intake rate were fastest for ripe fruits and slowest

for woody foods such as pith and wood. Feeding rate on ripe fruits was faster than that on pith (Dunn's post-hoc test: p=0.03), and energy intake rate of ripe fruits was faster than that of young leaves (p=0.04) and pith (p=0.005).

Table 4-1: Feeding rates and energy intake rates by food type

Food type	Feeding rate (dry g/min)	Range for feeding rate	Energy intake rate (Kcal/min)	Range for energy intake rate	N
Ripe fruit					
(drupe + fig)	3.4±0.4	0.4-10.8	10.7±1.3	1.5-36.3	36
Drupe fruits	3.0±0.6	4-10.8	9.9±1.8	1.5-36.3	24
Fig fruits	4.2±0.5	1.6-7.6	12.5±1.5	4.1-22.8	12
Young leaves	2.1±0.2	0.7-4.2	6.2±0.6	1.9-11.1	19
Pith	1.8±0.2	1.0-3.1	3.4±2.2	2.3-9.1	13
Unripe fruit	3.0±0.8	1.0-5.9	9.0±3.4	2.5-16.5	7
Flower	2.7±0.3	1.8-3.5	7.7±1.0	4.3-10.1	7
Seed	2.3±1.9	0.3-8.1	6.9±5.7	0.9-23.8	4
Bark	2.9±2.1	0.8-5.1	5.7±4.3	1.5-11.1	2
Wood	0.3±0.1	0.1-0.3	0.6±0.1	0.5-0.9	3

Average intake rates for adult female chimpanzees of the Kanyawara community. Cells show mean ± standard error. Food types are arranged from the most frequently consumed through the least consumed plant parts. Differences among the 8 major plant parts analysed were significant in each of the variables measured: Kruskal wallis test (H); feeding rate: H=17.0, df=7, p=0.02; energy intake rate: H=18.2, df=7, p=0.01. N = number of species.

Feeding rate on figs was faster than on drupes (H=5.05, df=1, p=0.03; Table 4.1). By contrast, the difference between energy intake rate for figs and drupe was not quite significant (H=3.7, df=1, p=0.06) (Table 4.1).

Macronutrient composition varied considerably among food types (Table 4.2). Lipid content was greater in seeds than in young leaves, pith, bark and wood. Available protein was greater in young leaves, seeds and flowers than in ripe fruit, pith, unripe fruit and bark. WSC content was greater in ripe fruit than in all foods with the exception of pith and seeds. TNC content was greater in ripe fruit than in young leaves, seed, bark and wood. Fibre content also varied among food types. NDF, ADF, hemicellulose and cellulose contents were greater in pith and woody food types than in ripe fruits.

Table 4-2: Macronutrient concentrations (% OM) of foods eaten by female chimpanzees

Food type	%Lipid	%AP	%NDF	%TNC	%WSC	%ADF	%Ls	%HC	%Cs	N
RF	4.6±1.3	9.3±1.1	41.5±2.4	44.6±2.7	16.5±1.7	28.5±2.3	13.0±1.5	12.9±0.8	15.5±1.2	36
Figs	3.5±0.7	6.8±1.9	49.0±3.8	40.7±3.6	9.2±1.2	38.0±3.7	17.3±2.7	11.0±1.1	20.6±1.4	12
Drupes	5.2±1.9	10.6±1.3	37.7±2.9	46.6±3.7	20.1±1.2	23.8±2.5	10.9±1.7	13.9±1.1	12.9±1.4	24
YL	0.5±0.2	25.9±1.9	43.1±2.8	30.5±3.1	5.1±0.5	27.7±2.5	10.4±1.5	15.4±1.6	17.2±1.4	19
PT	0.4±0.2	7.5±2.0	58.1±3.1	33.9±2.9	15.5±2.7	32.8±1.8	5.1±0.5	25.3±1.7	27.7±1.6	13
UF	2.9±1.0	7.1±2.3	51.1 ±4.0	38.8±3.0	8.9±1.8	37.1±6.0	17.8±4.6	13.9±2.9	19.3±2.0	7
FL	2.8±1.3	28.4±3.8	55.5±4.1	13.2±4.0	4.5±0.4	37.5±4.0	23.3±3.0	18.0±1.1	14.1±1.1	7
SD	5.3±1.4	30.4±7.5	48.4±4.8	15.8±4.6	11.2±3.1	21.8±2.3	9.3±1.2	26.6±3.5	12.5±1.5	4
BK	0.0±0.0	13.8±5.1	87.0±3.3	1.7±0.7	1.9±0.5	45.8±4.2	7.1±2.5	41.1±0.9	38.7±6.7	2
WD	0.0±0.0	12.0±11.9	71.9±19.5	16.0±7.6	1.9±0.9	40.5±0.0	19.1±0.0	31.4±0.9	21.4±0.1	3

Data source: same as for Table 4.1. Cells show mean ± standard error.

RF, ripe fruit; YL, young leaves; PT, pith; UF, unripe fruit; FL, flower; SD, seed; BK, bark, WD, wood. AP, Available protein; WSC, Water soluble carbohydrates; NDF, Neutral detergent fiber; TNC, Total non-structural carbohydrates; Ls, Lignin; ADF, Acid detergent fiber; HC, Hemicellulose; Cs, Cellulose. All values represent percentage of organic matter.

As expected, the concentration of WSC was greater in drupes than in figs, whereas some of the fibre indices such as NDF, ADF and cellulose content were greater in figs than in drupes. For the rest of the macronutrients, there was no significant difference in their composition among the fruit types (Table 4.2).

4.3.2 Contrasts in behavior and intakes between drupe-months and fig-months

Based on the fruit abundance indices, four months were identified as drupe-months and 14 months as fig-months (Table 4.3).

Table 4-3: Summary of fruit abundant tree species, feeding observations and group size used in the analysis

Month	Fruit-month	[a]Dominant fruit available	[b]Total number of feeding bouts	No. of food types eaten	Average group size	FAI
January 2014	Drupe	*Mimusops bagshawei* S.Moore	70	18	19	12.4
February 2014	Fig	Figs	81	20	27	7.3
March 2014	Fig	Figs	87	25	13	9.0

Month	Fruit-month	[a]Dominant fruit available	[b]Total number of feeding bouts	No. of food types eaten	Average group size	FAI
April 2014	Fig	*Ficus dawei* Hutchinson	138	30	11	7.9
May 2014	Fig	*Ficus dawei* Hutchinson	55	23	17	7.9
June 2014	Drupe	*Aningeria altissima* A. Chev and *Uvariopsis congensis* Robyns & Ghesq	94	30	15	7.3
July 2014	Fig	*Ficus natalensis* Hochst	137	39	14	8.4
August 2014	Fig	*Ficus capensis* Thunb	121	28	8	5.1
September 2014	Fig	*Ficus natalensis* Hochst	126	36	4	6.7
October 2014	Drupe	*Celtis gomphopylla* Baker	100	29	5	15.7
November 2014	Fig	Figs	86	22	6	12.4
December 2014	Fig	Figs	103	25	6	13.4
January 2015	Fig	*Ficus natalensis* Hochst	79	24	9	8.9
February 2015	Fig	*Ficus brachylepis* Welw. ex Hiern	127	25	11	9.0
March 2015	Fig	Figs	77	26	10	14.0
April 2015	Fig	Figs	70	24	4	10.1
May 2015	Fig	Figs	68	24	14	18.0
June 2015	Drupe	*Uvariopsis congensis* Robyns & Ghesq	80	15	20	24.7

[a]*Dominant fruit available was based on the FAI for each month. In some of the months, more than one fruit species was abundant. If they were all Ficus species, then the dominant fruit available was scored as "figs".* [b]*Total number of feeding bouts represents the number of times a particular food item was continuously fed on for atleast 5 minutes or more before the focal individual ate a different food item.*

Although the monthly proportion of trees in fruit was consistently lower than the proportion containing young leaves or flowers (Figure 4.1a), ripe fruit dominated the diet of chimpanzees (62% ripe fruit, 21% young leaves, and 1 % flowers: based on grams ingested) (Figure 4.1b). Mean foraging group size was larger during drupe-months (13±2 chimpanzees) than in fig-months (10±1 chimpanzees), but the difference was not significant ($F_{1,139}=3.2$, $p=0.07$).

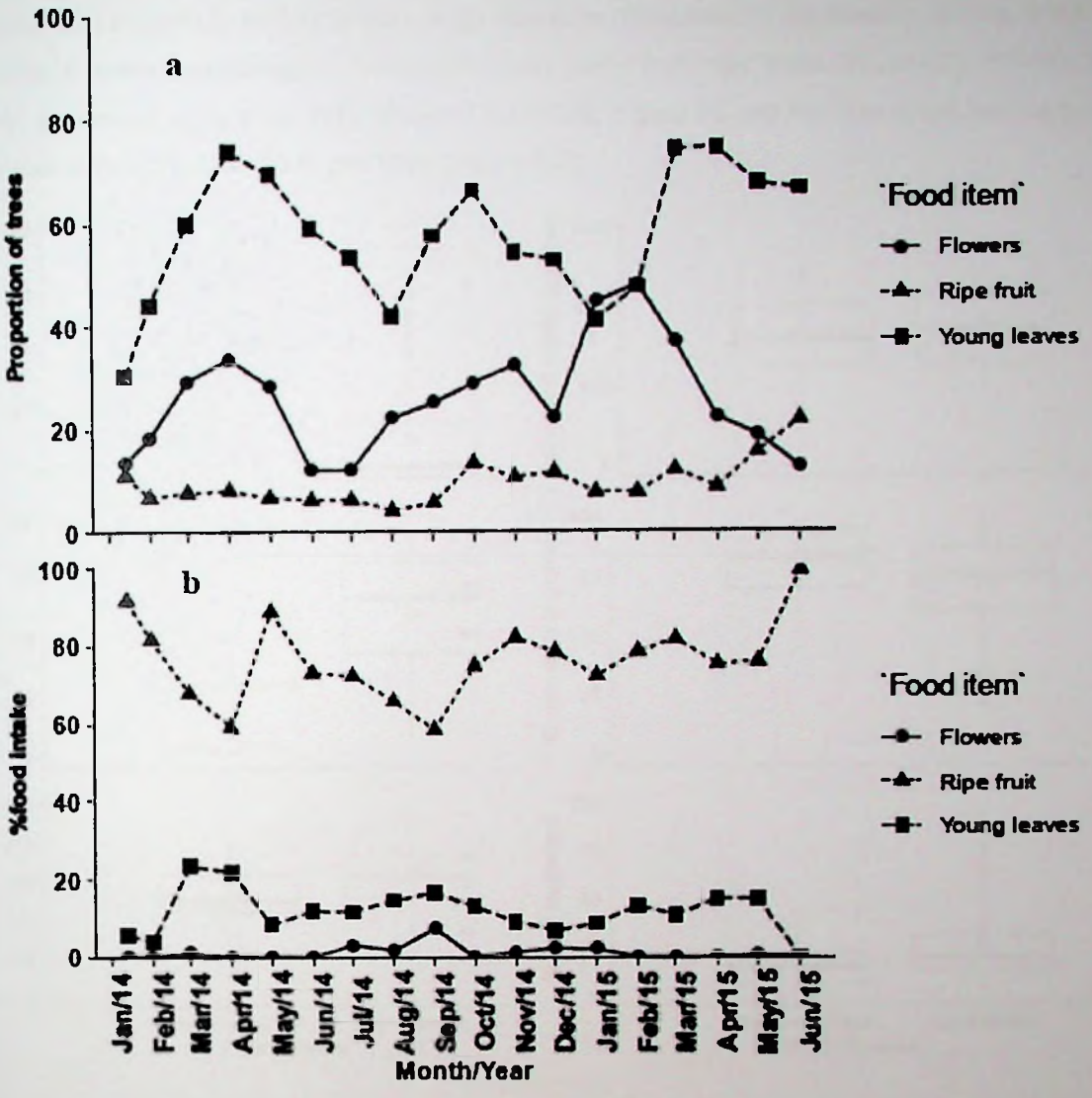

Figure 4-1: Fluctuations in flower, ripe fruit and young leaves (a) availability and (b) intake (based on weight) between January 2014 and June 2015. *Number of monitored trees for phenology =207 trees representing 19 species.*

Across all the months, the mean daily time spent feeding, dry mass ingested and energy intake were 308.7±85 mins, 872.6±289 g, and 2479.4±858.1 Kcal respectively. Throughout the study period, figs accounted for the largest proportion of ripe fruit intake (69.2%). Drupe fruits accounted for a larger proportion in drupe-months than in fig-months ($F_{1,17}$=18.9, p=0.001), whereas figs accounted for the largest proportion during fig-months ($F_{1,17}$=12.5, p=0.003) (Figure 2). The total dry weight of food ingested per day did not vary between drupe-months and

fig-months ($F_{1,139}$=0.2, p=0.6) (Figure 4.2). However, compared to fig-months, during drupe-months, a greater percentage of dry-weight intake came from ripe fruits ($F_{1,139}$=5.2, p=0.02), a lower percentage came from THV ($F_{1,139}$=5.7, p=0.02; Figure 2), and the time spent feeding per day was 20% less ($F_{1,139}$=10.0, p=0.002) (Figure 4.2).

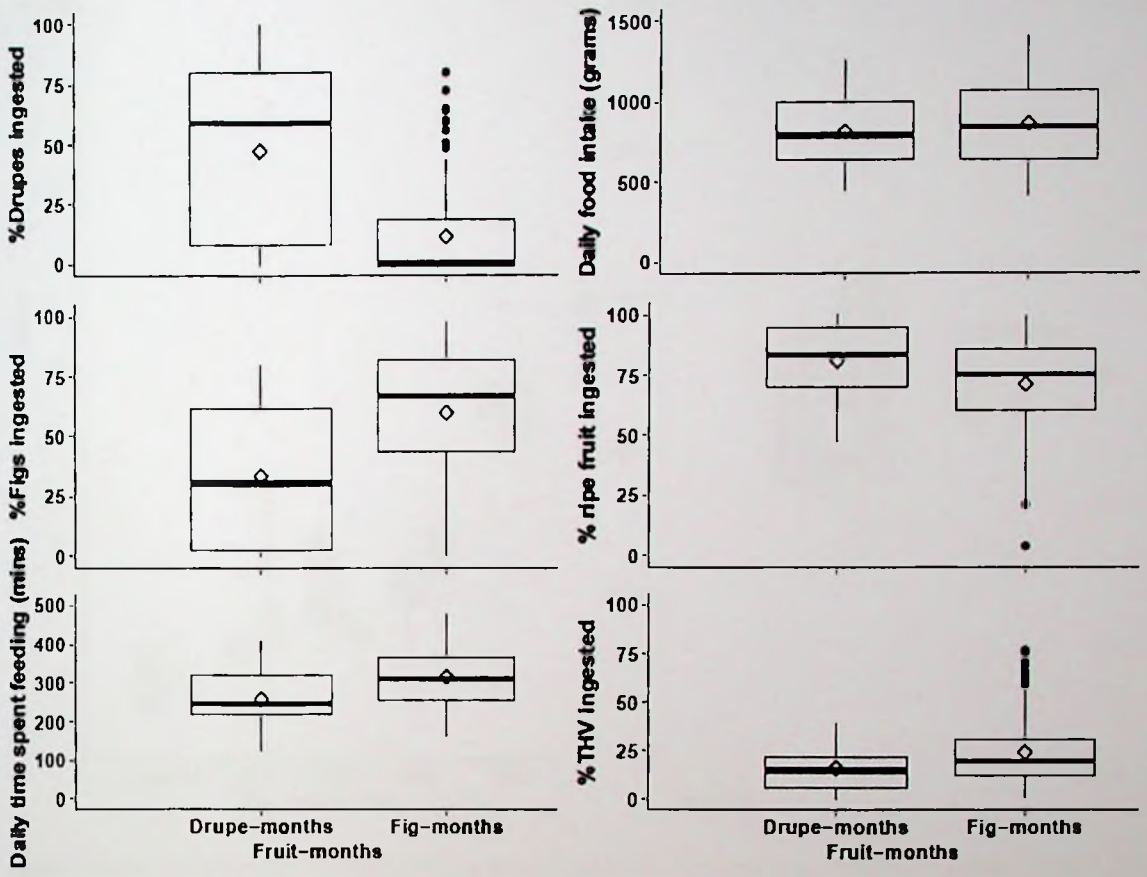

Figure 4-2: Variation in the proportion of drupes and figs ingested, time spent feeding and daily food intake and the proportion of ripe fruit and THV consumed between the fruit months. *N for drupe-months and fig-months= 4 and 14 months respectively. The diamond symbol indicates the mean; boxes show the lower and upper quartiles, horizontal middle line indicates the median; whiskers denote the minimum and maximum values; black circles denote the outliers.*

As with food intake, metabolisable energy intake did not differ significantly between drupe-months and fig-months ($F_{1,139}$=0.01, p=0.9; Figure 4.3). Nutrient composition did vary, however, in drupe-months female chimpanzees consumed more WSC and lipid and less NDF (Kcal/day) than in fig-months (WSC: $F_{1,139}$=13.2, p=0.0004, lipid: $F_{1,139}$=4.5, p=0.04; NDF: $F_{1,139}$=4.0,

p=0.05). In drupe-months intake of AP (Kcal/day) was also slightly less than in fig-months ($F_{1,139}$=3.6, p=0.06). TNC intake did not vary by type of fruit-month (TNC: $F_{1,139}$ = 0.9, p=0.3) (Figure 4.3).

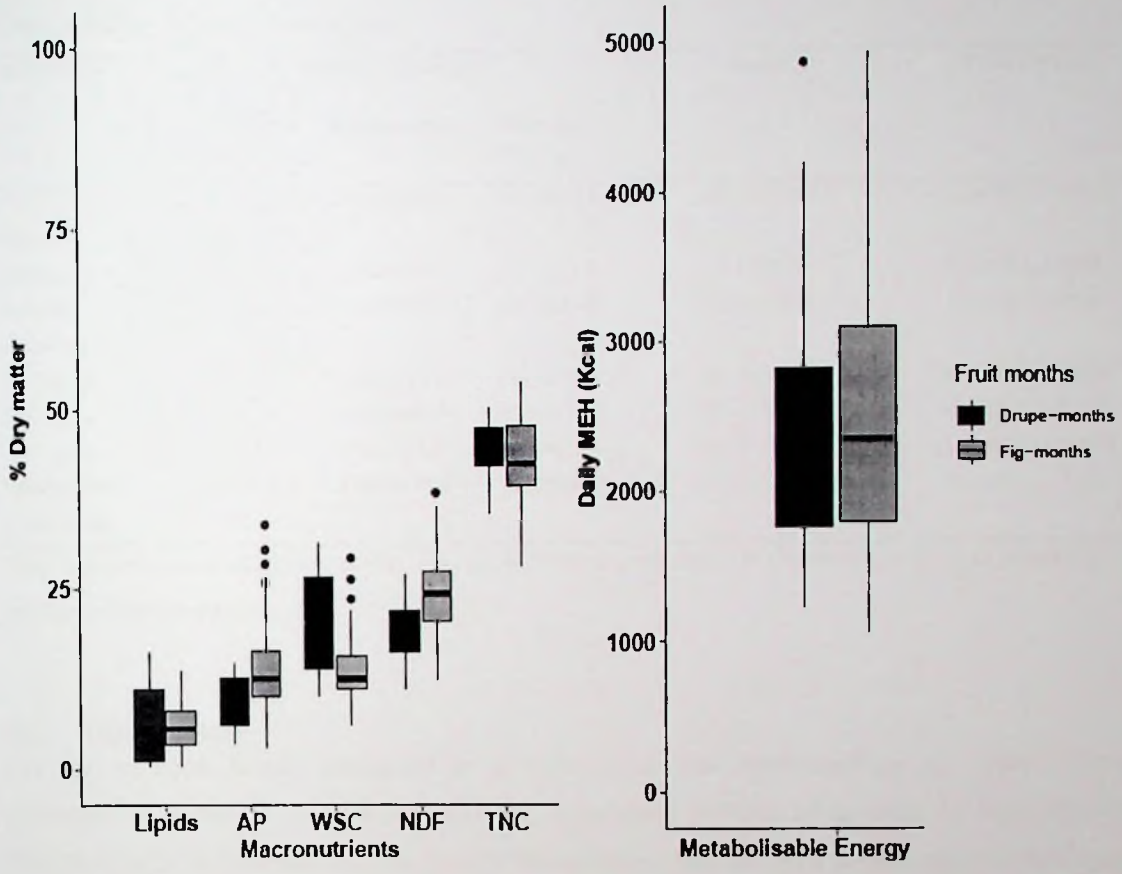

Figure 4-3: Variation of average daily metabolizable energy and macronutrient intake across the fruit months. N for drupe and fig-months= 4 months and 14 months respectively. *The boxes show the lower and upper quartiles, horizontal middle line indicates the median; whiskers denote the minimum and maximum values; black circles denote the outliers.*

In addition to comparing feeding success between months, the effect of diet composition between days on intake was considered. The findings show that on drupe-days female chimpanzees ingested more food (dry weight) and metabolizable energy than on THV-days (Table 4.4). Intake of WSC was greater on drupe-days than on either fig-days or THV-days, whereas available protein intake was greater on THV-days than on drupe-days or fig-days. TNC intake on drupe-days and fig-days was greater than that on THV-days. Intake of NDF was

greater on fig-days than on THV-days. Lipid intake did not vary among the days dominated by different food types (Table 4.4).

Table 4-4: Variation in daily food, macronutrient and metabolisable energy intake among days dominated by different food types

Daily intake	Dominant food type			Range	F and p-value
	Non-fig days (22)	Fig days (76)	THV days (43)		
Food ingested (grams)	930.7±70.9	924.7±32.2	750.8±37.8	409.0-1716.7	$F_{2,138}$=5.9, p=0.004
Lipid (Kcal)	202.8±49.5	200.6±14.4	149.5±12.7	8.1-726.2	$F_{2,138}$=2.1, p=0.13
Available protein (Kcal)	317.7±38.5	340.9±14.5	410.3±31.0	92.2-1420.4	$F_{2,138}$=3.3, p=0.04
WSC (Kcal)	792.3±89.2	400.2±19.3	344.4±31.4	83.2-2033.3	$F_{2,138}$=29.6, p=0.0001
TNC (Kcal)	1547.8±138.3	1325.2±60.9	1073.9±74.3	453.1-3373.8	$F_{2,138}$=6.1, p=0.003
NDF (Kcal)	638.0±46.7	722.9±25.5	534.9±27.8	243.9-1390.2	$F_{2,138}$=11.0, p=0.0001
Metabolisable energy (Kcal)	2706.2±221.4	2589.5±94.5	2168.6±113.7	1240.3-4931.0	$F_{2,138}$=4.4, p=0.01

Cells show mean ± standard error. The number in parenthesis is the number of days when that food type dominated the diet.

4.4 Discussion

The diet of adult female chimpanzees in Kanyawara was dominated by ripe fruits whether calculated in terms of contributing species, time spent feeding or amount of food ingested. Nevertheless as in previous studies, female chimpanzees also fed on a diverse array of food types from different plant species including young leaves, pith and unripe fruit (Basabose, 2002; Newton-Fisher, 1999; Watts, Potts, Lwanga, & Mitani, 2012).

Ripe fruits are high-quality foods with high soluble sugar content and low fibre content compared to other diet items that were eaten by female chimpanzees (Conklin-Brittain et al., 1998; Wrangham et al., 1998). While ripe fruits are an important source of calories in the form of digestible carbohydrates, they have lower levels of protein and minerals. Therefore, despite being ripe fruit specialists, chimpanzees may have to complement and balance their fruit-based diet with other foods such as young leaves which are rich in protein. Furthermore, it was noted that feeding rates of fibrous foods such as pith were generally slow compared to other food types. This is because high-fibre foods tend to require longer mastication, as has been demonstrated in mammalian herbivores such as deer and some primates (Oftedal, 1991; Spalinger, Hanley, & Robbins, 1988).

The findings are commensurate with previous studies of Kanyawara chimpanzees, in that energy intake rates of figs and drupes were comparable, and figs contained less soluble carbohydrates and more fibre than drupes (Conklin-Brittain & Wrangham, 1994; Wrangham et al., 1993). Additionally, the results show that female chimpanzees were likely to ingest more dry grams per minute when feeding on figs than when feeding on drupes, apparently due to the low handling cost for figs given that figs are normally consumed whole, without any prior processing (Leighton, 1993). However, the high water and fibre content of figs leads to lower energy contributions than drupe fruit (Leighton, 1993; Wrangham et al., 1993). Compared to gorillas who have a relatively longer hind-gut, chimpanzees may digest fibre less efficiently (National Research Council, 2003). High-fibre parts of the food were often either discarded by chimpanzees as a wadge or were passed out in faeces.

Compared to drupe-months, in fig-months female chimpanzees increased the proportion of fibrous foods in their diet (i.e. figs and THV), and spent more time feeding. However despite the increase in feeding time, there was no commensurate increase in food intake, presumably because the fibre-rich foods that were eaten in greater amounts were eaten more slowly (Oftedal, 1991). The foraging strategy employed by female chimpanzees during fig-months was thus typical of frugivorous primates during fruit-scarce periods, involving changes both in diet composition and in time spent feeding (Clink et al., 2017; Conklin-Brittain et al., 1998; Doran, 1997; Felton et al., 2008; Irwin et al., 2014; Tutin et al., 1997).

The fluctuations in drupe fruit availability resulted in monthly variations in macronutrient intake. Increased consumption of fig-fruits resulted in reduced intake of WSC and lipids. There was also an increased intake of available protein and NDF, with the increase in available protein coming from the greater intake of THV, whereas the increase in NDF intake came mainly from figs, and not from THV as is sometimes assumed (Conklin-Brittain et al., 1998; Wrangham et al., 1998). These adjustments in behavior and diet to reductions in diet-quality during fig-months allow chimpanzees to compensate for energy shortages in the diet (Chapman, Wrangham, & Chapman, 1995; Conklin-Brittain & Wrangham, 1994). The larger foraging group size during drupe-months may be an indication that larger groups have better quality diets and habitats (Wright et al., 2015).

The average daily calorie intake of female chimpanzees estimated in this study (2500 Kcal) was slightly greater than but comparable to the estimate from a previous study of Kanyawara chimpanzees (2340 Kcal) (Conklin-Brittain, Knott, & Wrangham, 2006). The difference might be due to the fact that the previous study combined feeding rates of both male and female

chimpanzees and did not estimate feeding rates for piths, which are some of the important fallback foods for chimpanzees. Also, in the previous studies present the average of all females irrespective of their reproductive state. Additionally, the study subjects were nursing mothers that might be consuming extra calories per day to meet the high energy costs of milk production (Gittleman & Thompson, 1988; Oftedal & Hudson, 1985). This partly explains why the estimated calorie intake was greater than that for human females at 2000 Kcal.

Critically, the results indicate that despite the variation in energy density among available foods, there was no monthly variation in metabolisable energy intake. This finding is commensurate with a previous study of Kanyawara chimpanzees (Conklin-Brittain, et al., 2006), and with results from mountain gorillas, western gorillas and western chimpanzees (Masi et al., 2015; N'guessan et al., 2009; Rothman et al., 2008; Wright et al., 2015).

The lack of significant monthly variation in metabolisable energy intake at Kanyawara may be due partly to the lack of mast fruiting periods, unlike those reported to cause large fluctuations in net caloric gain rates among Ngogo chimpanzees (10 km to the south of Kanyawara) and orangutans (Knott, 1998; Potts, Baken, Ortmann, Watts, & Wrangham, 2015). Additionally, unlike orangutans which feed on a 100% fruit based diet during the months of high fruit production (Knott, 1998), female chimpanzees included lower-quality fall back foods in their diet even when preferred foods were abundant, contrary to the prediction. The fact that female chimpanzees ingested more calories on days when the diets were dominated by ripe fruits (whether figs or drupes) than on days when THV dominated the diets is an indication that if female chimpanzees fed exclusively on ripe fruit when drupe or fig fruits are abundant, there would be significant peaks in energy intake across the fruit-months. However, it seems that female chimpanzees are not interested in maximizing energy intake at the expense of other macronutrients.

Although there was no difference in energy intake between drupe-months and fig-months, there were two other changes that could be important. Firstly, macronutrient composition changed: there was reduced intake of WSC and lipids during fig-months. An indication that chimpanzees just like other primates such as orangutans, red colobus monkeys (*Piliocolobus trephosceles*), black howler monkeys (*Alouatta pigra*), and yellow baboons (*Papio cynocephalus*) are nutritionally stressed when preferred foods are scarce (Behie, Pavelka, & Chapman, 2010; Chapman, Saj, & Snaith, 2007; Gesquiere et al., 2008).

Secondly, time spent feeding was reduced during drupe-months, suggesting that there was a reduction in foraging costs. This would likely result in increased positive energy balance during

drupe-months. And since increased intake of digestible carbohydrates seems to fluctuate in parallel with environmental food abundance, increased intake of WSC and lipids could in theory serve as a cue to trigger increased reproductive effort (Emery Thompson, 2013). The findings thus suggest that variation in energy intake may not be the only reason why reproductive effort is associated with diet quality, as indicated in chimpanzees and other primates such as Hanuman langurs (*Presbytis entellus*), Assamese macaques (*Macaca assamensis*) (Emery Thompson & Wrangham, 2008; Heesen, Rogahn, Ostner, & Schülke, 2013; Koenig, Borries, Chalise, & Winkler, 1997; Wallis, 1995). Further research is needed to test the idea that macronutrient composition, and foraging costs imposed by increasing feeding time, can affect reproductive effort independently of energy intake.

4.5 Conclusion

The findings reveal that on days when more ripe fruit were eaten the amount of metabolisable energy ingested by female chimpanzees was greater. In contrast to the comparison among days, however, comparisons among months (drupe-months versus fig-months) suggest that females maintained a consistent mean energy intake of around 2500 Kcal per day. The fact that mean energy intake did not vary in relation to monthly changes in the availability of preferred foods requires further investigations of the commonly found positive correlations between reproductive performance and food quality. Variations in macronutrient composition and time spent foraging provide candidate explanations.

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CHAPTER FIVE: NUTRITIONAL STRATEGIES OF FEMALE CHIMPANZEES (PAN TROGLODYTES)

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ABSTRACT

Primate diets are comprised of various food components that are composed of different macronutrients which vary in time and space. Therefore, primates are daily faced with a challenge of choosing foods which will help them achieve their nutrient intake target. By using the geometric framework for nutrition, this study sought to understand how Kanyawara female chimpanzees achieve their nutrient intake target in the face of ecologically driven nutritional constraints. Three objectives were explored, to: examine the contribution of the various food types to chimpanzee diet; investigate how the balance of non-protein energy (NPE) and protein (P) varies according to fluctuations in diet composition; and determine whether the mean daily ratio of NPE to P of female chimpanzee is similar to that of frugivorous spider monkeys. Female chimpanzees achieved a statistically indistinguishable nutrient intake on fruit-days regardless of whether drupes or figs were the dominant fruit, and to do so they changed their intake of non-fruit foods (THV) to balance the diet. Even on days when fruits were scarce and protein rich foods were abundant (THV-days), chimpanzees did not overconsume protein but instead regulated its intake tightly. These findings suggest that just like spider monkeys, chimpanzees tightly regulated protein intake but allowed energy intake to vary following variation in diet composition. This study demonstrates that female chimpanzees reached their intake target (balance between protein and nonprotein energy intake) by consuming nutritionally balanced foods (figs and drupes) or by alternating between nutritionally complementary foods (fruits and THV).

Key words: geometric framework of nutrition, protein, non-protein energy, rule of compromise

5.1 Introduction

To fully understand how primates meet their nutritional needs, one needs to decipher the ways in which animals respond to an ecologically-driven fluctuating diet, and its nutritional implications. Animal diets are comprised of numerous foods which are comprised of different nutrients. The particular nutrients and quantity required by the animal might change with circumstances such as health, growth stage and reproductive state (Raubenheimer & Simpson, 2016). Similar to humans, nutrient imbalance, deficiencies, or overconsumption affect the activity, health, growth, reproduction and survival of non-human primates (Barboza, Parker, & Hume, 2009; Oftedal, Whiten, Southgate, & Soest, 1991). Consequently, primates tend to ingest foods that maximize health and fitness. For example, the consumption of carbohydrate rich foods has been associated with increased rate of sexual swellings and ovulations among female chimpanzees (*Pan troglodytes schweinfurthii*) (Emery Thompson & Wrangham, 2008). In blue monkeys (*Cercopithecus mitis*), increase in energetic stress is associated to a shift in diet to fallback foods and other non-preferred food items (Foerster, Cords, & Monfort, 2012). The lifetime fitness of baboons (*Papio anubis*) can be predicted by dietary energy and protein (Altmann, 1991, 1998).

According to optimal foraging theory, animals should optimize intake of energy or protein to maximize fitness (Pyke, Pulliam, & Charnov, 1977; Stephens & Krebs, 1986). However, given the complexity of primate diets coupled with the complexity of nutrients that they provide as well the complexity of consumers' responses to changes in the diets, it is seems unlikely that a single optimization strategy, such as energy can account for food choices. More recently, the application of nutritional geometry (Simpson & Raubenheimer, 2012) has demonstrated that primates use several optimization strategies to achieve a particular daily nutrient 'intake target', often in terms of protein and non-protein energy. For example, frugivorous Bolivian spider monkeys (*Ateles chamek*) have an intake target of non-protein energy to protein ratio that is 8:1 (Felton, Felton, Wood, et al., 2009), while more folivorous mountain gorillas (*Gorilla beringei*) have a target NPE to P of 4:1 during fruit abundant seasons (Rothman, Raubenheimer, & Chapman, 2011).

However, due to fluctuations in food availability, primates may not be able to easily reach their intake targets in all seasons or environments. In such cases the animal is forced to trade-off between over-eating and/or under-eating some nutrients (Raubenheimer and Simpson, 2009). For example, mountain gorillas consume more available protein than they need to meet an energy target when faced with seasonal fruit fluctuations (Rothman et al., 2011; Rothman, Dierenfeld,

Hintz, & Pell, 2008). Frugivorous spider monkeys maintain a stable daily protein intake while overconsuming non-protein energy (available carbohydrates and fats) during fruit-abundant seasons; perhaps to ensure they meet protein needs as they maximize available energy (Felton, Felton, Raubenheimer, et al., 2009; Felton, Felton, Wood, et al., 2009). Unlike folivorous gorillas, folivorous diademed sifakas (*Propithecus diadema*) maintain nutrient balance irrespective of the fluctuations in fruit availability while varying the total macronutrient intake (Irwin *et al.*, 2015). The trade-off, called the "rule of compromise" and intake target, is expected to differ among species according to their particular ecological circumstances. For example, even though gorillas and sifakas are both folivorous, their rule of compromise is different. Hence, it is imperative that we understand the intake target and rule of compromise for different primate species, as well as the reasons behind a species rule of compromise.

Chimpanzee diet is complex in that it is comprised of different food items and types (Basabose, 2002; Tutin, Ham, White, & Harrison, 1997; Watts, Potts, Lwanga, & Mitani, 2012; Wrangham et al., 1991). As ripe fruit specialists, chimpanzees frequently select and ingest large volumes of fruits that are rich in non-fibrous carbohydrates and calories (Conklin-Brittain, *et al.*, 2006; 1998; Wrangham *et al.*, 1998). Variations in diet composition and nutrient intake in chimpanzees are attributed to temporal fluctuations in fruit availability, specifically preferred fruits (Basabose, 2002; Conklin-Brittain, Knott, & Wrangham, 2006; Conklin-Brittain, et al., 1998; Furuichi, Hashimoto, & Tashiro, 2001; Tutin et al., 1997). When preferred fruits are scarce, chimpanzees adjust their behavior and foraging strategy by increasing the dietary diversity which leads to increased intake of fibrous foods such as young leaves, pith and staple fallback foods such as figs (Tutin et al., 1997; Watts et al., 2012; Yamagiwa & Basabose, 2006; Yamakoshi, 1998).

Kanyawara chimpanzees are reported to prefer drupe-fruits (hereafter referred to as drupes), which are high quality foods due to the fact that they are rich in digestible energy (Conklin-Brittain *et al.*, 1998; Wrangham *et al.*, 1993). Unlike fig fruits (hereafter referred to as figs) which are available and relatively abundant all year, drupes are rare and their availability is very inconsistent (Chapman *et al.*, 1994; Wrangham *et al.*, 1991). To this end, chimpanzees are reported to experience a 46% reduction in energy intake following fluctuations in fruit-availability (Conklin-Brittain, *et al.*, 2006). In a recent study, it was revealed that female chimpanzees experience large daily variation in energy intake following changes in diet composition (Uwimbabazi et al., 2019). Despite the fair documentation on macronutrient and energy intake in chimpanzees (Conklin-Brittain, et al., 2006, 1998; Wrangham, Conklin-Brittain, & Hunt, 1998), it remains unclear how chimpanzees respond to nutrient reductions during the

drupe-fruit scarce seasons. This study therefore sought to understand the intake target in terms of protein (P) and non-protein energy (NPE) and rule of compromise of chimpanzees using the geometric framework.

The aim of this study was to understand the intake target and rule of compromise of the Kanyawara female chimpanzees in Kibale National Park, Uganda. The specific objectives were to: 1) examine how various food sources contribute nutritionally to the chimpanzee diet by comparing the proportions of the various food sources in the diet to the proportions of daily nutrients they provide; 2) examine whether the mean daily ratio of NPE to P is similar to other frugivorous primates such as spider monkeys (Felton, Felton, Wood, et al., 2009); and 3) investigate how the balance of NPE and P vary according to environmentally driven fluctuations in ripe drupes. Fruits are expected to provide the most dietary sugar and fat, while terrestrial herbaceous vegetation are expected to provide the most daily protein (Masi et al., 2015; Rothman et al., 2011). Furthermore, it was expected that P intake to be less variable than NPE intake because chimpanzees regularly prefer seasonal fruit over terrestrial herbaceous vegetation (Wrangham et al., 1996, Newton-Fisher et al., 1999, Basabose 2002).

5.2 Methods

This chapter builds on the preceding chapter and therefore the same data set and approach for field data collection was used. The detailed descriptions are included in sections 4.2.1, 4.2.2, 4.2.3, 4.2.4, 4.2.5 and 4.2.6 of Chapter Four.

5.2.1 Food and nutrient intake calculations

In addition to the variables used in Chapter Four, the following variables were calculated:

1) The proportion of daily nutrient from different food types was calculated as:

$$(DN_i \div TDaily\ Energy\ Intake) * 100$$

where DN_i is the daily amount of nutrient from food type i (young leaves, ripe fruit, pith, unripe fruit, flowers and seeds).

2) Daily non-protein energy (NPE) = TNC (Kcal) + [illegible] (Kcal) + NDF (Kcal)

3) Daily available protein = [illegible] AP (Kcal) per day

5.2.2 Statistical analysis

Two-way ANOVA was used to compare the proportions of nutrients contributed by the different food items to daily nutrient intake. Welch's test was used because the data violated the assumption for equal variances and Games-Howell's posthoc tests were used for pairwise comparisons. Linear mixed effect models were used to analyse if: 1) the contribution of different

macronutrients to total metabolizable energy intake (response variables) differed due to daily diet composition or due to fruit availability (fixed factors), and 2) daily available protein and non-protein energy intake (response variables) differed due to variations in dominant food type or fruit available (fixed factors). All models included the identity of the individuals as a random factor. The models were fitted by REML (Restricted Maximum Likelihood criterion) using nlme package (R Core Team, 2015). The Akaike (AIC) selection criterion was used to identify the best model. The relative percentage contributions (% of total energy) to the diet by available protein, carbohydrate (NDF+TNC) and fat were also examined using three variable right angled mixtures (Raubenheimer, 2011).

5.3 Results

5.3.1 Feeding behavior and Diet Composition

The contrasts in feeding behavior and diet composition between the fruit-months and among days dominated by different food types are reported in section 4.3.2. However, to ease readability, some of the information is repeated in this section as it will be referred to in the subsequent sections in this chapter.

Daily time spent feeding increased by 20% during the fig-months but this did not translate in increased dry matter intake in the fig-months (refer to Figure 4.2). On a daily basis however, chimpanzees spent more time feeding and ingested less dry matter on THV-days than on fig or drupe-days (refer to Figure 4.2). The daily diet of female chimpanzees varied in that it was comprised of different food items of which ripe fruits accounted for the largest proportion. Additionally, the dominant food type varied on a daily basis whereby figs dominated the diet for most days followed by terrestrial herbaceous vegetation (piths, young leaves, flowers and seeds) and lastly drupes. Furthermore, the diet of female chimpanzees varied following fluctuations in fruit availability whereby drupes accounted for largest proportion of the diet during drupe months (drupes: 47%, figs: 33% of dry matter) and large amounts of figs were consumed during the fig-months (figs: 60%, drupes: 11.4% of dry matter). The diet of female chimpanzees was dominated by ripe fruit irrespective of the fruit-months (drupe-months: 81% and fig-months: 71%). However, they consumed more THV during fig-months than drupe-months (24% > 16% of dry matter) ($F_{1, 128}=4.0$, $p=0.04$) (Figure 4.2).

For the days dominated by different food types: ripe fruit consumption on drupe (84%) and fig-days (80%) was greater than on THV-days (55%) ($F_{2, 128}=41.8$, $p=0.0001$). In contrast, chimpanzees consumed greater amount of THV on THV-days (38%) than on drupe (12%) or fig-days (17%) ($F_{2, 128}=38.4$, $p=0.0001$).

5.3.2 Nutritional contributions to the diet

Contributions of nutrients by different food items to daily energy intake

Ripe fruit contributed the largest proportion of lipids, carbohydrates and fibre compared to all the other food items (Table 5.1). Young leaves and ripe fruit contributed comparable and largest proportion of available protein to the daily energy intake (Table 5.1). In regards to ripe fruit, figs supplied female chimpanzees with majority of their lipids, protein, TNC and NDF (Table 5.1).

Table 5-1: Weight based intakes of different food items and proportion of nutrients contributed food items to daily energy intake

Food item	Lipid (%) ($F_{8,468}=61.2$, $p=0.001$)	AP (%) ($F_{8,468}=31.4$, $p=0.01$)	NDF (%) ($F_{8,468}=141.8$, $p=0.003$)	TNC (%) ($F_{8,468}=263.9$, $p=0.001$)	P:NPE ($F_{6,89}=16.8$, $p=0.001$)
Ripe fruit	6.0±0.4	6.5±0.3	19.6±0.7	41.3±1.2	0.14
Drupes	2.5±0.5	3.1±0.3	6.6±0.9	21.8±2.3	0.15
Figs	5.1±0.3	5.3±0.3	17.6±0.8	32.0±1.4	0.10
Young leaves	0.1±0.0	7.1±0.6	3.5±0.3	5.7±0.4	0.59
Pith	0.0±0.0	0.8±0.1	2.6±0.3	2.9±0.3	0.14
Unripe fruit	1.4±0.3	1.3±0.3	2.8±0.6	5.1±1.1	0.11
Seed	1.6±0.5	2.8±0.6	1.6±0.7	1.4±0.6	0.75
Flowers	1.7±0.8	3.6±0.7	3.3±0.9	2.5±1.0	0.79
Bark	0.0±0.0	1.9±0.6	3.4±1.1	0.2±0.1	0.38
Wood	0.0±0.0	0.0±0.0	0.6±0.2	0.1±0.0	0.27
Mature leaves	1.0±0.2	2.8±0.7	2.6±0.6	4.4±1.1	0.3

Cells represent mean ±SE, ***P:NPE*** *is the mean for the ratio between protein and nonprotein energy (TNC+Lipids+NDF) for the different food types*

5.3.3 Nutrient balancing strategies

Using right-angled mixture triangles (RMTs), we found that on a daily basis, female chimpanzees consumed a diet which contained a variable contribution of carbohydrates (TNC+NDF) to metabolizable energy, a relatively consistent contribution of lipids and protein contribution (Figure 5.1).

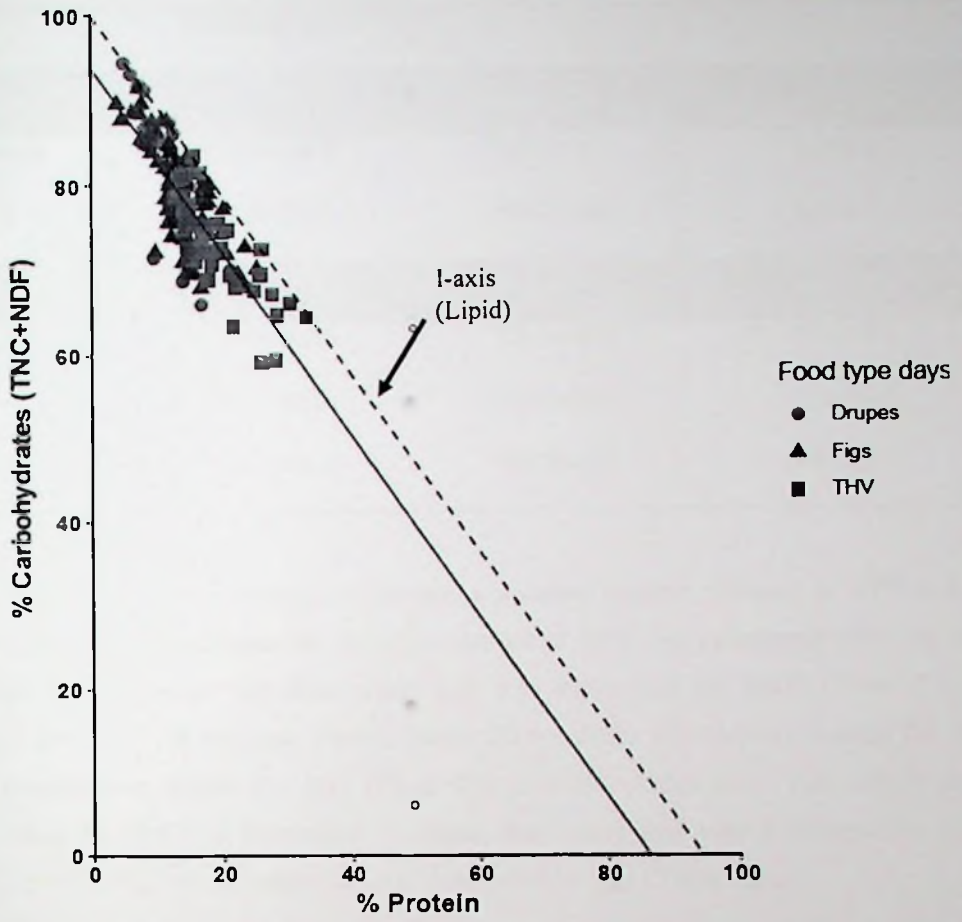

Figure 5-1: Right-Angled Mixture Triangle (RMT) showing the mean relative components of metabolizable energy (ME) from the dominant food types. X-axis: is % ME from protein, Y-axis: % ME from carbohydrates (TNC+NDF), I-axis (implicit axis): R^2 of 0.65, slope is -1.09.

Protein and non-protein energy intake

Daily intake of protein and NPE averaged at 354.5 ±12.3 (Kcal) and 2099.0 ± 66.2 (Kcal) respectively. Daily protein and non-protein energy (NPE) did not differ among fruit-months (LMM ANOVA p>0.05) (Table 5.2). As reported in Chapter Four, total daily energy intake did not differ among the fruit-months ($F_{1,129}=0.5$, $p=0.49$). Yet, the ratio NPE:P differed significantly among the fruit-months being larger during the drupe-months than in the fig-months ($F_{1,127}=6.6$, $p=0.001$) (Table 5.2).

Table 5-2: Mean intakes of NPE and protein across fruit-months and days dominated by different food types

	Non-protein energy	Protein (Kcal)	NPE:P

	(NPE) (Kcal)		
Fruit-month			
Drupe-month	2253.0±168.7	309.7±34.5	8.5±0.8
Fig-month	2067.3±71.9	363.7±12.9	6.4±0.3
Dominant food type			
Drupe-days	2384.0±192.9	326.5±45.5	9.1±1.0
Fig-days	2203.7±88.1	338.0±15.0	7.2±0.4
THV-days	1795.1±103.3	394.9±20.2	4.9±0.3

On a daily basis however, female chimpanzees consumed varying amounts of NPE and protein depending on the diet composition. A larger amount of NPE was consumed when the diet was dominated by drupes or figs than when diet was dominated by THV (Table 5.2) (NPE: $F_{2,128}=5.7$, $p=0.004$). In contrast, protein intake did not differ significantly despite the variation in diet composition across the days ($F_{2,128}=2.6$, $p=0.08$) (Table 5.2). The NPE:P ratio was greater when the diet was dominated by drupes than when diet was dominated by THV ($F_{2,128}=16.7$, $p=0.0001$), but not when diet was dominated by figs (Table 5.2).

Visualisation of data using NPE:P ratio shows that female chimpanzees maintained stable protein intake but varied intake of NPE following variations in diet composition (Figure 5.2). Diet compositions are represented as Cartesian points (proportions of AP and NPE in the diet) and the nutritional rails (vectors passing through the origin) represented the AP: NPE balance for the food ingested.

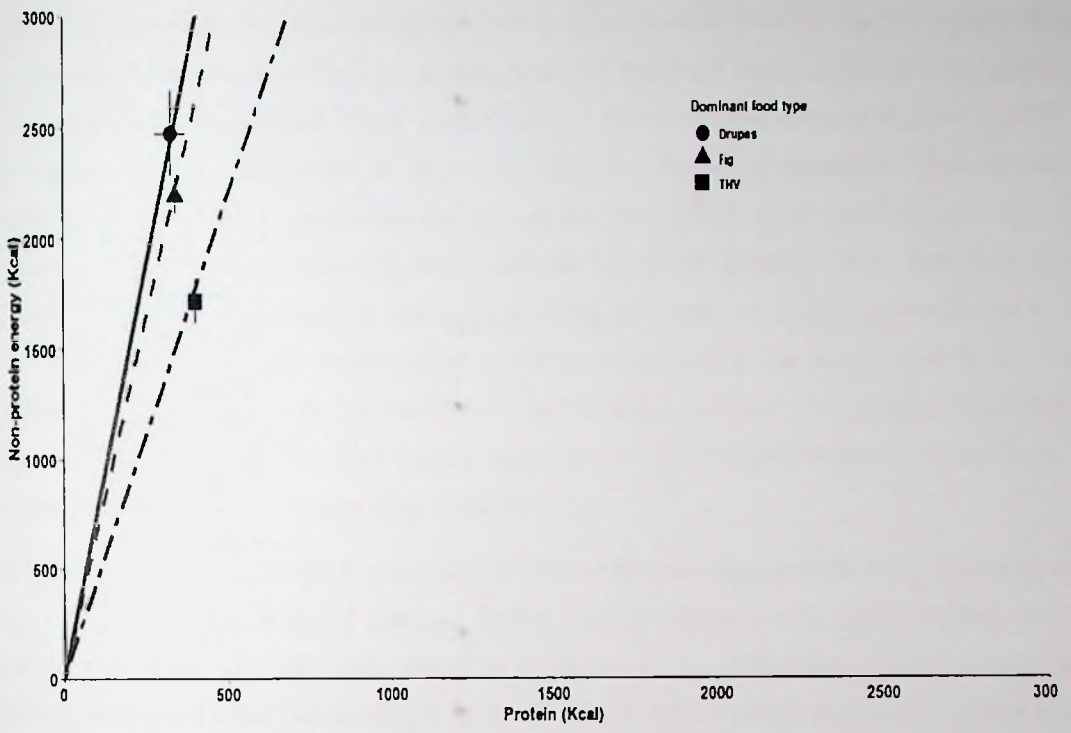

Figure 5-2: A geometric plot of mean daily intake (±SE) of non-protein energy (NPE) vs protein (P) following variation in diet composition. The solid, dashed and two-dashed lines represent the ratio of NPE:P when diet was dominated by drupes, figs and THV respectively.

5.4 Discussion

This study aimed to examine the nutrient balancing strategies of female chimpanzees using a Geometric Framework for Nutrition (GFN) to test a specific hypothesis regarding the pattern of nutrient regulation in the face of fluctuating fruit resources.

In this study, resource fluctuation was measured at two levels. First, there was variation in the availability of drupes, figs and THV across months (Uwimbabazi et al., 2019). This variation did not, however, deterministically map onto actual dietary intakes, because ripe fruit dominated the diet regardless of whether it was a fruit scarce month (fig-months) or not. Since the GFN measures the influence of actual dietary composition on nutrient intakes, the daily diet composition (proportions of the respective food categories) were considered as the categorical factor for tests, rather than the monthly classifications derived from the fruit availability index.

In line with findings from other studies and as predicted, ripe fruits contributed larger proportions of carbohydrates and lipids (Felton, Felton, Raubenheimer, et al., 2009; Masi et al., 2015; Rothman et al., 2008). But contrary to one of the predictions, young leaves did not

significantly contribute more protein to absolute nutrient intakes than all the food types though they contained larger proportions of protein than all the food types. With the exception of protein, ripe fruits contributed larger proportions of all the macronutrients including NDF to daily nutrient intake. This might be due to the fact that female chimpanzees ingested larger proportions of ripe fruit compared to the rest of the food items. This also explains why figs contributed larger amounts of carbohydrates and the rest of the macronutrients than drupes, yet figs have lower contents of protein and carbohydrates compared to drupes (Uwimbabazi et al., 2019). An indication that the proportion of nutrients contributed to the overall diet by any food item does not always tally with the nutrient content of that food item. This suggests that female chimpanzees may be able to extract large proportions of all macronutrients from ripe fruits by ingesting more ripe fruits than any other food item.

As expected, the results showed that the NPE:P ratio of female chimpanzees at 7:1 is comparable to that of spider monkeys at 8:1 (Felton, Felton, Raubenheimer, et al., 2009; Felton, Felton, Wood, et al., 2009). The difference could be attributed to the difference of food species that contribute nutrients for the two primate species. However, the closeness in the ratio values might be an indication that frugivorous-hindgut fermenters are likely to use the same nutritional strategy.

Furthermore, the analysis provides strong evidence that the rule of compromise for chimpanzees is protein regulation while maximizing NPE, just like in spider monkeys (Felton, Felton, Raubenheimer, et al., 2009; Felton, Felton, Wood, et al., 2009). This is seen from the fact that on days when proteinaceous foods (THV) dominated the diet, protein intake remained relatively stable. However, chimpanzees consumed significantly greater amount of NPE on fruit-days compared to THV-days. Although female chimpanzees spent more time feeding on THV-days, they ingested less dry matter compared to that on fruit-days, this partly explains why protein-intake was not significantly greater on THV-days than on fruit-days. The lower intake of dry matter on THV- days was probably due to the longer mastication periods required for high-fibre foods which tends to lead to lower their intake rates (Oftedal, 1991; Spalinger, Hanley, & Robbins, 1988).

While it has been commonly assumed that frugivores are energy maximisers, the analysis disputes this theory concerning female chimpanzees using these two explanations. Firstly, if female chimpanzees were energy maximisers, they would have consumed drupes or figs only when these foods were abundant there by maximizing (NPE); but instead, they also consumed substantial portions of protein rich foods. Secondly, since drupes are richer in water soluble

carbohydrates compared to figs, chimpanzees would have consumed drupes only during drupe-months to maximise NPE intake but this was not the case. Instead they included a significant portions of figs in their diet during drupe-months (33% based on dry weight (Uwimbabazi et al., 2019)

Much as drupes are richer in water soluble carbohydrates compared to figs (Conklin-Brittain & Wrangham, 1994; Uwimbabazi et al.; 2019; Wrangham et al., 1993), the results suggest that chimpanzees achieved similar intake of NPE on drupe and fig-days. Since the P:NPE ratio for figs and drupes is not significantly different, chimpanzees might able to reach their NPE intake target by consuming either of the fruit categories. Additionally, chimpanzees may achieve their protein intake target from a fruit-based diet by ingesting more fruits. But because fruits are deficient in protein compared to other food types such as young leaves, flowers and seeds, chimpanzees have to include a portion of THV in their diet even during fruit abundant periods (Milton, 1999). According to Uwimbabazi et al. (2019), drupes contain more protein than figs. Therefore, it seems that female chimpanzees consumed less THV during drupe-months/days (16%) because they could meet their protein intake target by consuming less THV in addition to drupes. On the other hand, since figs contain less protein, chimpanzees had to ingest more THV during fig-months/days (24%) in order to meet their protein intake target.

In this case THV were serving as nutritionally complementary foods, which the chimpanzees combined in the diet with figs or drupes to achieve the same intake target on the respective feeding days. Thus, unlike spider monkeys, chimpanzees supplemented their frugivorous diet with THV to reach their daily protein target (Felton, Felton, Raubenheimer, et al., 2009; Felton, Felton, Wood, et al., 2009). In contrast, on days when neither fruit category dominated the diet, the female chimpanzees maintained the same protein intake, but in order to do so consumed smaller amounts of NPE. This same response was observed in spider monkeys (Felton, Felton, Raubenheimer, et al., 2009; Felton, Felton, Wood, et al., 2009).

Figs provide a staple fallback food for chimpanzees and were consumed in significant amounts even when the preferred drupes were available (Felton, Felton, Wood, & Lindenmayer, 2008; Marshall & Wrangham, 2007). Several studies have highlighted the relative importance of figs to frugivorous primates not just as staple fall back foods but because they are nutritionally balanced (Conklin-Brittain & Wrangham, 1994; Felton, Felton, Wood, et al., 2009; Wrangham et al., 1991). Hence the nutrient balance of figs may far outweigh the low quality of individual concentrations of macronutrients (Conklin-Brittain & Wrangham, 1994). Figs also contain high concentration of available calcium which is critical for maintenance and reproduction (Silver,

Ostro, Yeager, & Dierenfeld, 2000; Wendelin, Runkle, & Kalko, 2000). These factors might explain why chimpanzees fed on figs even when drupes were abundant and why they dominated the diet of female chimpanzees throughout the study period.

Tight regulation of protein intake in chimpanzees as well as in humans and other vertebrate and invertebrate species is important because the costs of failing to regulate protein intake outweigh the costs of either eating excesses or deficits of NPE (Cheng *et al.*, 2008; Simpson and Raubenheimer, 2012). One likely reason that animals tend not to over-eat protein is that, in contrast with NPE, there is no mechanism to store excess protein to draw on when dietary protein is low. Another is that ingested excesses of protein might be associated with accelerated ageing, and early on onset of some diseases, as suggested for humans (Le Couteur *et al.*, 2016). In the extreme, excessive protein consumption is associated to fitness costs and can eventually lead to death (Bilsborough & Mann, 2006). Nonetheless, protein is an important macronutrient that needs to be consumed in sufficient quantities on a daily basis. For example, protein is important for maintenance, growth and repair and for milk production in females.

5.5 Conclusion

Overall, the patterns of macronutrient intake by female chimpanzees that were observed in the present study suggest the following interpretation. The intake target – meaning the ratio and amounts of macronutrients that the animals specifically target during foraging – is represented by the intakes that were observed on fruit-days. This is suggested by the fact that they reached a statistically indistinguishable nutrient intake on those days regardless of whether drupes or figs was the available fruit, and to do so they changed their intake of non-fruit foods (THV) to balance the diet. Specifically, since figs contained a lower proportion of protein energy than drupes, when eating figs, female chimpanzees increased their intake of THV and achieved the same macronutrient intakes as on drupe days.

In contrast, on THV days, they were constrained to a diet with proportionately higher protein content than on fruit days, and their response to this constraint was to prioritise protein intake thereby under-ingesting NPE. Hence, the importance of THV is not just to provide alternative sources of energy but are important sources of protein for chimpanzees which mainly subsist on a fruit-based diet which is protein deficient.

Figs were a substantial component of chimpanzees' diet. This might be because figs constitute a nutritionally rewarding food resource especially in terms of NPE that is available all year round. Hence, figs do not only assist chimpanzees to overcome drupe-scarce periods as often assumed.

As nutritionally balanced foods which are used extensively by chimpanzees and other frugivores, figs need special attention in wild habitats when it comes to conservation planning, such as selecting them as priority species for enrichment planting.

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CHAPTER SIX: SEASONALITY OF REPRODUCTIVE EVENTS IN FEMALE CHIMPANZEES AS A FUNCTION OF MACRONUTRIEN AND ENERGY INTAKE

Abstract

Reproduction in female mammals is energy demanding because females carry the bulk of the reproductive costs. While seasonality in reproductive events in chimpanzees has been associated with variations in diet-quality, the extent to which variations in macronutrient and energy intake influence reproduction remains unclear. In Kanyawara community, high rates of sexual swellings and conceptions have been linked to drupe-fruit abundance under the assumption that this relates to high energy intake. In this chapter, the relationship between frequency of reproductive events and diet quality plus climatic factors was investigated. The sample included demographic data for 5.8 years (63 maximal sexual-swellings, 18 conceptions and 19 births) along with feeding data. The objectives were three-fold, to determine whether: 1) there was predictable seasonal variation in energy intake by female chimpanzees, 2) reproductive events were distributed in a predictable seasonal pattern, and 3) reproductive events were associated with energy intake, rainfall and temperature. Results demonstrated that the variation in energy or macronutrient intake was not consistent across the years, fruit-months or climate-seasons. Using circular statistics, it was revealed that the peak month for sexual-swellings is April, for conceptions is June and for births is February. However, compared to other months, the rates of sexual-swellings were not significantly higher in April, nor were those of conceptions higher in June or those of births in February, implying that the seasonality was not strict. Relatedly, rates of reproductive events were not higher in drupe-months or second-dry season as expected but instead seemed to be occur opportunistically. Although the association was not strong, it was noted that there were high rates of maximal swellings (12% & 8%) and conceptions (14%) were during the first-wet and second-dry seasons indicating that reproductive events could be tracking diet quality. Findings from the model suggest that sexual-swellings and births are limited by energy intake and that all reproductive events might be constrained by minimum temperature. This study supports previous evidence that reproduction is Kanyawara chimpanzees is limited by food quality and also suggests that climatic factors may explain some of the trends observed in rates of reproductive events. The lack of consistency in the linkages between diet-quality and reproductive events warrants more investigations in the seasonality in reproductive events of Kanyawara female chimpanzees.

6.1 Introduction

Evidence about the energetics of reproduction in chimpanzees suggests that diet quality and energy balance are critical elements of reproductive function in females (Emery Thompson, 2013; Emery Thompson & McCabe, 2013; Knott, 2001; Murray, Lonsdorf, Eberly, & Pusey, 2009). Female chimpanzees are found to be typical capital breeders, using a risk averse reproductive strategy such that reproductive effort is dependent on maternal condition (Brockman & van Schaik, 2005; Emery Thompson & McCabe, 2013; Janson & Verdolin, 2005). In other words female chimpanzees have to maintain a positive energy balance before they initiate reproduction (Knott, 2005). Energy balance is defined as energy intake minus energy expended through basal metabolic processes, plus the added metabolic demands of activity and reproductive state. A female's energy balance plays an important role in reproductive processes that influence ovulation (Ellison, 1990). Hence energy intake in terms of nutrition has been cited as one of the key factors limiting reproduction in female primates (as is the case in most female mammals) (Lee, 1987).

Within various species females that maintain a relatively high-quality diet are found to give birth early, have shorter gestation and lactation periods, have shorter interbirth intervals and reach menarche age early (Bercovitch & Strum, 1993; Borries, Sommer, & Srivastava, 1991; Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007). For example, it has been reported that females which occupy the most productive home ranges have relatively high ovarian function and shorter interbirth intervals, and that their infants are more likely to survive (Emery Thompson et al., 2007; Pusey, 1997; Wallis, 1997). Also, consumption of high-quality foods influences the rates of maximal-swellings and conceptions (Anderson, Nordheim, & Boesch, 2006; Emery Thompson & Wrangham, 2008). Such studies generally assume that consumption of high-quality foods results in increased energy intake, which would therefore elevate energetic status of the female individual. Despite the mounting evidence showing diet quality and energy balance to be significant predictors of reproductive function in female chimpanzees, no study of seasonal variation in chimpanzee reproductive performance has actually quantified variation in energy intake.

Food is especially important to female primates due to the high metabolic costs associated with gestation and especially lactation (Lee, 1987). Toward the end of their pregnancy, female primates must eat enough food to nourish both themselves and the foetuses developing in their womb, as well as maintaining the body fat they will need to support nursing infants (Strier, 2000). However, primates living in tropical forests may be constrained by fluctuations in preferred food availability which results in fluctuations in macronutrient and energy intake

(Conklin-Brittain, Knott, & Wrangham, 2006; Hanya et al., 2011; Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2014; Knott, 1998; Wallace, 2005). Hence, females have to adjust their behaviours in food scarce seasons in order to acquire adequate nutrition. For example, pregnant females may select high quality diets, spend more time feeding, or ingest larger amounts of food than their non-pregnant counterparts (Boinski, 1988; Hemingway, 1999; Koenig, Borries, Chalise, & Winkler, 1997; McCabe & Fedigan, 2007).

The various patterns of seasonality in foods and reproductive events in several primate species have received fair documentation (Brockman & van Schaik, 2005). The intensity of seasonality of reproductive events in primates varies greatly across species; certain species exhibit very concentrated birthing seasons, while others give birth throughout the year (Lindburg, 1987). Seasonal breeding is characteristic of income breeders, which time the most energetically demanding phases i.e. late gestation and early lactations, to coincide with periods of maximal energy availability thereby maximising survival for the mother and/or the weanling (Carnegie, Fedigan, & Melin, 2011; Emery Thompson, 2013; Janson & Verdolin, 2005). For example, in vervet monkeys, the first three months of the infant's life which is the time of high lactational burden coincide with periods of high dietary quality (Lee, 1987). Many lemurs have two to three week long breeding seasons which coincide with the seasonal food abundant seasons (Kappeler, 1996).

Much more variability in reproductive patterns exists for primates inhabiting seasonally unpredictable environments. This is common in capital breeders such as great apes (e.g. orangutans, chimpanzees, and humans), where females have to acquire a certain energy threshold before they can initiate reproduction (Seidman, Ever-Hadani, & Gale, 1989; Wich et al., 2004). Ovarian activity in capital breeders is cued endogenously, unlike the exogenous cuing in income-breeders. Due to the long gestation periods in apes, the factors that influence ovulation or conception may not be present by the time of births. Hence, the predictors of reproduction in great apes remain unclear.

Although food availability has the most significant influence on reproduction in mammals, several environmental factors such as photoperiodism and climate are known to be important also (Bronson, 1989). Climate may influence reproductive cycles directly through thermoregulation or indirectly by affecting food production. Evidence from captive chimpanzees in North America suggests that rainfall and/or temperature may have an effect on the estrous cycle by influencing thermoregulation (Young and Yerkes 1943). While it is difficult to discern if climatic variables influence reproductive cycles of wild primates, especially in the tropics

where climate is relatively stable, some studies have shown that reproductive events are associated to climate. For example, in western chimpanzees it was reported that the number of maximal-swellings was negatively related to mean rainfall in the two preceding months and the mean high temperature (Anderson et al., 2006).

Kanyawara chimpanzees exhibit diet fluctuations that are not seasonally predictable. This is partly due to vagaries in the fruiting patterns of major fruit species that contribute to the chimpanzee diet at Kanyawara (Chapman et al., 2005; Wrangham et al., 1996). Although figs provide fruit resources throughout the year at Kanyawara, there is seasonality in availability of drupes (Wrangham *et al.*, 1991). This seasonality has been associated with some of the reproductive events in female chimpanzees such as increased rates of conceptions and maximal-swellings (Emery Thompson & Wrangham, 2008). Similarly, findings from other chimpanzee sites show that there are seasonal peaks in sexual receptivity (i.e. sexual swellings) and conceptions (Tai: (Anderson et al., 2006; Boesch & Boesch-Achermann, 2000); Gombe: (Matsumoto-Oda, Hosaka, Huffman, & Kawanaka, 1998; Janette Wallis, 1995)). These studies suggest that the increase in rates of sexual receptivity during fruit abundant periods is due to increased energy intake.

According to (Knott, 2001), apes have evolved, as did humans, to time reproduction so that conceptions are more likely to occur in periods when the female maintains positive energy balance. At Kanyawara, availability of drupes has been associated with positive energy balance in male chimpanzees (Emery Thompson, Muller, Wrangham, Lwanga, & Potts, 2009). An indication that chimpanzees are likely to resume cycling when drupes are abundant. Therefore, this study seeks to examine whether the timing of reproductive events of Kanyawara chimpanzees is linked to diet quality in terms of energy or nutrient quality or whether they are cued to climatic factors (temperature and rainfall).

The specific objectives were to determine whether: (1) there is predictable seasonal variation in energy and macronutrient intake by Kanyawara female chimpanzees, (2) reproductive events are distributed in a predictable seasonal pattern, and (3) the timing of reproductive events is associated with environmental factors (diet composition and climate). The underlying hypothesis of this study is that since chimpanzee diets are highly diverse, chimpanzees use foods with different phenological patterns and therefore will not show consistent seasonal variation in energy and macronutrient intake.

6.2 Methods

6.2.1 Study site and subjects

This information in this chapter is based on the same study site as in Chapter Four. In addition to the female chimpanzees which were observed between January 2014 to June 2015, this chapter includes long term data (5.3 years) for all adult female chimpanzees between the ages of 13 to 55 years which were continuously observed for at least 10 hours between September 2009 to December 2013.

6.2.2 Behavioral and feeding data

In addition to the behavioral and feeding data collected between January 2014 to June 2015 (see chapter 4.2.2), behavioral and feeding events for the period between September 2009 to December 2013 were used. Data from September 2009 was considered because that is the month when Kibale Chimpanzee Project (KCP) started conducting continuous focal follows on focal individuals.

From the 70 months, there were 368 focal observation days representing 255216.8 observation hours. The total number of feeding bouts was 3902.

6.2.3 Climate data

Weather data has been collected at Kanyawara field station since 1970s. The rainfall and temperature for the years 2009 to 2014 is summarized in Figure 6.1. And it shows, just like previous studies in Kibale region, a bimodal rainfall distribution pattern (Chapman et al., 2005; Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999). The dry seasons were from December to February (first-dry) and June to August (second-dry). The wet seasons were from March to May (first-wet) and September to November (second-wet). Average monthly rainfall was 137.4 mm ranging from 9 mm to 307.3 mm. The mean annual rainfall was 1648.8 mm ranging from 1461.5 to 1831.0 mm. Despite these bimodal trends, there was marked year-to-year variation in the magnitude, onset, and duration of wet and dry seasons (Appendix I). Mean daily temperature ranged from 14.8°C (minimum) to 25.9°C (maximum). Equally, there was marked year to year variation in the monthly patterns of minimum and maximum temperature (Appendix II & III).

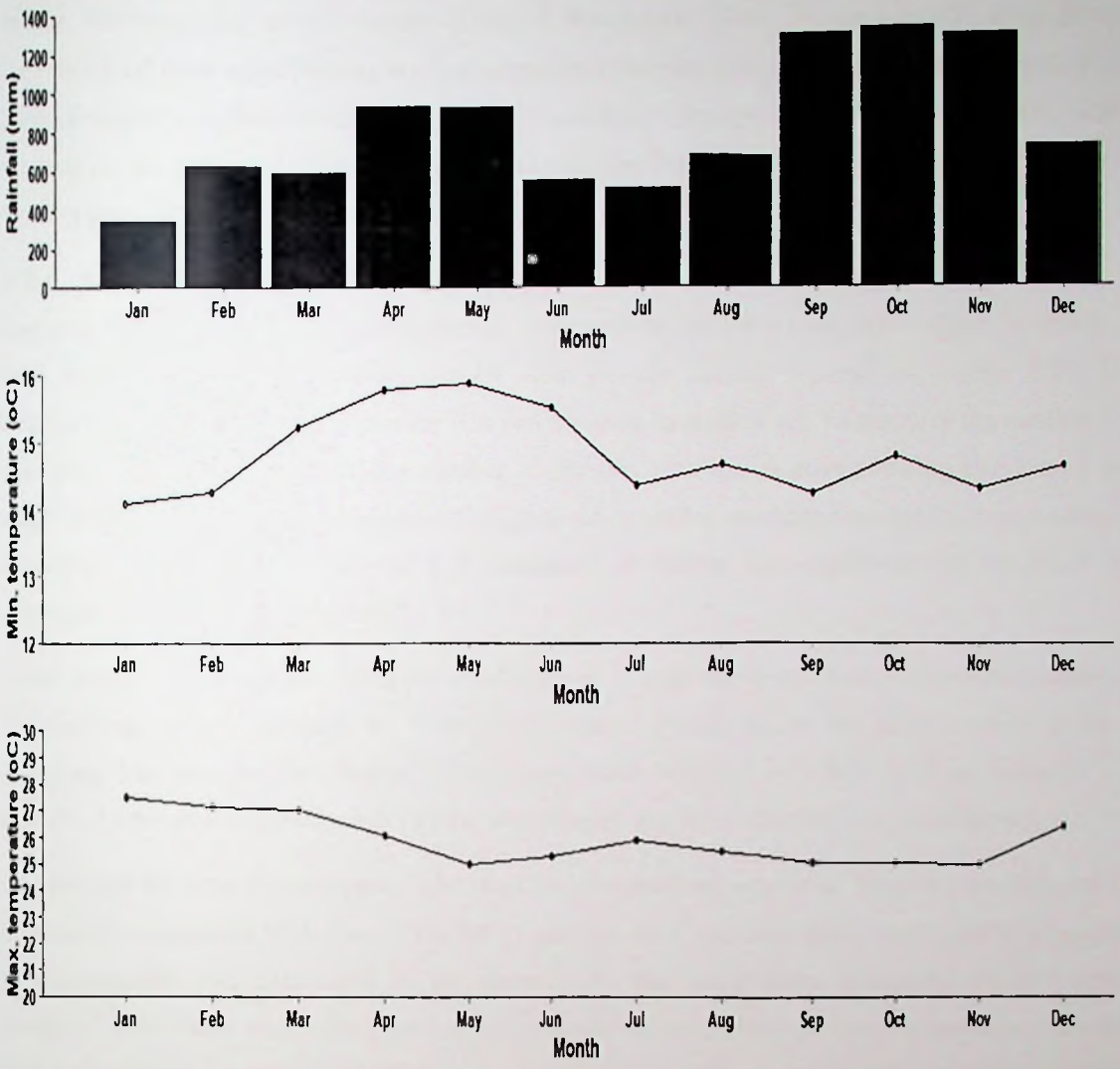

Figure 6-1: Rainfall and temperature data for Kanyawara, Kibale National Park for the years 2009 to 2014. Source: Prof. Colin Chapman's lab.

6.2.4 Measurement of fruit availability

Usually, phenology data is used in primate seasonality studies to show variation in food abundance. However, there was no consistent data for the 52 months (September 2009 to December 2013). Therefore, a method that was previously used by primatologists to show fluctuations in fruit availability was adopted in this section. In this method, the proportion of drupes in the diet is used as a proxy for diet quality (Emery Thompson & Wrangham, 2008; Gilby & Wrangham, 2007). This method is based on the premise that the proportion of fruit in the chimpanzee diet at Kanyawara is significantly correlated with fruit availability calculated from phenological transects as evidenced from previous studies (Wrangham et al., 1996, 1991).

Hence, following the method used by (Gilby & Wrangham, 2007), for each month, using group data, the total time spent feeding was calculated and the percent time spent feeding on each fruit species was determined. Months in which chimpanzees spent ≥40 percent of their feeding time feeding on drupes are termed as drupe-month whereas those months when they spent <40% of feeding time on drupes are termed as fig-month.

6.2.5 Reproductive variables

Reproductive states of female chimpanzees were ascertained by visual observations, pregnancy tests and back calculations. Demographic data for the period between September 2009 to February 2015 was extracted from the Kanyawara long term data set. To quantify the number of maximal-swellings in a month, the number of females with the relative swelling size scored as stage 3 (i.e. when the sexual skin swelling has no wrinkles and appears tight) were counted. Experimental studies have shown that anogenital swellings are largest around the time of ovulation (Emery & Whitten, 2003).

Urine samples for pregnancy tests were collected by Kibale field staff from female chimpanzees by pipetting from vegetation or from plastic sheets placed under the subject when it was urinating. The samples were stored in leak-proof tubes, labelled with date, time, and identity of subject. At the end of the day, hCG strips were dipped into the sample to test for pregnancy.

To estimate the time of conception, a back-calculation method was used. Whereby the difference between the estimated birth date of the infant and 225 days which is the average gestation length in chimpanzees was calculated. In the absence of other information indicating when a birth occurred, birth dates were determined as the midpoint of the period between the last day a female was seen without an infant and the first day she was seen with an infant. Also, some birth dates were estimated based on the size of the infant when it was first observed. There were 19 conceptions and 18 infants born during this period.

6.2.6 Food and macronutrient intake calculations

The approach used in section 4.2.6 was used for food intake and nutrient intake calculations for the September 2009 to June 2015 focal data.

6.2.7 Statistical analysis

Contrasts of macronutrient and energy intake as well as frequency reproductive events were conducted on three fronts: across the months, fruit-months and climate seasons. These were analysed using one-way ANOVA with Welch's test because the data violated the assumption for equal variances. Games-Howell's posthoc tests were used for pairwise comparisons. Kruskal-

Wallis (H) tests and Dunn's post-hoc tests for pairwise comparisons ($\alpha = 0.05$) were used to assess the variation of reproductive events among fruit-abundant periods and climate seasons. These tests were chosen because of the small sample sizes for the categorical variables (fruit-months and climate-seasons) and the fact that our dependent variables did not conform to normality and homoscedasticity assumptions. Log linear regression using a quasi-Poisson distribution was used to determine if the frequency of reproductive events (maximal-swellings, conceptions and births) in any given month was influenced by diet composition in a given month or climate (rainfall, maximum and minimum temperature) and macronutrient/or energy intake. All the above statistical analyses were performed using SPSS 20.0 statistical software and R version 3.5.1.

Rayleigh's Uniformity Test (Z) in the circular statistical program Oriana ver. 4 was used to show whether reproductive events (maximal-swellings, conceptions and births) were distributed in a predictable seasonal pattern (Kovach, 2011). Circular statistics allows one to examine the distribution of data that can be plotted on a circular scale such as compass directions or months of a year, where there is no 0 point and the axis is divided equally into angles $\leq 360°$ (Fisher, 1993; Zar, 1999). For example, when investigating monthly seasonality, the total length of the circular axis is one year, creating an axis divided into 12 equal sections, with each sector being 30° wide. If the observations are available on a monthly basis, each month is converted to the numeric value of the month of the year, e.g., to a maximum of 12, then converted to an angle that divides the circle into equal sections (Zar 1999). For example, January would be represented at the midpoint of the first section at 15°, February at 45°, and December at 345°.

Each observation, e.g., the number of births in a month, is converted to a vector with an angle, a, and a length, r, and analysis of all the vectors, using trigonometric functions (Zar 1999), results in a mean vector angle and a mean vector length of r. The mean angle can be converted back to a mean date, which provides information on when the variable of interest is most concentrated, e.g., in June. The mean vector length, r, gives an indication of how closely spaced the observations are on the axis ranging from 0 to 1.0, with 0 meaning there is a perfectly equal distribution around the axis and 1.0 meaning that all observations occurred in the same interval.

6.3 Results

Focal observations on the study subjects that lasted for a minimum of 10 observation hours were included in the analysis. In total, 368 days of focal observations from September 2009 to June 2015 which yielded 4253.6 observation hours of which 1836.4 hrs accounted for time spent

feeding were included. The mean observation time for complete focal observations was 11 hrs per day.

According to the >40% or <40% criteria of time spent feeding on different fruit species (Appendix IV), 18 months are classified as drupe-months whereas 52 months are classified as fig-months. This was used as a proxy of drupe abundance (drupe-months) or drupe scarcity (fig-months).

Graphical visualization shows that there was marked variation in drupe abundance but it did not follow a consistent pattern across the years. Figs dominated the diet of female chimpanzees across the years (Figure 6.2).

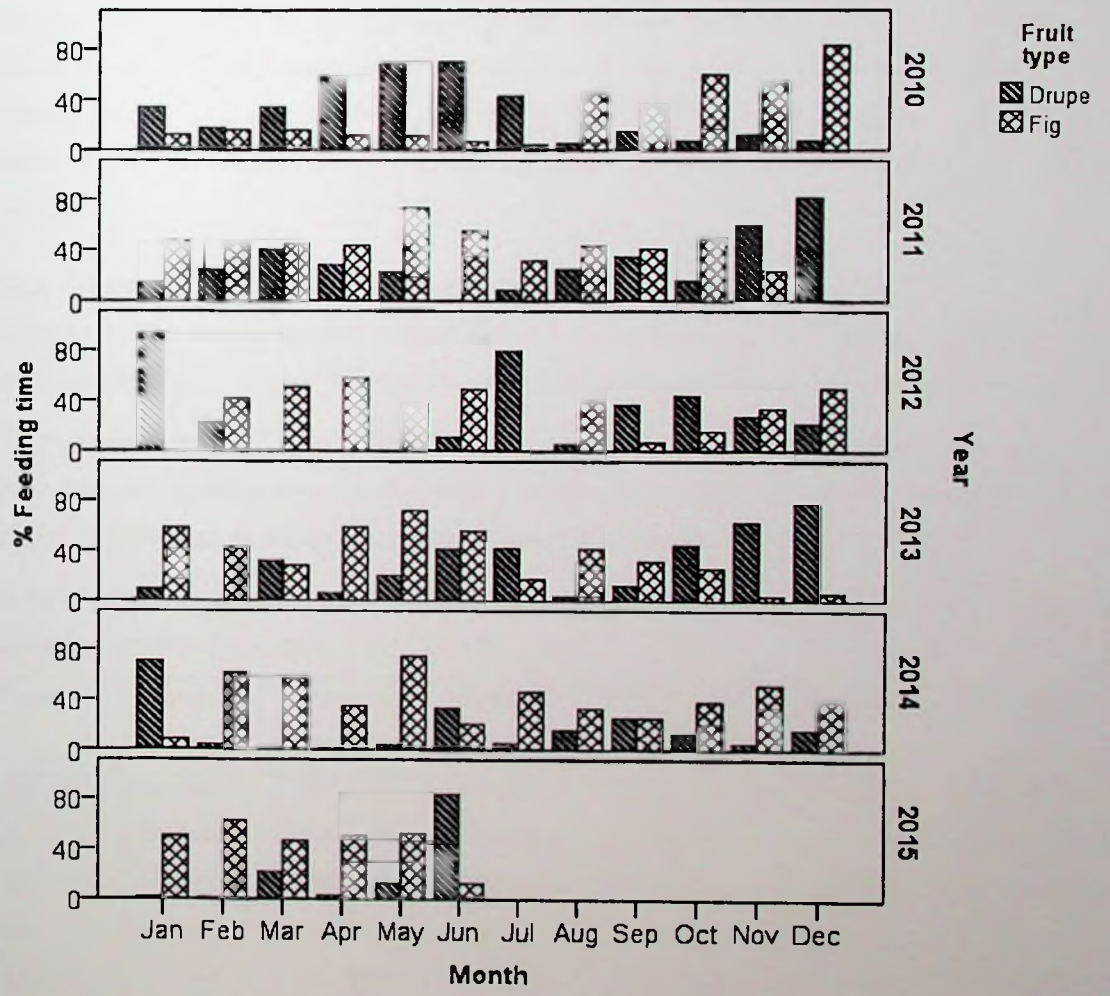

Figure 6-2: Percentage time spent feeding on drupe and fig fruits per month. The drupe-months (N=18 mo) are those where time spent feeding on drupes in a given month was >40% and those months where time spent feeding on drupes was <40 % are classified as fig-months (N=52 mo). This data represents the period between September 2009 and June 2015.

6.3.1 Variation in behavior and diet composition across fruit-months and climate-seasons

On average, female chimpanzees spent 291 minutes feeding, and consumed 883 g of food and 2521.9 Kcal of metabolisable energy on a daily basis. In line with findings from Chapter Four, female chimpanzees spent more time feeding during fig-months (305.8±4.9 mins) than in drupe-months (257.1±7.4 mins) and yet ingested more food in drupe-months (905.4±32.4 g) than in fig-months (876.0±18.8 g). They consumed more ripe fruit (82%) and less THV (18%) during the drupe-months than in the fig-months (ripe fruit:69% and THV: 30%). Considering the climate seasons, the findings show that time spent feeding and dry matter consumed across the bimodal seasons were not significantly different. However, female chimpanzees consumed more drupes during the second-dry season than the first-wet and second-wet seasons ($F_{3,364}=3.9$, $p=0.009$).

6.3.2 Variation in macronutrient and energy intake

Variation in macronutrient and energy intake was analysed on three fronts, as a subject of months, fruit-months (drupe fruit abundance) and climate seasons (bimodal rainfall patterns).

Monthly variation

There were no significant peaks or declines in the intake of macronutrients and energy across months in individual years nor in combined years ($p>0.05$) (Table 6.2).

Table 6-1: Mean monthly macronutrient and energy intake across the years for the period September 2009 to June 2015

Month	Lipid (Kcal)	Protein (Kcal)	WSC (Kcal)	NDF (Kcal)	TNC (Kcal)	ME (Kcal)
Jan	130.7±24.1	307.6±35.4	610.6±62.2	609.1±41.4	1289.4±99.2	2336.8±154.4
Feb	122.2±28.0	368.0±53.3	403.6±45.9	709.0±60.9	1271.1±141.0	2465.8±238.3
Mar	111.1±15.5	386.2±28.4	529.7±91.1	602.8±37.2	1365.4±136.2	2465.4±180.4
Apr	168.0±24.4	433.8±27.6	451.5±55.7	666.9±43.5	1222.2±79.8	2491.0±135.7
May	196.0±24.7	353.7±23.3	447.7±65.7	507.4±31.3	1161.6±100.6	2218.7±134.6
Jun	277.6±42.0	438.9±25.9	527.1±64.6	561.0±31.8	1363.2±116.1	2640.6±189.0

Month	Lipid (Kcal)	Protein (Kcal)	WSC (Kcal)	NDF (Kcal)	TNC (Kcal)	ME (Kcal)
Jul	213.5±37.9	463.5±55.3	464.9±57.6	540.4±33.5	1208.1±107.2	2425.4±194.7
Aug	204.3±29.1	519.4±48.9	445.9±48.0	638.8±47.3	1291.0±112.4	2674.3±209.8
Sep	221.2±30.3	452.9±33.1	479.3±45.8	566.5±28.1	1275.3±98.8	2521.9±153.1
Oct	267.0±26.9	448.0±36.6	542.8±56.9	627.5±46.7	1494.6±132.0	2853.2±229.1
Nov	195.5±23.8	350.6±32.7	603.7±80.0	607.2±35.3	1530.4±104.2	2683.7±158.9
Dec	185.8±28.1	445.5±48.8	644.0±67.0	602.1±38.8	1611.0±107.1	2855.7±181.3

Cells represent mean +/-SEM

Variation between the fruit-months

In line with findings in Chapter Four, daily intake of metabolisable energy did not vary among the fruit-months ($F_{1,366}$=0.61, p=0.44) (**Figure 6.3**). However, the pattern of daily macronutrient intake was not entirely similar to the findings in Chapter four. More TNC and WSC was consumed during drupe-months than in fig-months (TNC: $F_{1,366}=10.8$, $p=0.01$) (Figure 6.3). On the other hand, average intake of lipid and available protein during the fig-months was greater than in the drupe-months (lipid: $F_{1,366}=6.8$, $p=0.009$, available protein: $F_{1,366}=9.3$, $p=0.002$) (Figure 6.3).

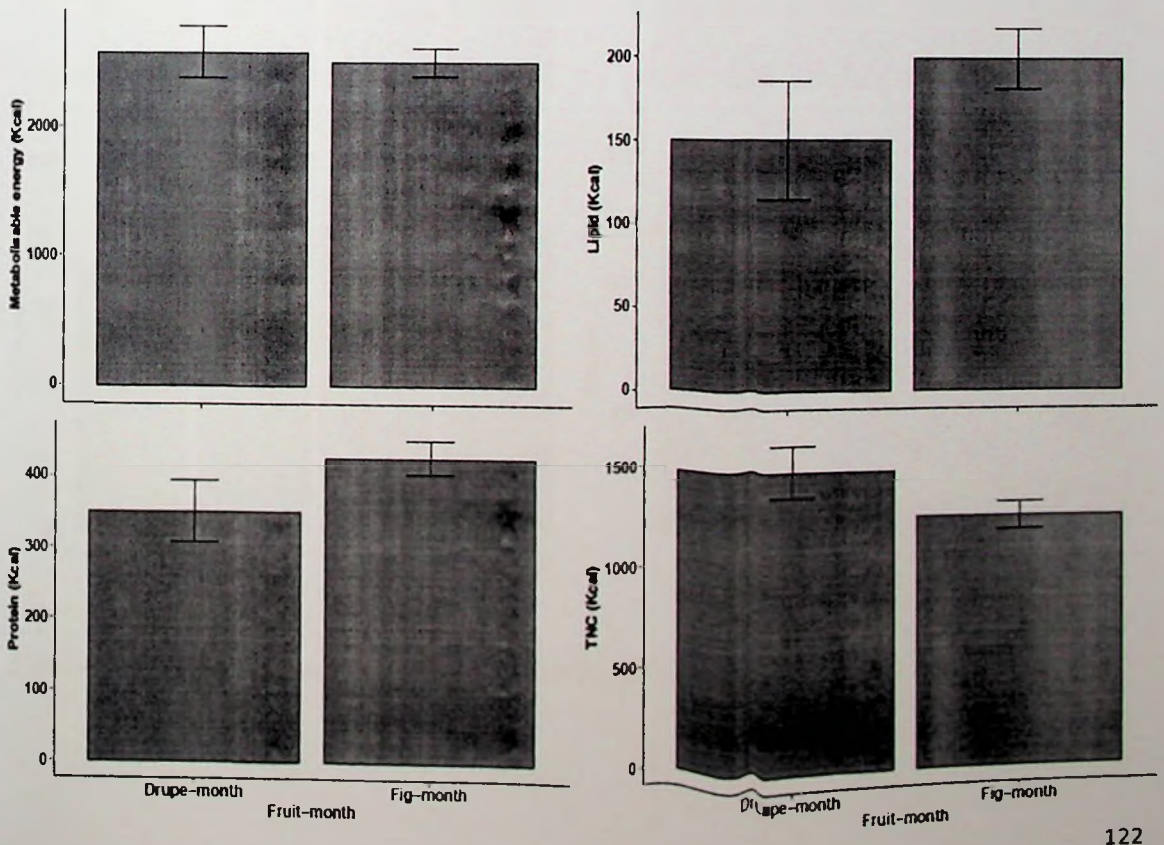

Figure 6-3: Variation in metabolisable energy and macronutrient intakes across the fruit-months. $N_{drupe\text{-}month}$=18 months, $N_{fig\text{-}month}$=52 months

Intake of lipid during the second-dry and second-wet seasons was greater than that in the first-dry and first-wet seasons (lipid: $F_{3,362}=7.5$, $p=0.0001$). Protein intake during the second-dry season was greater than that in the first-dry season ($F_{3,362}=3.5$, $p=0.02$). For the rest of the macronutrients and metabolizable energy intake, there was no significant difference ($p>0.05$) (**Figure 6.4**).

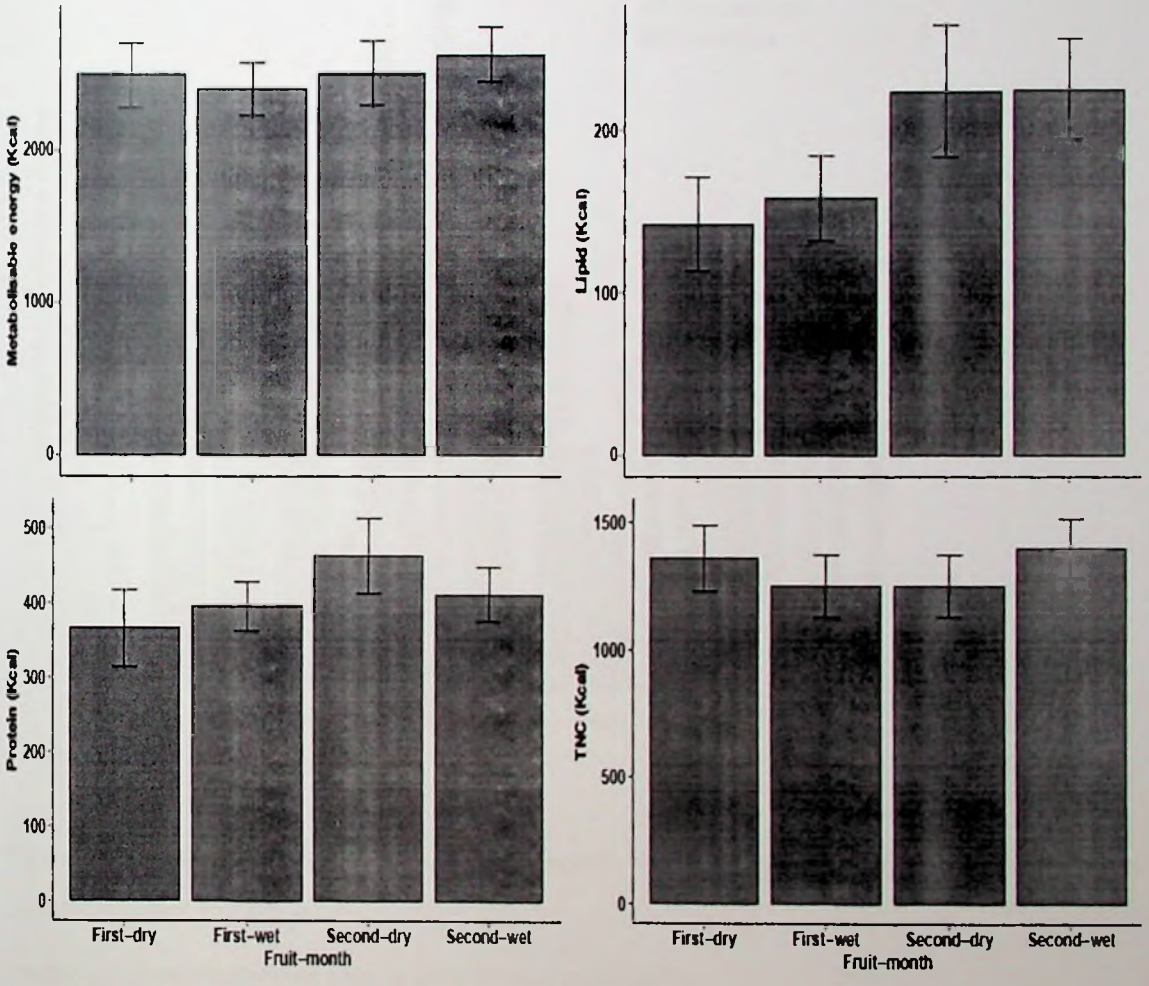

Figure 6-4: Mean macronutrient and energy intake among the climate seasons.

6.3.3 Seasonality of reproductive events

Monthly variation of reproductive events

There was marked year to year variation in the distribution of number of maximal-swellings, conceptions and infant births across each year (Appendix V). Even when combined, there was no significant difference in the number of swellings or conceptions or births among the months ($p>0.05$).

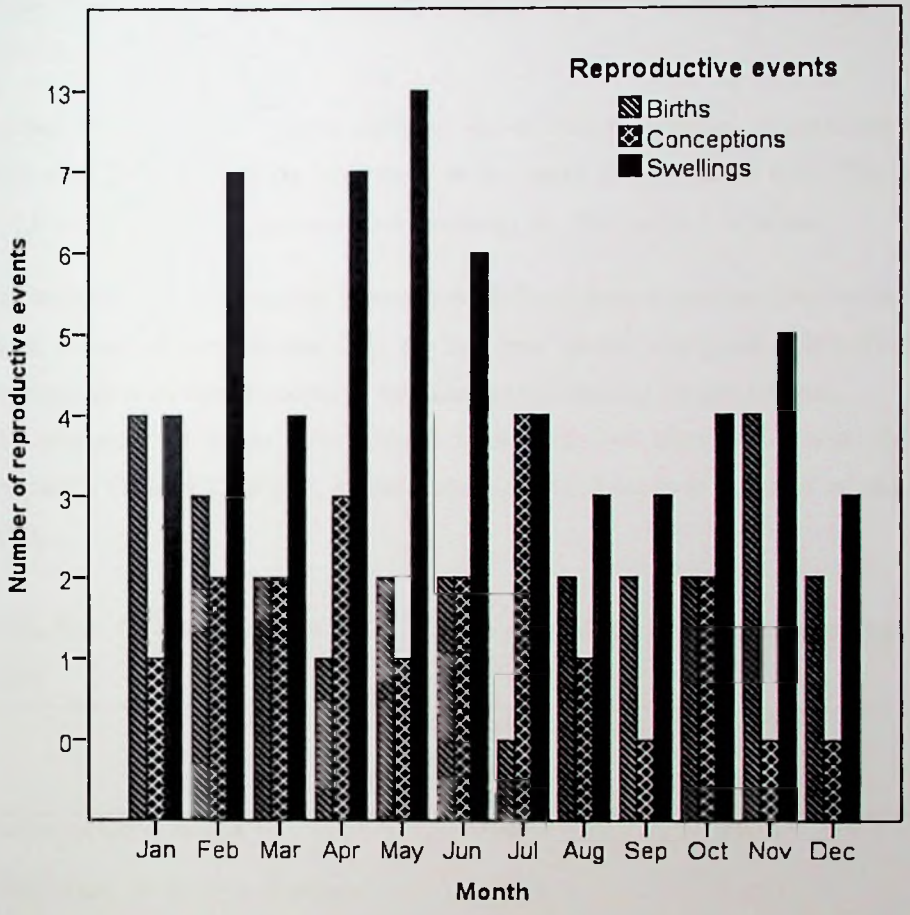

Figure 6-5: Monthly distribution of reproductive events combined for all the years from September 2009 to June 2015.

Variation of reproductive events due to fruit availability

The proportion of swellings that occurred during the drupe-months (9%) was not significantly higher than that in fig-months (8%) ($H=0.20$, $df=1$, $p=0.66$). The same trend was found in conceptions (drupe-months:4%, fig-months: 12%) ($H=1.77$, $df=1$, $p=0.18$) and births (drupe-months: 13%, fig-months: 4%) ($H=0.37$, $df=1$, $p=0.55$).

Variation of reproductive events among climate seasons

Frequency of females with maximal swellings was significantly higher in the first-wet season (12%) than the rest of the seasons (first-dry: 8%, second-dry: 8%, second-wet: 4%) (*H=9.5, df=3, p=0.02*). Although there were more conceptions during the first-wet (14%) and second-dry seasons (14%) than in the first-dry (3%) or second-wet (6%), the difference was not statistically significant (*H=3.9, df=3, p=0.3*). Similarly, the number of births did not differ significantly across the climate-seasons (first-dry: 6%, first-wet 4%, second-dry: 6%, second-wet: 8%) (*H=3.2, df=3, p=0.4*).

Further analysis using circular statistics shows that the number of maximal-swellings differed from a random distribution with April as the mean month (Table 6.3). The low r-value (Table 6.3) is an indicator that the maximal-swellings are not clustered in April.

The frequency of chimpanzee conceptions differed from a random distribution (Table 6.3). The mean month of conceptions over the 5.8 year period evaluated (2009–2015) was June, but conceptions were not clustered in this month as evidenced by low r-value.

The frequency of births also differed from a random distribution with the mean month as February (Table 6.3). Again, births were distributed all over the year as shown by the low r-value.

Table 6-2: Circular statistics results for the distribution of maximal-swellings, conceptions and births

	Maximal-swellings	**Conceptions**	**Births**
Number of Observations	600	700	700
Group Width (& Number of Groups)	30(12)	30 (12)	30(12)
Mean Vector (μ)	97.4	154.54	34.35
Mean month	April	June	February
Length of Mean Vector (r)[a]	**0.29**	**0.38**	**0.18**
Concentration	0.59	0.82	0.36
Circular Variance	0.71	0.62	0.82
Circular Standard Deviation	90.67	79.56	106.78

	Maximal-swellings	Conceptions	Births
Rayleigh Test (Z)	49.04	101.82	21.71
Rayleigh Test (p)	<0.0001	<0.0001	<0.0001

[a]*The mean vector r gives an indication of the degree of clustering around the mean group on a 0–1 scale, where 0 indicates that frequencies are spread perfectly evenly across months (i.e. no clustering) and 1 indicates that all events occur at exactly the same time.*

6.3.4 Relationship between environmental factors and reproductive events

The number of swellings was positively associated to energy intake and minimum temperature but negatively associated to protein intake (Table 6.4). The frequency of conceptions was also influenced by minimum temperature (Table 6.4). The number of births were not affected by minimum temperature but were positively associated with energy intake and negatively associated with macronutrient intake (Table 6.4).

Table 6-3: Loglinear regression results for relationship between macronutrient intake and conceptions/ maximal-swellings

	Conceptions			Swellings			Births		
	Estimate	t-value	P-value	Estimate	t-value	P-value	Estimate	t-value	P-value
Macronutrient									
Lipid	-0.05	-0.60	0.39	0.04	1.13	0.36	-0.06	-2.26	0.03*
TNC	0.25	1.57	0.93	0.09	1.05	0.74	-0.05	-2.09	0.04*
AP	-0.12	-1.11	0.55	-0.18	-2.92	0.05*	-0.05	-2.00	0.05*
NDF	-0.17	-1.05	0.99	-0.03	-0.38	0.55	-0.05	2.06	0.04*
ME	0.00	1.11	0.30	0.00	1.03	0.005**	0.05	2.11	0.04*
Diet composition									
% Drupes	-0.02	-1.06	0.29	0.009	1.90	0.06	0.03	1.46	0.13
% THV	0.006	0.19	0.84	-0.006	-0.36	0.72	-0.03	-1.22	0.22
Climatic factors									
Rainfall	-0.008	-1.12	0.43	-0.002	-1.05	0.18	-0.003	-0.58	0.56
Min-Temp	0.74	1.69	0.05*	0.35	2.39	0.03*	-0.32	-0.87	0.38
Max-Temp	-0.03	-0.10	0.92	0.14	1.32	0.19	-0.42	-1.52	0.14

*represents α level at 0.05, ** α-level at 0.01

6.4 Discussion

The availability of long-term demographic and feeding data enabled the evaluation of patterns of reproductive events in relation to ripe fruit abundance and to test the predictions that energy intake is associated with the timing of these reproductive events. The results show that there was no predictable seasonal variation in intakes of energy or easily digestible nutrients (lipids, proteins and TNC). Yet, the rates of maximal-swellings and conceptions tended to follow a seasonal pattern although this was not exactly associated with periods of high-quality diet.

6.4.1 Seasonality in diet composition, macronutrient and energy intake

Monthly variation in diet composition in terms of ripe fruit and THV as well as macronutrient and energy intake did not follow a consistent pattern across the years. Hence, there is no predictable monthly trend in ripe fruit or drupe fruit as well as energy intake for Kanyawara chimpanzees.

In line with findings in Chapters Four and Five, female chimpanzees spent less time feeding, consumed larger amounts of ripe fruit and less THV during the drupe-months compared to fig-months. Contrary to what was expected, ripe fruit intake was not greater during the second-dry (June-August) which is said to be the fruit-peak season at Kanyawara, instead drupe consumption was significantly more in this season. But this did not result in increased energy intake or WSC or TNC as one would expect. Instead the findings further show that intake of lipids increased during the dry seasons (both June-August and December-February periods).

Generally, the trends in macronutrient and energy intake across the months or fruit-months or climate-seasons are not consistent. This is an indication that macronutrient and energy intake does not follow any predictable pattern. This is largely attributed to the lack of clear pattern in drupe-fruit availability and rainfall patterns across the years. The extent and severity of fruit fluctuations at Kanyawara is not as severe as what is reported in other habitats such as the South-Asian forests where there are significant mast fruiting periods (Conklin-Brittain, Wrangham, & Hunt, 1998; Knott, 1998; Wrangham et al., 1996). This is partly due to the bimodal rainfall distribution which ensures availability of fruit in the Kanyawara habitat all year round. As such, there are no significant peaks in macronutrient and energy intake across the year.

6.4.2 Seasonality in reproductive events

Although all the reproductive events occurred throughout the year, circular statistics reveal that there is some level of seasonality. The mean month for sexually receptive females (April) preceded the mean month for conceptions (June). The highest proportion of maximal-swellings was in the first-wet season (Mar-May) that precedes the second-dry (June-August) during which

more drupes were consumed. Similarly, the highest proportion of conceptions were in March-May and June-August period. The second-dry and wet seasons were also periods when chimpanzees consumed more lipid and protein. This suggests that swellings and conceptions are timed to coincide with a period of ripe fruit abundance when high-quality macronutrients can be accessed in large amounts. An indication these reproductive events are strongly associated to diet-quality as reported in previous studies (Anderson et al., 2006; Emery Thompson & Wrangham, 2008; Wallis, 1997).

The peak month for births (February) precedes the first-wet and second-dry seasons when protein rich (young leaves) and energy rich foods (ripe fruits) are likely to be abundant. So, although infant births do not coincide with the fruit-abundant period (June-August), there is a likelihood that births occur just before the protein-rich (young-leaves) and fruit-abundant period so that the demanding lactation phase coincides with the good food period. Nonetheless, the low r-value (*0.18*) shows that there is reduced birth seasonality in chimpanzees as is the case for Gombe and Mahale chimpanzees (*r-value:0.08*) (see review by Janson and Verdolin, 2005). This is expected of species with long gestation periods that live in less seasonal environments such as the Kanyawara habitat.

Growing evidence suggests that just like in humans, female reproductive hormones in non-human primates respond to changes in nutrient intake, energy expenditure and energy balance (Ellison, 1990; Knott, 2001, 2005). The findings seem to suggest that is a relationship between macronutrient intake and some of the reproductive events, though the linkage is not so clear.

6.4.3 Relationship between reproductive events and environmental factors

There was no consistent pattern in the relationship between environmental factors and the proportion of reproductive events. However, further analysis shows that the occurrence of maximal-swellings (and not conceptions) was positively associated with metabolizable energy intake. This supports previous studies which show that maximal-swellings in primates are linked to continuous consumption of high-diet quality (Anderson *et al.*, 2006; Emery Thompson and Wrangham, 2008; Takahashi, 2002; Wallis, 1995).

The fact that there was no positive association between swellings with the drupe-months and yet they were related to energy intake is an indication that maximal-swellings are not timed to coincide with any fruit-period but overall energy intake plays a vital role in the estrus cycle. The estrus cycle is energetically demanding physiologically but also due to the fact that females have to put up with the sexual competition from males while at the same time they have to feed.

Hence at this stage, females may maximise energy intake at the expense of other nutrients like protein. Births were also positively associated with total energy intake and not any macronutrients, possibly because lactation is energy demanding (Emery Thompson, Muller, & Wrangham, 2012; Gittleman & Thompson, 1988).

Much as it is known that maximal-swellings, conceptions and lactation are energy demanding, the fact that female chimpanzees use a capital breeding mechanism whereby they can accumulate energy over a period of time before they initiate reproduction, makes it difficult to show a direct association between energy intake and reproductive events (Brockman & van Schaik, 2005; Knott, 2005). Since female chimpanzees maintain a relatively stable energy intake over the months, the influence of the same on timing of reproductive events is difficult to ascertain. Therefore, the rates of maximal-swellings or conceptions or births in a month might be due to accumulated energy consumed in the previous months.

The findings in Chapter Four show that during drupe-months, female chimpanzees spend less time feeding and increase intake of energy and TNC. This could mean that females are able to maintain a positive energy balance during drupe months just like males (Emery Thompson et al., 2009). If they maintain a positive energy balance, then females are likely to resume cycling (Emery Thompson, 2013; Potts, 2013). This would explain the concentration of maximal-swellings and conceptions in months when drupes are said to be abundant at Kanyawara (Chapman et al., 1999; Emery Thompson & Wrangham, 2008).

Also, minimum temperature was positively associated with the rates of maximal-swellings and conceptions, in line with previous findings (Anderson et al., 2006). Evidence from phenology studies at Kanyawara and elsewhere suggest that fruiting is negatively correlated to minimum temperature (Chapman et al., 1999; Tutin & Fernandez, 1993). The relationship between maximal-swellings and conceptions to climatic conditions are not clearly understood, thus it remains unclear whether female chimpanzees respond to the temperature cues in relation to fruit availability or whether it is linked to thermoregulation.

6.6 Conclusion

The findings in this study are in line with our hypothesis that there would be no consistent seasonal variation in energy and macronutrient intake due the fact that drupe-fruit availability did not follow a consistent pattern over the years. Overall, the generalist feeding behavior of chimpanzees allows them to reproduce throughout the year, whereby the timing of reproductive events seems to be opportunistic, in that the rates of maximal-swellings, conceptions and births

tend to track the diet-quality. The other indirect factors such as minimum temperature may serve as a cue to indicate fruit availability in the next season.

The lack of strict seasonality in the reproductive events either in terms of annual patterns or fruit-months or climate-seasons attests to the fact that female chimpanzees are capital breeders which accumulate energy reserves over some period and resumption of cycling is dependent on the energetic condition of the individual (Knott, 2001, 2005; Potts, 2013). Through their generalist feeding strategy, chimpanzees are able to maintain a relatively stable energy intake and balance nutrients; as such the influence of energy and macronutrient intake on reproductive cycle does not stand out clearly.

Some of the chemical contents of diet such as phytoestrogens are said to change the reproductive physiology of animals and can have an influence on seasonal breeding or even disrupt the reproductive function (Shutt, 1976; Whitten & Naftolin, 1992). Influence of phytoestrogens has been reported in human populations. Near the end of World War II, people in Holland consumed large quantities of tulip bulbs due to severe food shortage. Tulip bulbs are high in estrogenic activities and many women who ate them showed manifestations of estrogen imbalance including uterine bleeding and abnormalities of the menstrual cycle (Bickoff, 1963). These studies confirm the possibility that diet can directly affect mammalian reproductive physiology. It is also possible that chimpanzees may be avoiding phytoestrogens in some foods and this would lead to seasonal changes in diet which eventually translate in seasonal changes seen in reproductive variables observed in Kanyawara chimpanzees.

In order to clearly ascertain whether energy/macronutrient intake influences the reproductive cycle of female chimpanzees, one would need to continuously track the daily food intake and activity budget of individual female chimpanzee throughout their reproductive cycle. This can be easily done for those in captivity but may be difficult in the wild. Furthermore, as capital breeders, female chimpanzees will only resume cycling when positive energy balance is maintained (Emery Thompson, 2013; Knott, 2005; Potts, 2013). In order to fully examine if energy intake influences the reproductive cycle, it is necessary to consider energy expenditure. Future studies need to fully explore the all chemical contents of available foods (including plant secondary metabolites) to ascertain whether the seasonality in diet quality is due to avoidance or regulation of some of the undesirable food compounds.

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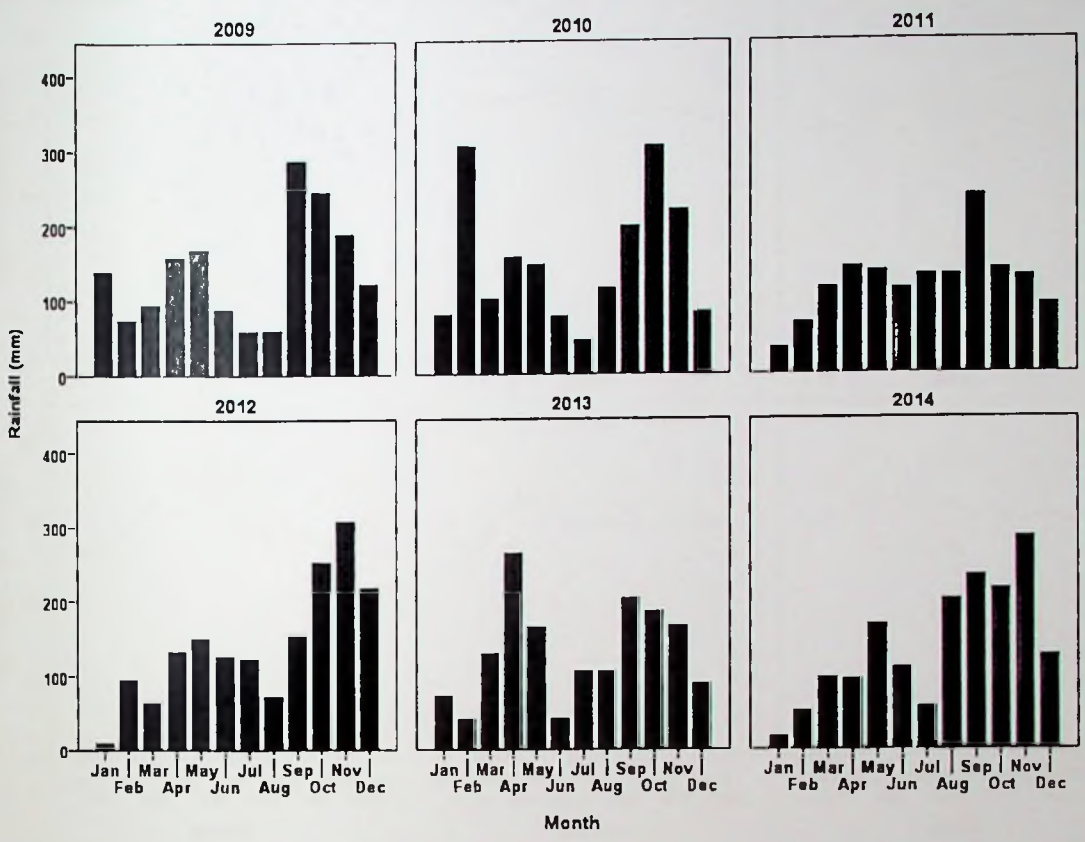
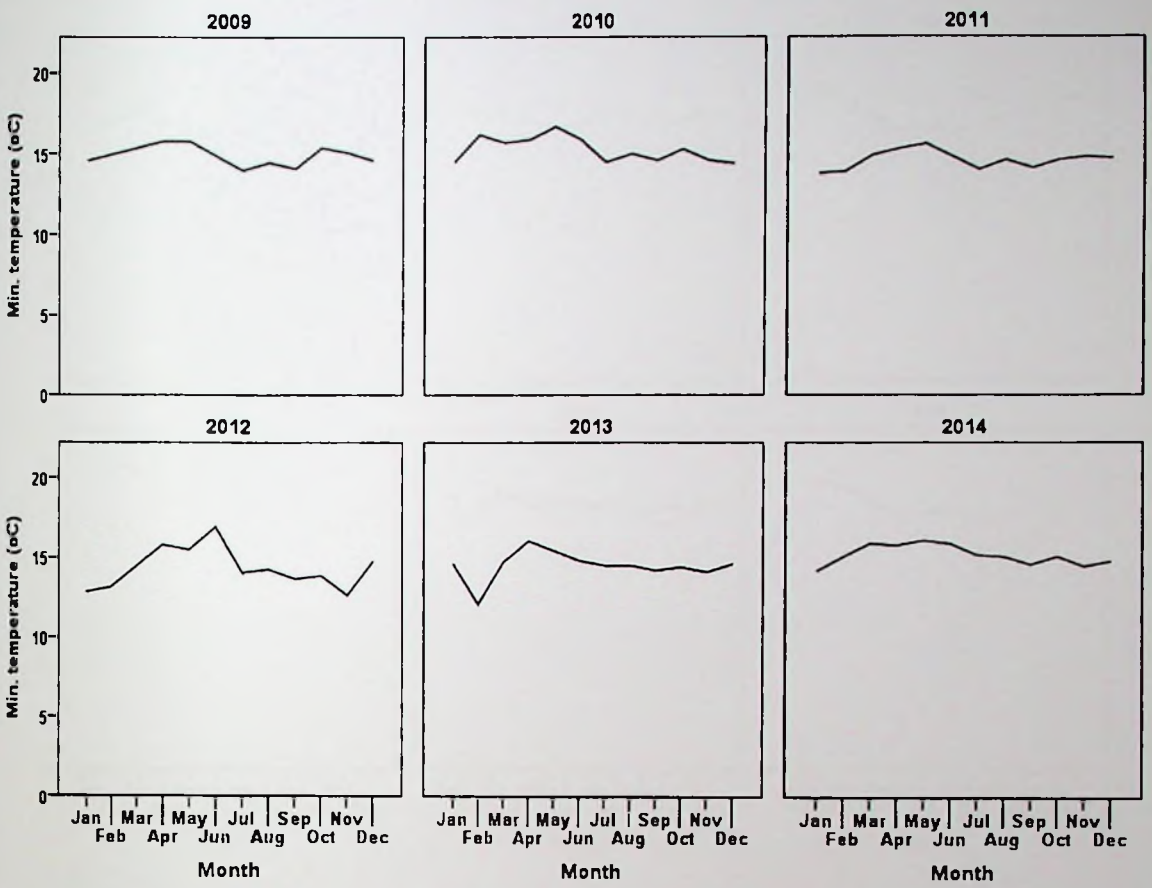
APPENDIXES

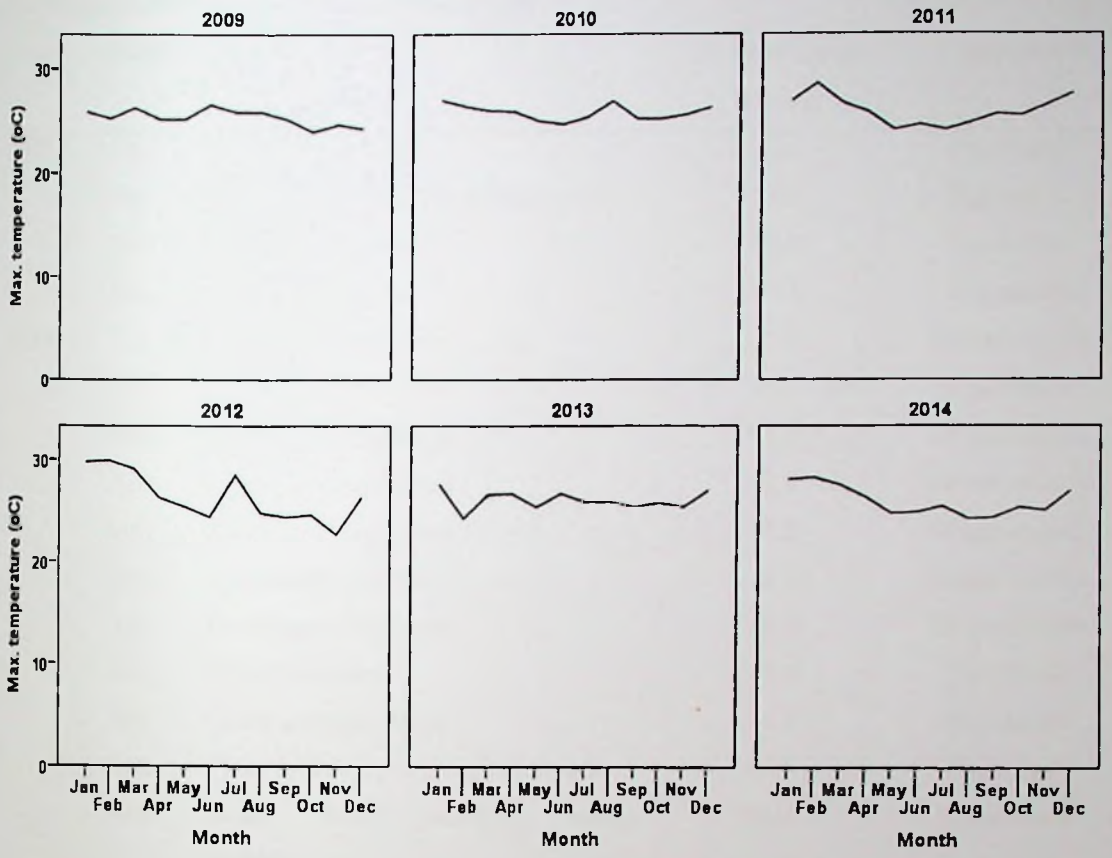
Appendix I: Annual rainfall distribution across the years 2009-2014



Appendix II: Annual trend of minimum temperature across the years 2009-2014



Appendix III: Annual trend of maximum temperature across the years 2009-2014



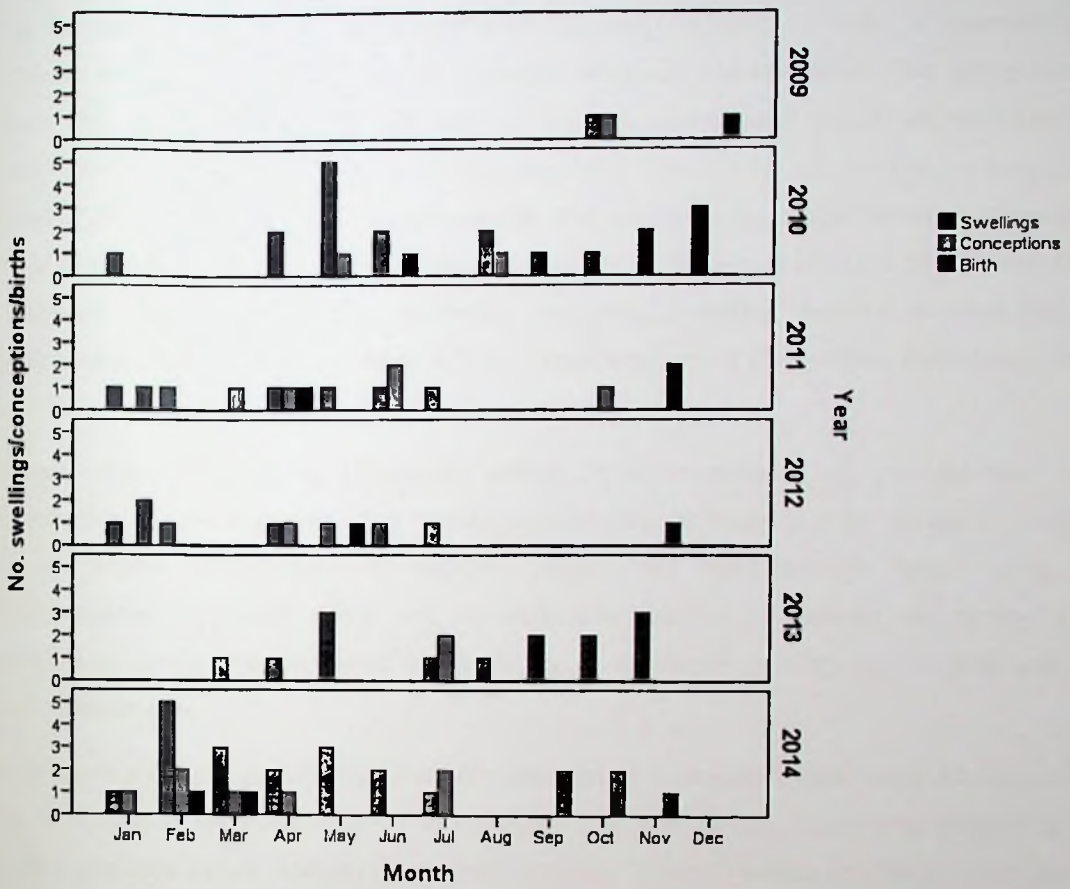
Appendix IV: Fruit availability indices using fruit species which accounted for highest percentage of time spent feeding in each month

Year	Month	Fruit specie	% time spent feeding	Fruit-month
2009	Sep	*Ficus brachylepis*	73	Fig-month
	Oct	*Ficus brachylepis/Ficus natalensis*	53.9	Fig-month
	Nov	*Ficus brachylepis*	50.0	Fig-month
	Dec	*Ficus brachylepis*	46.4	Fig-month
2010	Jan	*Pseudospondias microcarpa*	47.3	Drupe-month
	Feb	*Ficus natalensis*	35.3	Fig-month
	Mar	*Mimusops bagshawei*	51.0	Drupe-month
	Apr	*Mimusops bagshawei*	68.9	Drupe-month
	May	*Mimusops bagshawei*	76.3	Drupe-month
	Jun	*Uvariopsis congensis*	76.7	Drupe-month
	Jul	*Uvariopsis congensis*	45.4	Drupe-month
	Aug	*Ficus natalensis*	33.6	Fig-month
	Sep	*Celtis gomphophylla*	46.8	Fig-month
	Oct	*Ficus brachylepis/Ficus natalensis*	65.8	Fig-month
	Nov	*Ficus brachylepis/Ficus vallis-choudae*	61.4	Fig-month
	Dec	*Ficus exasperata*	89.7	Fig-month
2011	Jan	*Ficus natalensis*	65.3	Fig-month
	Feb	*Ficus natalensis*	71.0	Fig-month
	Mar	*Ficus natalensis*	86.7	Fig-month
	Apr	*Ficus dawei (saussureana)*	68.4	Fig-month
	May	*Ficus dawei (saussureana)*	60.3	Fig-month
	Jun	*Ficus capensis (sur)*	70.1	Fig-month
	Jul	*Ficus capensis (sur)*	55.0	Fig-month
	Aug	*Ficus natalensis*	65.2	Fig-month
	Sep	*Ficus natalensis*	58.3	Fig-month
	Oct	*Ficus capensis (sur)*	60.1	Fig-month
	Nov	*Mimusops bagshawei*	70.2	Drupe-month
	Dec	*Mimusops bagshawei*	68.8	Drupe-month

2012	Jan	*Mimusops bagshawei*	78.2	Drupe-month
	Feb	*Ficus natalensis*	76.3	Fig-month
	Mar	*Ficus dawei (saussureana)*	49.2	Fig-month
	Apr	*Ficus dawei (saussureana)*	56.0	Fig-month
	May	*Ficus capensis (sur)*	37.6	Fig-month
	Jun	*Uvariopsis congensis*	63.2	Drupe-month
	Jul	*Uvariopsis congensis*	66.4	Drupe-month
	Aug	*Ficus dawei (saussureana)*	55.1	Fig-month
	Sep	*Ficus brachylepis*	43.0	Fig-month
	Oct	*Ficus dawei (saussureana)*	62.0	Fig-month
	Nov	*Ficus brachylepis*	62.5	Fig-month
	Dec	*Ficus brachylepis*	70.1	Fig-month
2013	Jan	*Ficus capensis (sur)*	69.7	Fig-month
	Feb	*Ficus natalensis*	53.9	Fig-month
	Mar	*Ficus natalensis*	57.2	Fig-month
	Apr	*Ficus capensis (sur)*	62.4	Fig-month
	May	*Ficus exasperata*	69.2	Fig-month
	Jun	*Uvariopsis congensis*	75.9	Drupe-month
	Jul	*Ficus brachylepis*	65.0	Fig-month
	Aug	*Ficus dawei (saussureana)*	47.1	Fig-month
	Sep	*Ficus brachylepis*	67.4	Fig-month
	Oct	*Mimusops bagshawei*	65.7	Drupe-month
	Nov	*Mimusops bagshawei*	75.6	Drupe-month
	Dec	*Mimusops bagshawei*	74.8	Drupe-month
2014	Jan	*Mimusops bagshawei*	78.6	Drupe-month
	Feb	*Ficus vallis-choudae*	58.9	Fig-month
	Mar	*Ficus brachylepis*	59.2	Fig-month
	Apr	*Ficus dawei (saussureana)*	35.0	Fig-month
	May	*Ficus capensis (sur)*	79.5	Fig-month
	Jun	*Uvariopsis congensis*	55.4	Drupe-month
	Jul	*Ficus natalensis*	57.7	Fig-month
	Aug	*Ficus capensis (sur)*	49.1	Fig-month
	Sep	*Ficus capensis (sur)*	53.0	Fig-month
	Oct	*Mimusops bagshawei*	51.8	Drupe-month

	Nov	*Ficus brachylepis*	57.9	Fig-month
	Dec	*Ficus brachylepis*	51.3	Fig-month
2015	Jan	*Ficus natalensis*	54.3	Fig-month
	Feb	*Ficus natalensis*	64.2	Fig-month
	Mar	*Mimusops bagshawei*	69.7	Fig-month
	Apr	*Ficus brachylepis*	51.3	Fig-month
	May	*Ficus exasperata*	64.3	Fig-month
	Jun	*Uvariopsis congensis*	79.6	Drupe-month

Appendix V: Annual distribution of reproductive events (swellings, conceptions and births): ($N_{swellings}$=63, $N_{conceptions}$=18, N_{births}=19).



CHAPTER 7: GENERAL DISCUSSION and CONCLUSION

7.1 General Discussion

Although feeding ecology among chimpanzees has been fairly well studied, the nutritional ecology of chimpanzees has not been widely investigated. In this dissertation, the response of female chimpanzees to temporal variation of preferred fruit availability in terms of macronutrient and energy intake and its significance on reproductive events was examined. This was assessed through field observations of feeding behavior of Kanyawara adult female chimpanzees in Kibale National Park, Uganda for 18 mo (January 2014-June 2015). Additionally, a long-term data set of feeding events of female chimpanzees was used from the period between September 2009 to December 2013 as well as demographic data from the period between September 2009 to February 2015. Several data collection methods, including behavioral observation, phenological surveys of fruit abundance and nutritional analyses of chimpanzee plant foods were employed.

The study objectives were to 1) examine effects of fruit-seasonality on macronutrient and metabolisable energy intake by adult female chimpanzees; 2) determine the foraging strategy used by female chimpanzees to regulate energy and macronutrient intake using a multidimensional approach (GF); and 3) determine whether variations in energy and macronutrient intake are associated to the timing of maximal-swellings and conceptions in female chimpanzees

This research therefore provides new insights into female chimpanzee nutritional ecology with wider implications for other frugivorous primates. The aim of this concluding chapter is to provide a synthesis of key findings from earlier chapters. To avoid undue repetition, this chapter is presented as a short synopsis of key findings.

7.1.1 Influence of fruit availability on macronutrient and energy intake by female chimpanzees

Fruit availability fluctuated across the study period whereby some months were classified as drupe-months (when drupes were abundant) and some as fig-months (when drupes were scarce). Throughout the different fruit-months, the diet of chimpanzees was dominated by ripe fruit and often complemented with other food items such as young leaves, piths or flowers as has been reported previously (Basabose, 2002; Newton-Fisher, 1999; Tutin & Fernandez, 1993; Watts, Potts, Lwanga, & Mitani, 2012; Yamakoshi, 1998). While ripe fruits are an important source of calories, they have lower levels of protein and minerals and therefore chimpanzees are forced to

subsist on low-quality fibrous proteinaceous foods. These foods varied in terms of feeding and energy intake rates as well as macronutrient content. As such, time spent feeding on the different food types was not commensurate with food intake or macronutrient intake. This supports the notion that feeding rates should be incorporated in the estimation of food intake equations for wild animals (Nakagawa, 2008, 2009; Schülke, Chalise, & Koenig, 2006). Furthermore, the findings agree with previous studies that energy intake rates for figs and drupes are comparable despite the fact that figs have low sugar content (WSC and TNC) compared to drupes (Conklin-Brittain & Wrangham, 1994; Wrangham et al., 1993). However, drupes provide a high quality diet since they are rich in the high quality macronutrients and therefore provide more energy than figs.

The results demonstrated that the behavior of female chimpanzees during fig-months is typical of frugivorous primates during fruit-scarce periods (Clink, Dillis, Feilen, Beaudrot, & Marshall, 2017; Conklin-Brittain, Wrangham, & Hunt, 1998; Doran, 1997; Tutin, Ham, White, & Harrison, 1997). Female chimpanzees experienced nutrient-quality reductions during fig-months, in that intake of WSC and lipid reduced while AP and NDF intake increased. To this end, they adjusted their feeding behavior during fig-months to compensate for the low nutrient quality of figs and THV which were abundant during that period. They spent more time feeding and increased the proportion of fibrous foods in their diet during fig-months, however there was no commensurate increase in food intake or energy intake probably because fibre foods take long to be digested (Oftedal, 1991). Instead the increased consumption of fibre compensates for energy shortages since chimpanzees are able to digest fibre to some extent (Conklin-Brittain *et al.*, 2006).

Despite the fluctuations in fruit availability, female chimpanzees maintained a relatively stable energy intake across the fruit-months. This is partly due to lack of mast fruiting seasons at Kanyawara and the fact that figs provide a high-quality fallback food unlike other sites like Ngogo (Potts *et al.*, 2015). However, variations in daily diet composition led to marked variation in daily energy intake, whereby energy intake on drupe-days (when drupes dominated the diet) was significantly greater than on THV days. This further supports previous evidence that drupes are high-quality foods compared to figs.

Overall, the findings suggest that differences in diet quality between drupes and figs can have important effects on frugivore foraging, and that they influence net energy gain more by their effects on macronutrient composition or foraging cost than by their direct impact on energy intake.

7.1.2 Nutritional strategy of female chimpanzees

Using the geometric framework for nutrition, this study shows how female chimpanzees achieve their nutrient intake target in the face of fluctuating food resources. The nutritional strategy of female chimpanzees is protein prioritization similar to that of frugivorous spider monkeys.

The adjustments in feeding behavior and switching of diet by female chimpanzees was geared towards meeting their nutrient intake target in the face of fluctuating food resources. As ripe fruit specialists, chimpanzees were expected to subsist solely on a ripe fruit diet especially when ripe fruit is abundant. But this was not the case, chimpanzees consumed significant portions of low-quality herbaceous vegetation when drupes (20% THV) or figs (28.6%) were abundant. This suggests that their nutritional strategy was not energy maximization as commonly assumed of frugivorous animals.

The findings further suggest that female chimpanzees could reach their intake target by solely feeding on a fruit-based diet, if they consumed large amounts of ripe fruits. However, this is a longer process of meeting an individual's nutrient requirements because ripe fruit is deficient in proteins and is not as abundant as herbaceous vegetation. Thus female chimpanzees consumed as much protein from easily digestible ripe fruits and obtained the balance by feeding on small quantities of hard to digest but protein rich foods such as young leaves, flowers etc in order to meet their protein requirements (Milton, 1999). So unlike spider monkeys which subsist on a ripe fruit during fruit-abundant seasons, chimpanzees feed on low-quality fibrous foods (THV) even when preferred fruits are abundant (drupe-months) (Felton, Felton, Raubenheimer, et al., 2009). This suggests that although drupes and figs of Kanyawara contain some protein, the content is not enough to meet the protein target of chimpanzees.

Just like spider monkeys, chimpanzees tightly regulated protein intake while maximizing NPE intake irrespective of whether protein rich foods were abundant or scarce (Felton, Felton, Raubenheimer, et al., 2009; Felton, Felton, Wood, et al., 2009). They did this by adjusting their feeding behavior, in that during drupe-months they consumed low amounts of THV (protein-rich foods) but during fig-months, they increased the proportion of THV in their diet. This is because drupes are richer in protein than figs (Uwimbabazi et al., in press). Furthermore, the NPE:P ratio of female chimpanzees at 7:1 is close to that of spider monkeys at 8:1, an indication that frugivorous-hindgut fermenters are likely to use a similar nutritional strategy (Felton, Felton, Raubenheimer, et al., 2009).

Contrary to the common assumption that figs are fall back foods whose consumption increases when drupes are scarce, this study shows that as nutritionally balanced foods, figs are a crucial

part of the diet of frugivorous primates (Lambert & Rothman, 2015; Marshall & Wrangham, 2007). Although they are more fibrous than drupes, they contain high concentration of available calcium which is critical for maintenance and reproduction (Silver, Ostro, Yeager, & Dierenfeld, 2000; Wendelin, Runkle, & Kalko, 2000). Hence their nutrient balance may far outweigh the low quality of individual concentrations of macronutrients (Conklin-Brittain & Wrangham, 1994). Relatedly, fallback foods such as THV are not necessarily alternative sources of energy (Wrangham et al., 1991, 1993), but instead are vital sources of protein which allow chimpanzees to meet their protein intake target.

Female chimpanzees tightly regulated intake of protein while allowing NPE to vary depending on the available food types. The less regulation of NPE intake compared to protein intake might be because animals can store excess energy and can draw on it on days of negative balance or for reproduction (Emery Thompson, 2013; Knott, 2001). However, no such buffer exists for protein.

7.1.3 Influence of energy and macronutrient intake variability on seasonality of sexual swellings and conception in female chimpanzees

The analysis from the long-term data set (5.8 years) shows that there was no predictable seasonality in the intakes of energy and macronutrients despite the variation in diet-quality. This was due to lack of strict annual trends in the availability of drupe-fruits and in the onset of climate-seasons. Also, the bimodal rainfall distribution ensures availability of fruit in the Kanyawara habitat all year round and as such female chimpanzees are able to reproduce throughout the year.

On the contrary there was some level of seasonality in reproductive events and this was partly associated to diet quality (in terms of fruit type and macronutrient or energy intake) and climatic factors (Anderson, Nordheim, & Boesch, 2006; Wallis, 1995). Nonetheless, maximal-swellings, conceptions and births occurred throughout the year and there was no marked year to year variation in their distribution. The lack of strict seasonality in reproductive events is partly linked to the lack of significant variation in macronutrient and energy intake. The findings further agree with previous studies that reproductive events are limited by nutrient and energy intake as well as climatic factors (Anderson et al., 2006; Ellison, 1990; Knott, 2001).

The flexibility in feeding behavior coupled with their ability to exploit different foods with different phenological patterns enables female chimpanzees to maintain a relatively stable intake of energy across the years. Accordingly, individual female chimpanzees might be able to resume cycling regardless of the fruit-season. Therefore, unlike strict income-breeders, it is likely that female chimpanzees accumulate energy by taking advantage of ripe fruit abundant periods to

consume large amounts of carbohydrates which trigger the resumption of cycling. This partly explains why maximal-swellings and births were positively associated to energy intake.

Furthermore, the frequency of reproductive events in a month may be influenced by energy intake in previous months. As capital breeders, female chimpanzees can accumulate energy in their fat reserves and draw from that energy once they are ready to resume cycling (once they have reached a positive energy balance). This explains why there is no clear relationship between energy/macronutrient intake and conceptions.

7.2 General Conclusion

In the context of the nutritional ecology of female chimpanzees, this study adds to the documentation of behavioral responses to variation in fruit availability and the nutritional properties of food. As ripe fruit specialists, chimpanzees mainly subsisted on a ripe fruit diet. But they also fed on other foods such as unripe fruit, young leaves, pith and flowers.

In the face of fluctuating food resources with dynamic nutrient quality and quantity, female chimpanzees adjusted their feeding behavior and mixed resources to regulate protein and maximise NPE intake. Through use of feeding rates, this study revealed that time spent feeding is not commensurate with food and macronutrient intake for different food types.

The findings support previous evidence that drupes are high-quality foods due to the fact that chimpanzees experience nutrient reductions and increase foraging costs when drupes are scarce (fig-months). The behavioural and dietary flexibility exhibited by female chimpanzees enables them to maintain relatively stable energy-intake across the fruit-periods but there are marked variations in macronutrient intake.

The findings further suggest that figs and THV which are normally referred to as fallback foods for frugivorous primates are incomporated in the diet of female chimpanzees as supplementary and complementary foods to help the individuals meet their NPE and P target. The value of figs is further highlighted by the fact that even when preferred foods were abundant, chimpanzees included a significant portion of drupes in the diet (drupes-47%, figs-33%).

Although there were no significant patterns or trends in energy and/or macronutrient intake, the results agree with previous findings that there is tendency to concentrate reproductive events, especially maximal-swellings and conceptions in periods when high quality diet is abundant. From the model, it was evident that sexual-swellings and birth may be limited by energy intake. Additionally, the findings suggest that climatic factors may partly explain the seasonality in reproductive events.

7.3 Recommendations and Broader applications

7.3.1 Recommendations

This study highlights the relevance of different plant foods in the diet of female chimpanzees. The community of chimpanzees studied is in a protected area with minimal anthropogenic disturbances. Hence, the food resource base in the study community is fairly stable, although there has been indications that there is fruit decline in tropical forests in relation to climate change (Babweteera et al., 2018; Chapman et al., 2005). However, in the face of high deforestation rates in Uganda, there is a likelihood of significant loss of food resources in chimpanzee habitats particularly those outside protected areas.

Therefore, enrichment planting of degraded forest sites with drupe species such as *Cordia mellenii, Mimusops bagshawei, Uvariopsis congensis, Aningeria altissima* and several ficus species is recommended in order to conserve and manage sustainable populations of frugivorous primates in the wild.

The dietary flexibility and ability to fallback on low-quality foods may facilitate chimpanzees to survive in degraded habitats, this partly suggests that chimpanzees can tolerate human induced change. However, it might lead to negative consequences such as increased rates of crop-raiding and associated human-wildlife conflicts (McLennan, 2008, 2013). Therefore, it is important to restore the degraded forest ecosystems with the relevant food tree species of chimpanzees and other primate species. Reafforestation of degraded habitats will also contribute to curbing global warming, thereby reducing the effects of climate change on fruit production.

7.3.2 Limitations of the study and broader applications

While this study provided a detailed of seasonal changes in the diet and macronutrient intake of female chimpanzees over the years, it by no means represents the complete range of variation possible for this species and not even all female reproductive stages. The female subjects considered in this study were lactating females because they were fairly easy to locate and they occurred in large numbers compared to nulliparous and pregnant females. The response of nulliparous and pregnant females to variations in diet quality may not be similar to those of lactating females. But even among lactating females, the lactational burden is known to vary as the infant matures. As such, nutrient requirements may vary depending on the lactational stage of the female.

Furthermore, this study did not explore all the chemical components of foods such as micronutrients, toxins and other antifeedants. Yet there is a likelihood that the foraging behavior exhibited by female chimpanzees may be partly to avoid or regulating some toxic elements in

some foods. Probably the non-desirable components such as PSMs or phytoestrogens in plant foods may also explain the seasonality in reproductive events better. Also micronutrients are essential components of foods which are sought after by consumers and may explain the foraging strategy of the consumer.

There is significant variation in food types or items and their phenology among chimpanzee sites, the findings from this study may not be holistically applied to other chimpanzee populations or sites. For example, it has been noted that there is significant dietary diversity and phenology patterns for chimpanzees within Kibale National Park, that is Ngogo which about 12 km south east of Kanyawara (C. A. Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999; Potts, Chapman, & Lwanga, 2009). Nonetheless, there are some similarities in behavioral and foraging responses to fruit scarcity for the Kanyawara and Ngogo chimpanzees (Watts, Potts, Lwanga, & Mitani, 2012b) and other frugivorous primates.

The lack of strict seasonality in the timing of reproductive events for Kanyawara chimpanzees is mainly associated with their dietary flexibility which allows them to utilize foods with different phenological patterns. Linked to this is the lack of energy peaks across the years or even between fruit-periods. This trend is expected for chimpanzee sites or primates living in less seasonal habitats.

7.4 Future research

As shown from previous studies, the foraging strategy of different primate species, even in the same functional group (e.g. frugivores) varies depending on the habitat or other physiological differences. Therefore, more research is needed on chimpanzees in different habitat types before one concludes that their nutritional strategy is protein prioritization.

Furthermore, more studies are needed to compare the nutritional analysis of foods eaten and foods not eaten by chimpanzees. Because often times, according to the phenology analysis, some fruits which are abundant are not eaten. Relatedly, complete chemical analysis should be done for all chimpanzee foods in order to show if there is a pattern in intake of PSMs or antifeedants as well as micro and macronutrients and if this might explain seasonality in some of the behavior and physiological aspects in chimpanzees.

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