Feeding ecology of black and white colobus monkeys from south coastal Kenya: the influence of spatial availability, nutritional composition, and mechanical properties of food items

DISSERTATION

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ABSTRACT

Identifying the degree to which primates alter their behavior and diets to different ecological conditions has significant implications for examining functional morphology, modeling socioecology and feeding competition, and developing primate conservation strategies. This study seeks to determine if Angola black and white colobus monkeys (*Colobus angolensis palliatus*) employ consistent dietary section criteria by investigating the behavior and diet of three groups inhabiting ecologically distinct areas of Kenya's Diani Forest. The primary goals of this research are to examine feeding ecology, dietary flexibility, and food selection in relation to 1) seasonal and spatial availability, 2) mechanical toughness, and 3) nutritional composition of food items.

Behavioral data were collected on three habituated groups (Ujamaa, Ufalme, and Nyumbani) over 267 days from July 2014 – December 2015. Behavioral data were recorded using a combination of instantaneous scan sampling and focal follows. Food availability was estimated by combining tree species composition profiles of home ranges with phenology data. Mechanical toughness was recorded with a portable test instrument. Nutritional composition of food items was calculated using a combination of traditional wet chemistry assays and near-infrared reflectance spectroscopy (NIRS) predictive models.

Home ranges of the three groups differed significantly with regard to tree species composition and food availability. Diets differed considerably with regard to plant species and species-specific plant parts: only three species ranked in the top 20 food species for all three groups and mean monthly dietary overlap was just 10.4% among all groups. Dietary idiosyncrasies were not readily explained by differences in spatial and temporal availability of the most abundant tree species within the groups' home ranges (i.e., all groups selected rare tree species and plant parts from their ranges). Leaf toughness was not a strong predictor of food selection; however, toughness significantly impacted foraging efficiency. Leaf toughness negatively correlated with ingestion rate (i.e., g/min) and positively correlated with masticatory investment (i.e., chews/g). NIRS models of nutritional components had strong predictive power despite the highly heterogeneous sample set. Conventional fiber limitation and protein to fiber ratio maximization models explained leaf selection in two of the three groups and one of the three groups, respectively. Despite significant differences in consumption of species-specific plant parts and quantity of kilocalories consumed per day, individuals of different groups balanced their intake of non-protein energy (NPE) and available protein energy (AP) to a consistent ratio of approximately 2:1.

This study emphasizes that aspects of behavior and diet can vary considerably among groups living in different areas within the same forest. While availability, mechanical toughness, and nutritional composition of plant parts influenced food selection to varying degrees, maintaining a consistent NPE to AP intake (i.e., intake target) was the only consistent pattern among all three groups. Intake targets can be achieved by consistently consuming foods whose nutritional composition is close to or equal to that of the target or by consuming foods with disparate, yet complementary nutritional compositions. Unlike traditional models of food selection (e.g. protein maximization), the Geometric Framework provides a theoretical approach that can be universally applied to all investigations of primate feeding ecology.

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Publications

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2016 Dunham NT, Lambert AL. The role of leaf toughness on foraging efficiency in Angola black and white colobus monkeys (*Colobus angolensis palliatus*). *American Journal of Physical Anthropology* 161:343-354.

2016 Dunham NT, Opere PO. A unique case of extra-group infant adoption in free-ranging Angola black and white colobus monkeys (*Colobus angolensis palliatus*). *Primates* 56:183-192.

2016 Dunham NT, Kane EE, Rodriguez-Saona LE. Quantifying soluble carbohydrates in tropical leaves using a portable mid-infrared sensor: implications for primate feeding ecology. *American Journal of Primatology* 78:701-706.

2015 Dunham NT, Kane EE, McGraw WS. Scapular morphology and forelimb use during foraging in four sympatric cercopithecids. *Folia Primatologica* 86:474-489.

2015 Dunham NT. Ontogeny of positional behavior and support use in *Colobus angolensis palliatus* of the Diani Forest, Kenya. *Primates* 56:183-192.

2014 Dunham NT, McGraw WS. Positional behavior and habitat use of Peters' Angola black and white colobus monkey (*Colobus angolensis palliatus*) in structurally distinct areas of the Diani Forest, Kenya. *African Primates* 9:1-14.

Fields of Study

Major Field: Anthropology

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CHAPTER 1: INTRODUCTION TO FOOD SELECTION: THE INFLUENCE OF SPATIAL AND SEASONAL AVAILABILITY, MECHANICAL TOUGHNESS, AND NUTRITIONAL COMPOSITION OF FOOD ITEMS

INTRODUCTION

Studies of primate feeding ecology have shown that diets can differ greatly among closely related taxa, intraspecifically among groups inhabiting different habitats or areas within a forest, and interanually within a single group (Chapman and Chapman 1999; Chapman et al. 2002a, b, c; Chaves and Bicca-Marques 2013; Harris and Chapman 2007; Harris et al. 2010; Snaith and Chapman 2008). Identifying the degree to which primates alter their behavior and diets to different ecological conditions has significant implications for examining form-function relationships (e.g., linking diet to craniofacial and dentognathic traits), modeling socioecology and feeding competition, and developing primate conservation strategies (Jones 2005; McGraw and Daegling 2012; Snaith and Chapman 2007).

Researchers have utilized a variety of models and theoretical approaches to explain why primates select certain food items while excluding or minimizing the intake of others. It is clear that primate food selection is influenced to varying degrees by several variables including: availability, seasonality, density, size, strata location, odor, color, texture, predation risk, competition, mechanical properties, and nutritional/chemical composition of foods (Dominy et al. 2001; Lambert and Rothman 2015; Leighton 1993). This study seeks to determine if Angola black and white colobus monkeys (*Colobus angolensis palliatus*) employ consistent dietary selection criteria across structurally and ecologically distinct areas of Kenya's Diani Forest. The Diani Forest is characterized by extensive anthropgenic disturbance resulting in relatively intact forest areas adjacent to highly degraded areas. This forest structure provides the basis for a natural experiment in which I investigate how different ecological conditions influence feeding behavior and food selection in *Colobus angolensis palliatus*. The goal of this research is to examine feeding ecology, dietary flexibility, and food selection in relation to 1) seasonal and spatial availability 2) mechanical toughness, and 3) nutritional composition of food items. Particular emphasis is placed on understanding relationships among food selection and nutritional composition of food items. In doing so, I compare conventional food selection models based on protein maximization, fiber limitation, and protein to fiber ratio maximization typically used to explain colobine monkey food selection with a more recent theoretical approach, known as the Geometric Framework of nutrition, that examines the interactions of multiple macronutrients simultaneously (Felton et al. 2009; Simpson and Raubenheimer 2012).

Spatial and Seasonal Availability

Food availability fluctuates over spatial and temporal dimensions within a given habitat, and primates adjust their behavior and diets in response to this variability (Chapman et al. 1999, 2005; van Schaik et al. 1993). Differences in food availability contribute to intra- and interspecific dietary variation in African colobines (Chapman and Chapman 1999; Fashing 2001; Harris and Chapman 2007; Maisels et al. 1994; Wong et al. 2006). One area that has received considerable attention has involved comparing the behavior and diets of a particular colobine species inhabiting larger and/or more intact forest environments to those of groups inhabiting more disturbed forest areas or fragments (Milich et al. 2014; Onderdonk and Chapman 2000; Wong et al. 2006). In response to reduced food availability, colobine groups are known to increase time spent feeding, increase dietary diversity, and/or increase the number of food patches visited per day relative to nearby populations inhabiting more intact forest areas (Onderdonk and Chapman 2000; Wong et al. 2006; Milich et al. 2014). Furthermore, an abundance of trees from the Leguminosae family, have been associated with substantial seed predation by some African colobine monkeys including populations of *C. angolensis* (Harrison 1986; Maisels et al. 1994; McKey et al. 1981).

Chapter 2 examines how the spatial and seasonal availability of potential food items influence dietary selection in three groups of *C. a. palliatus*. This chapter also assesses the extent to which diets vary among groups inhabiting structurally distinct habitats.

Mechanical Toughness

Within the domain of materials science, toughness is defined as the work required to propagate a crack over a unit area (Lucas et al. 2012). This mechanical property has been increasingly studied in relation to the evolution of various craniofacial and dentognathic traits among living primates with the expectation that the processing of tougher food items requires morphological and/or behavioral specializations (Marshall et al. 2009). Toughness is related to a plant tissue's cell wall configuration and may correlate with some measures of fiber content (Dominy et al. 2001; Lucas et al. 1995). Because fiber is largely undetectable during ingestion, primates may assess the digestibility of food items based on the amount of work required to sufficiently comminute the material (i.e., toughness) (Hill and Lucas 1996; Teaford et al. 2006; Lucas et al. 2012). While it has been proposed that toughness (and not fiber concentration) influences food selection (Dominy et al. 2001), few studies have explicitly examined the relationship between toughness and food selection in free-ranging primates (Elgart-Berry 2004; McGraw et al. 2015; Teaford et al. 2006; Vogel et al. 2014; Wright et al. 2008; Yamashita et al. 2009). Colobines are well adapted to process tough food items due to their large bilophodont molars with high shearing crests (Lucas and Teaford 1994). It is largely assumed that tougher foods should be more costly to sufficiently break down through mastication. Thus, primates should preferentially select foods with lower toughness values and only consume tougher foods when more preferred foods are unavailable (Marshall et al. 2009). While this claim is largely assumed, it has lacked explicit testing in the literature (Venkataraman et al. 2014).

The primary objectives of Chapter 3 are to examine the relationship between food selection and leaf toughness of several species commonly consumed by *C. a. palliatus* and to test whether changes in leaf toughness influence foraging efficiency in terms of ingestion rate (grams consumed per minute), masticatory investment (chews per gram consumed), and chewing rate (chews per minute).

Nutritional Composition

Efforts to explain primate food selection have primarily focused on nutritional and chemical composition of potential food items. Many early primate feeding ecology studies utilized a theoretical framework based on optimal foraging theory (Charnov 1976; Post 1984). The most fundamental premise of this theory is that individuals will seek to optimize their foraging behavior in such a way that maximizes net energy gain (Macarthur and Pianka 1966). Thus, optimal foraging models are predominantly concerned with the caloric content of potential food items and the energy required to locate and process these items. Optimal foraging models have received considerable criticism primarily based on their assumptions that all resources are distributed homogeneously, individuals forage randomly through their home range, and that maximizing caloric intake is the primary driver of food selection. Instead, studies have demonstrated that home ranges are far from homogeneous and that the availability of different resources can be highly variable on spatial, seasonal, and annual scales (Chapman et al. 1999, 2005). Furthermore, there is also strong evidence that primates remember where food resources are located and when they are likely to be available (Dominy et al. 2001). Most importantly, optimal foraging models fail to account for the fact that “not all calories are created equal” and that individuals require certain quantities of various macro- and micronutrients (Garber 1987; Simpson and Raubenheimer 2012).

Consequently, several researchers began analyzing the nutritional content of primate foods in the 1970s and 1980s with the aim of identifying specific macronutrients that could explain why primates consistently selected certain foods while neglecting or limiting the intake of others. On the most basic level, macronutrients (i.e., major components of foods that provide caloric energy) can be divided into three categories: proteins, carbohydrates, and fats. Proteins are made up of amino acids and, in addition to providing metabolizable energy, are essential for an organism's growth and tissue maintenance (Lambert 2011). Several studies have shown that leaf selection in colobine monkeys positively correlated with protein content (Davies et al. 1988; Mowry et al. 1996; Koenig et al. 1998; Waterman et al. 1988; Yeager et al. 1997). This trend holds between plant species (i.e., leaves of some species have higher protein concentrations than those of other species) and within species as primates generally prefer more protein-rich young leaves compared to more fibrous mature leaves (Milton 1979; Dasilva 1994). With that said, many other studies did not find a positive relationship between protein content and leaf selection (Chapman et al. 2002c; Dasilva 1994; Kool 1992; McKey et al. 1981; Oates et al. 1980; Waterman et al. 1988).

Carbohydrates include a wide variety of compounds from the readily digestible water soluble monosaccharides (e.g., glucose and fructose) and disaccharides (e.g, sucrose), to starches with varying digestibility, to considerably less digestible structural carbohydrates which include fiber (composed of cellulose, hemicelluloses and lignin). Studies examining primate food selection in light of structural carbohydrate concentrations are far more ubiquitous due to their potential for digestion inhibition (Milton 1979; Felton et al. 2009; Rothman et al. 2012). This is not surprising given the fact that many structural carbohydrates are virtually indigestible for primates except those with specialized digestive anatomies (Kay and Davies 1994; Lambert 1998). Even though colobine monkeys have specialized digestive anatomies capable of processing fiber, several studies have documented that colobine monkeys select leaves with low fiber content or high protein to fiber ratios (Davies et al. 1988; Waterman et al. 1988; Mowry et al. 1996; Chapman and Chapman 2002c; Chapman et al. 2004; Fashing et al. 2007); however, it is clear that these trends do not apply to all colobine species and populations (Ganzhorn et al. 2016).

Fats are the most calorically dense macronutrient as they provide significantly more energy per unit weight compared to proteins and carbohydrates (Lambert 2011). Despite this fact, very few studies have explicitly examined the effect of fat concentration on primate food selection (Milton 1999). This is likely the case because many fruits and leaves consumed by primates have miniscule lipid concentrations (<1-5% by dry weight) (Simmen et al. 2014). Some fruits, seeds, and invertebrate and vertebrate prey have very high lipid concentrations though, and the importance of fat in the diets of primates may be understated (Righini et al. 2015; Reiner et al. 2014).

In addition to macronutrients, researchers have examined the influence of plant secondary metabolites (PSMs) on food selection. PSMs are a broad class of compounds that act as chemical defenses against insects and herbivores (Glander 1982; Burgess and Chapman 2005). While there are thought to be hundreds of thousands of unique PSMs, they are often grouped into categories based on chemical structure including: tannins, lignins, saponins, and cyanogenic glycosides (Freeland and Janzen 1974; Glander 1982). PSMs are sometimes inversely related to food selection (Oates et al. 1980; Dasilva 1994; Fashing et al. 2007) and in other cases appear to have no effect on food selection in colobines (Bocian 1997; Maisels et al. 1994; Mowry et al. 1996; Chapman and Chapman 2002).

Despite the methodological rigor and sophisticated laboratory analyses associated with many primate nutritional ecology studies of the past four decades, most of these studies lack an explicit and overarching theoretical framework. Instead, most studies examine one or a handful of macronutrient and PSM variables in relation to 1) whether foods are included vs. excluded in the diet and 2) preference/rank of those items consumed. The vast majority of these studies, particularly those of colobine monkeys, have focused on protein maximization, fiber limitation, protein to fiber ratio maximization, and/or PSM limitation or avoidance. While it is clear that these modes explain food selection for certain species or populations, they do not explain food selection universally across all primate species or even among all colobine species (Felton et al. 2009; Ganzhorn et al. 2016).

Within the past seven years the field of primate nutritional ecology has begun to transition from models examining how a specific macronutrient influences food selection to multidimensional models based on the interaction of multiple macronutrients and nutritional components. This approach originated in the early 1990s with Raubenheimer and Simpson's research on feeding behavior in locusts (Raubenheimer and Simpson 1993; Simpson and Raubenheimer 1993) and has since been applied to the study of a variety of animal taxa including several primate species (Felton et al. 2009; Rothman et al. 2011; Irwin et al. 2015; Johnson et al. 2013; Righini 2014; Vogel et al. 2016). This theoretical approach, called the Geometric Framework (GF) assumes that 1) different macro- and micronutrients serve different functions, 2) individuals require specific quantities of different nutrients, 3) individuals have evolved mechanisms to regulate/ balance nutrient intake to a specific target including mechanisms associated with taste receptors during ingestion and postingestive feedback from the digestive tract, 4) deviations from this target can negatively impact fitness, and 5) when individuals are prevented from reaching their intake target they must adopt various “rules of compromise” such as over consuming certain nutrients or under consuming certain nutrients (Simpson and Raubenheimer 2012). Thus, unlike more conventional models of food selection that emphasize maximizing or limiting the intake of a particular macronutrient, the GF records the quanities of nutrients consumed and emphasizes the importance of interactive effects among different nutrients.

The GF requires accurate estimates of daily food and macronutrient intake. Because it is often difficult to constantly monitor a single primate individual over a period of 10-12 hours, especially those inhabiting dense tropical forests, data on feeding rate can be combined with traditional scan sampling data of time spent feeding to estimate daily food intake (Felton et al. 2009). These daily intakes are then multiplied by the nutritional composition of food items to yield estimates of daily macronutrient intake (Rothman et al. 2012).

The GF works by plotting macronutrient intakes on x- and y-axes. For instance, protein intake is often plotted on the x-axis and nonprotein energy intake (i.e., calories from carbohydrates and fats) is often plotted on the y-axis. Each data point represents an individual’s total intake of nonprotein energy to protein energy for a given day and is plotted alongside other daily intakes to create a scatter plot. A regression line, forced through the origin, is then fitted to the points. The slope of this line represents the nonprotein energy to protein energy ratio or intake target (Simpson and Raubenheimer, 2012) (see Figure 1.1). When individuals are unable to achieve their intake target, there are a variety of methods used to determine which macronutrients are more tightly regulated vs. those that are under or overconsumed (e.g., comparing coefficients of variation and right-angled mixture triangles—discussed in Chapter 5).

Chapter 4 explains how nutritional compositions of various plant items were quantified using conventional wet chemistry assays as well as near infrared spectroscopy models. These values are then used to assess the relationships between food selection and protein maximization, fiber limitation, and protein to fiber ratio maximization models in Chapter 5. Chapter 5 also utilizes the GF to identify nonprotein energy to protein energy intake targets and rules of compromise for *C. a. palliatus*.

CONCLUSION

Chapter 6 employs a multivariate statistical model to assess how seasonal and spatial availability, mechanical toughness, and nutritional composition simultaneously influence food selection in *C. a. palliatus*. Finally, Chapter 7 concludes the dissertation by summarizing the major findings, discussing the significance of the research, and identifying important avenues for future research.

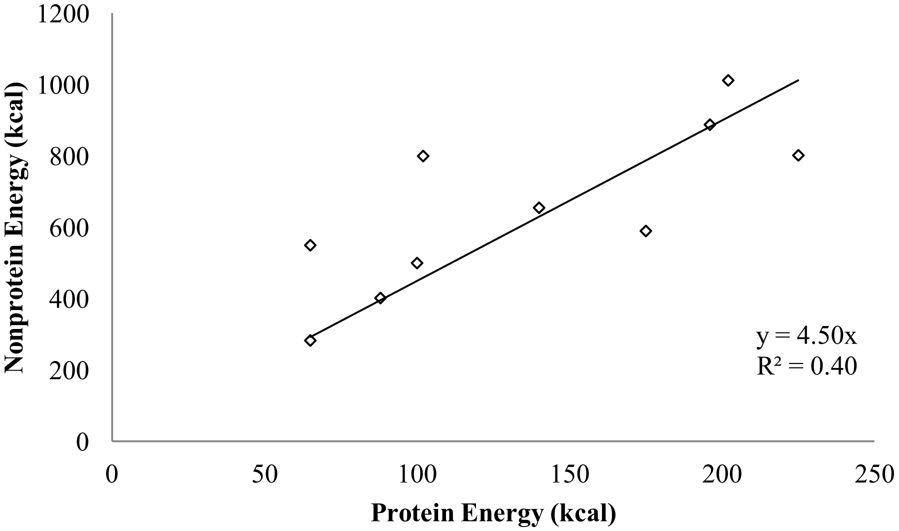

Figure 1.1. Example model of daily nutritional balancing based on ten days. Each of the ten data points represents a daily intake of nonprotein energy (y-axis) and protein energy (x-axis). A regression line is then fitted to the data points and forced through the origin. The slope of the line indicates that the intake ratio of nonprotein energy to protein energy is equal to 4.50.

CHAPTER 2: HOW DO SPATIAL AND TEMPORAL DIFFERENCES IN FOOD AVAILABILITY INFLUENCE DIETARY VARIATION AND FOOD SELECTION?

INTRODUCTION

It is well documented that the availability of different plant parts fluctuates over spatial and temporal scales with a given habitat and that primates adjust their behavior and diets in response to this variability (van Schaik et al. 1993; Chapman et al. 1999). Identifying the degree to which diets differ in response to changes in food availability remains an important research avenue for primatologists (Oates 1977; Milton 1980; Gautier-Hion 1980; Leighton 1993; Dasilva 1994; Fashing 2001). Comparisons of diet and differences in food availability among habitats provide important context for understanding intra- and interspecific dietary variation which in turn influences investigations of primate behavior, sociality, morphology, and conservation (Chapman et al. 2002b; Lambert and Rothman 2015).

The behavior and diet of African colobine monkeys has been the subject of extensive research (see Fashing 2011; Struhsaker 2010). Colobines are well known for their ruminant-like digestive systems characterized by a multi-chambered stomach equipped with symbiotic bacteria that function in foregut fermentation. These features enable more effective digestion of fibrous plant material (Kay and Davies 1994; Lambert 1998). While leaves constitute a significant proportion of the diet in all African colobines (i.e., 26%-92% of the annual diet) studied to date, it is clear that fruits, seeds, flowers, and other items often also make up large proportions of their overall diets (Fashing 2011). Differences in food availability and quality may, in part, explain some of the dietary variation among African colobine species and populations (Maisels et al. 1994; Fashing 2001).

Investigations of intraspecific dietary variation has often involved comparing the behavior and diets of a particular colobine species inhabiting larger and/or more intact forest environments to those of groups inhabiting more disturbed forest areas or fragments (Onderdonk and Chapman 2000; Wong et al. 2006; Milich et al. 2014). Logged forests and fragments are often characterized by reduced food availability for primates due to changes in forest structure including: reduction in the number of large trees and increases in the abundance of pioneer species, exotic species, and lianas (Lovejoy et al. 1986; DeWalt et al. 2000; Zhu et al. 2004). In many cases, populations inhabiting logged areas or forest fragments alter their behavior and diet by decreasing group size, increasing or decreasing daily path lengths, increasing time spent feeding, increasing dietary diversity, and/or increasing the number of food patches visited per day relative to nearby populations inhabiting more intact forest areas (Onderdonk and Chapman 2000; Wong et al. 2006; Milich et al. 2014). For instance, *Colobus vellerosus* groups inhabiting fragments outside the Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana fed more frequently on lianas and consumed several tree species not eaten by groups living in BFMS (Wong et al. 2006). Similarly, *Piliocolobus rufomitratus* achieved equal densities in logged vs. old growth areas of Kibale National Park. Groups inhabiting logged areas compensated for reduced food availability by increasing time spent foraging and dietary diversity (Milich et al. 2014).

Of the five species of black and white colobus monkeys (i.e., *Colobus* spp.), the Angola colobus (*Colobus angolensis*) is perhaps the least known with only a handful of long term field studies examining the behavior and diet of this species. In fact, despite its vast range spanning the majority of central Africa from Angola to Tanzania, there are only four published studies of *C. angolensis* behavior and feeding ecology that span 8 months or more: one of *C. a. angolensis* in Salonga National Park of Democratic Republic of Congo (DRC) (Maisels 1994), one of *C. a. cottoni* in the Ituri Forest of DRC (Bocian 1997), and two studies of *C. a. ruwenzorii* in the Nyungwe Forest, Rwanda (Fimbel et al. 2001; Vedder and Fashing 2002) (Table 2.1). From these studies, we have learned that the three subspecies rely heavily on seeds (i.e., 20%-50% of the overall diet) and may have craniofacial features more suited for granivory (Koyabu and Endo 2009). A six month study of *C. a. palliatus* from Diani, Kenya, suggests leaves (57.2%), fruits (21.4%), and flowers (10.7%) make up the majority of the diet with a much smaller contribution from seeds (10.7%) (Moreno-Black and Maples 1977).

This chapter builds on previous studies of *C. angolensis* diet and feeding behavior by examining three groups of *C. a. palliatus* inhabiting the Diani Forest, Kenya. The research seeks to assess the degree to which diets vary among three groups and examine the roles of spatial and temporal availability of potential food items on food selection.

I first compared differences in forest composition and food availability among the home ranges of three colobus groups inhabiting structurally distinct and nonadjacent ranges in the Diani Forest, Kenya: one group inhabited a relatively intact forest area with a mix of primary and secondary forest, and the other two groups inhabited more degraded forest areas dominated by exotic (i.e., non-indigenous) tree species. I then compared feeding behavior and diets of the three groups inhabiting these ranges. I predicted that the more intact forest area would be composed primarily of indigenous tree species and have greater food availability, while the more degraded forest areas would be structurally distinct in terms of tree species composition and would be associated with reduced food availability. In response to differences in forest composition and food availability among the home ranges, I predicted groups in the degraded areas would exhibit greater dietary diversity in terms of the number of plant species consumed such that the top plant species would contribute a smaller proportion of the overall diet. I also predicted that groups in the degraded areas would consume more lianas and exotic plant species.

METHODS

Study Site

The Diani Forest is located in south coastal Kenya and is one of the few remaining patches of biodiversity-rich coral rag forests in East Africa (Figure 2.1). The forest measures approximately 4.6 km^2, and is comprised of patches of intact forest interspersed with highly degraded areas (Anderson et al. 2007; Dunham and McGraw 2014; Dunham 2015). The climate is characterized by two rainy seasons, with short rains from October – December and long rains generally occurring from March – June (Mwamachi et al. 1995). The remaining months are markedly drier. Annual rainfall averaged 744 mm over a seven year period (Mwamachi et al. 1995); however the annual rainfall during this study was 1550 mm (i.e., January-December 2015) (Figure 2.2). High temperatures range from 35°C in dry seasons to 28°C in the rainy seasons and low temperatures range from 20°C - 24°C (Okanga et al. 2006). Several primate taxa inhabit the forest including small-eared galago (*Otolemur garnettii*), Kenya coast galago (*Galagoides cocos*), vervet monkeys (*Chlorocebus aethiops*), Sykes' monkeys (*Cercopithecus albogularis*), yellow baboons (*Papio cynocephalus*), and Peters' Angola colobus.

Study Species

Colobus angolensis typically live in groups of 2-20 members throughout their ranges in eastern and central Africa; however, *Colobus angolensis ruwenzorii* from Nyungwe, Rwanda, have been documented in groups of greater than 300 members (Fimbel et al. 2001; Fashing et al. 2007). Group size in the Diani Forest averages six individuals with groups typically consisting of one or two adult males, multiple adult females, and their offspring (Moreno-Black and Maples 1974; Dunham pers. observation). Like other *Colobus* spp., Diani Angola colobus monkeys are highly arboreal and spend much of their time feeding and resting in the main canopy (Dunham and McGraw 2014; Dunham 2015). This study focused on three groups (Ujamaa, Ufalme, and Nyumbani) inhabiting non-adjacent ranges with several colobus groups ranging between the three study group ranges. Group sizes ranged from 5 - 10 individuals but size and composition varied throughout the study period. The first group, Ujamaa, inhabited one of the most intact sections of the Diani Forest that is characterized by a mix of primary forest and secondary forest. Ufalme inhabited a more degraded forest area approximately 4.9 km north of the Ujamaa range. Lastly, Nyumbani ranged through another degraded forest patch dominated by invasive *Azadirachta indica* trees and lies roughly 1.0 km south of the Ujamaa range (Figure 2.3).

Forest Composition and Phenology

A GPS waypoint was recorded using a portable Garmin 62s at the start of each behavioral scan (i.e., every 15 minutes). Each waypoint was recorded approximately at the center of the study group to estimate the group's overall position (Cords 1987). ArcGIS software was used to plot the waypoints and map the home ranges from July 2014 - December 2015 for Ujamaa and Ufalme groups and from January - December 2015 for the Nyumbani group. Home ranges were mapped using the minimum convex polygon tool in Arc GIS.

Forest mapping around and within the study groups' home ranges was initiated in 2012 as part of another study examining the degree to which differences in forest composition and forest architecture among discrete areas of the Diani Forest influence *C. a. palliatus* positional behavior among the same three study groups (Dunham and McGraw 2014). Additional mapping was completed during May - November 2015 as the home ranges increased and/or changed slightly from the 2012 study to the 2014 -2015 study period. Using trails and forest edges as boundaries, the forest was divided into discrete quadrants of approximately 10 x 10 m in area. Within each quadrant, all trees >

10 cm at breast height (DBH) were recorded with regard to tree species name, DBH value, and GPS waypoint. The home ranges of the study groups and areas just outside their ranges were mapped and documented in this manner. After completing behavioral data collection in December 2015, home range maps were merged with forest composition maps. Using the home ranges as bounding areas, it was possible to select only the trees within group home ranges using ArcGIS. The basal area (BA) of each tree species was then calculated using the formula: BA = $[(0.5 \text{ X DBH})^2 \text{ x } \pi]$ (Vandercone et al. 2012).

Phenology data were collected twice per month on roughly the first and fifteenth day of each month. Data were collected on trees from three phenology trails, including one trail within each home range (n = 407 trees). The availability of young leaves (YL), mature leaves (ML), unripe fruit (UFR), ripe fruit (RFR), and flowers (FL) was scored on a whole number scale of 0 - 4. Scores were defined by the following: 0 = absent or 0% of tree canopy contains the particular plant item, 1 = ~1 - 25%, 2 = ~26 - 50%, 3 = ~51 - 75% and 4 = ~76 - 100% of the canopy was laden with a given plant part. Binoculars were used to assess phenology scores of upper canopy trees and those with particularly small fruits. Phenology was conducted in collaboration with a local botanist, John Ndege, who has extensive field experience in the coral rag forests of East Africa, including the Diani Forest.

Data on forest composition and phenology were combined to create a food availability index (FAI) for each tree species: FAI = [mean phenological score X BA]

(Dasilva 1994; Fashing 2001). Indices were generated for the top 20 ranking plant species in each group's overall diet.

Behavioral Methods

Behavioral data were collected on three habituated groups (i.e., Ujamaa, Ufalme, and Nyumbani) of *C. a. palliatus* (n = 267 full day follows). Behavioral data were recorded on Ujamaa and Ufalme from July 2014 - December 2015 and on Nyumbani from January - December 2015. Groups were followed on a weekly rotational basis such that each group was followed for 5 - 7 days per month. Activity budget and feeding data, including plant species and part consumed (i.e., YL, ML, UFR, RFR, FL, and other), were collected during 5 minute group scans at 15 minute intervals. Fruits were also classified as either whole fruit or seed depending on the plant species and whether colobus individuals consumed both the outer flesh and internal elements (i.e., whole fruit) or just the inner seeds (i.e., seed) (Fashing 2001). Each individual's behavior (i.e., resting, moving, feeding, socializing, other) was recorded instantaneously before rotating to another group member. A scan was completed after a maximum of 5 minutes or after the behavior of all individuals was recorded. Individuals were easily identified by a combination of facial features and tail morphology. This individual recognition, in addition to the cohesiveness of the small groups, enabled recording of all individuals for the vast majority of group scans. Only data of adult males and adult females are included in this analysis.

Statistical Methods

Wilcoxon signed rank tests using Bonferroni corrections were used to compare proportions of different plant parts among groups (Fashing, 2001). Each month represents a data point for a given plant part and group (n = 12 or 18). The Wilcoxon test determines if groups differ significantly in their consumption of different plant parts over the entire study period.

Dietary overlap (DO) among groups was calculated by summing the shared percentages of species-specific plants consumed between groups (Holmes and Pitelka 1968; Rudran 1978; Buzzard 2006). Percentage of dietary overlap was calculated each month between groups for each dyad. Monthly dietary overlaps were then averaged over the 18 months (i.e., Ujamaa vs. Ufalme) or 12 months (i.e., Ujamaa vs. Nyumbani; Ufalme vs. Nyumbani) to yield a mean dietary overlap between each dyad (Struhsaker and Oates 1975; Fashing 2001). Monthly dietary overlap was also calculated among all three groups per month and averaged over the 12 month period in which data are available for all groups.

Selection ratios (SR) were calculated to determine which plant species was eaten more frequently than expected based on its availability in a group's home range. SR = [% of feeding time spent on $\text{species}_{(t)}$ / % of total FAI contributed by $\text{species}_{(t)}$] (Dasilva 1994). Selection ratios greater than 1 indicate that a given species is selected more frequently than expected based on availability. Spearman rank-order correlations were used to examine the relationship between overall plant part availability and food selection as well as species-specific plant part availability and selection (Dasilva 1994; Fashing 2001).

RESULTS

Rainfall

The monthly rainfall during the study period is shown in Figure 2.3. Annual rainfall from July 2014 - June 2015 was 1426 mm. Rainfall from January - December 2015 was 1550 mm. These figures are considerably higher than the five-year rainfall mean of 744 mm reported by Mwamachi et al. (1995). The increased rainfall during the study period is likely the result of an El Niño event that affected much of East Africa during 2015. These rainfall data generally conform to the typical timing of precipitation for coastal Kenya in which rains are present from late March to early June and again from late October through November.

Forest Composition and Food Availability

Using the minimum convex polygon tool in ArcGIS home ranges sizes during the study period were 11.38 ha for Ujamaa, 5.99 ha for Ufalme, and 8.66 ha for Nyumbani. Ujamaa not only had the largest home range but their range also had the greatest number of tree species (n = 102) and individual trees greater than 10 cm DBH (n = 1,516 trees; 133.22 trees/ha). The Ufalme home range contained 55 trees species and 624 individual trees greater than 10 cm DBH (104.17 trees/ha). The Nyumbani home range consisted of 78 tree species and 1,260 trees greater than 10 cm DBH (145.50 trees/ha).

The top 20 most abundant tree species per home range are presented in Tables 2.2 – 2.4. Most notably, the Ujamma home range was dominated by indigenous tree species, particularly *Combretum schumannii* (Table 2.2). The Ufalme range contained a balance of exotic tree species, such as *Azadirachta indica* and *Delonix regia*, and indigenous trees, led by *Grewia plagiophylla*, *Lecaniodiscus fraxinifolius*, *Zanthoxylum chalybeum*, and *Adansonia digitata* (Table 2.3). More than half (i.e., 53.4%) of the Nyumbani home range biomass came from two exotic tree species: *Azadirachta indica* and *Delonix regia* (Table 2.4).

There was varying overlap among groups with regard to the 20 most abundant tree species in their home ranges. For instance, Ujamaa and Ufalme home ranges shared 7 out of 20 tree species. Ujamaa and Nyumbani home ranges were consistent in 12 out of 20 most abundant tree species. Finally, Ufalme and Nyumbani home ranges overlapped by 8 out of 20 tree species. Six tree species were among the 20 most abundant in all three home ranges: *Adansonia digitata*, *Carpodiptera africana*, *Delonix regia*, *Lecaniodiscus fraxinifolius*, *Millettia usaramensis*, and *Plumeria obtusa*.

In all three home ranges ML had the highest availability, followed by YL, then by varying amounts of FR and FL (Tables 2.5 – 2.7). When comparing among home ranges with Wilcoxon signed rank tests, food availability often differed significantly. The Ujamaa range had significantly higher availability of ML, YL, FR, and FL compared to the Ufalme range ($n = 18$; $p < 0.01$ for all tests). Similarly, the Ujamaa home range had a significantly greater availability of YL ($n = 12$; $p < 0.01$), and FR ($n = 12$; $p < 0.01$) compared to the Nyumbani range. The Ufalme range had significantly lower availability scores for ML and YL ($n = 12$; $p < 0.01$ for both comparisons) compared to the Nyumbani range. All other pairwise comparisons were non-significant.

Plant Parts and Plant Species Consumed

Pairwise comparisons of plant part consumption using Wilcoxon signed rank tests and Bonferroni corrections yielded no significant differences in plant part consumption among groups. Spearman rank-order correlation coefficients (r_s) were used to assess relationships between the phenological availability and consumption of different plant parts (i.e., YL, ML, total FR and FL). There were no significant correlations between overall plant part availability and monthly consumption for any of the study groups. The diets of all three groups consisted primarily of YL, ranging from 52.5 - 63.3% of the total diet (Table 2.8). ML comprised a considerably smaller portion of each group's diet (i.e., 11.6 - 15.4%). Both YL and ML were consumed from trees and lianas, as well as from indigenous and exotic plant species. Total fruit (FR) ranged from 11.8 - 16.4% of each group's total diet. The vast majority of FR consumed were UFR. Additionally, the majority of FR species consumed were seeds (SD) for Ufalme and Nyumbani groups (7.9 - 15.2%). SD comprised a smaller portion of the Ujamaa diet (5.6%) compared to whole fruit (WF) (8.6%). FL consumption varied from 11.4 - 17.7% of the total diet among groups. Flowers from indigenous tree species and lianas, as well as exotic flowering plants (e.g., *Delonix regia* and *Bougainvillea spectabilis*), were regularly consumed. Food items in the category "other" included fossilized coral, sand, soil, termite mounds, concrete, charcoal, and building plaster. Combined, these items constituted just 0.1 -

0.4% of each group's total diet. Individuals were also observed drinking from puddles a few times during the study period.

The top 20 plant species and plant parts consumed most frequently by each group are presented in Tables 2.9 – 2.11. All three groups differed in their most frequently consumed plant species: Ujamaa- *Pithecellobium dulce*; Ufalme- *Lecaniodiscus fraxinifolius*; Nyumbani- *Bougainvillea spectabilis*. The number two plant species consumed for all three groups was *Delonix regia*. The top 20 tree species varied considerably among groups. Ujamaa and Ufalme shared 7 out of 20 species, Ujamaa and Nyumbani shared 9 species, and Ufalme and Nyumbani overlapped on 7 out of 20 species. Only three plant species were ranked in the top 20 most consumed plants for all three groups: *Adansonia digitata, Bougainvillea spectabilis,* and *Delonix regia*. Combining data for the top 20 ranking plant species of all three groups (i.e., N = 60), SR < 1 for four species, SR > 1 for 37 species, and availability data were unavailable for 19 species of shrubs and lianas. Thus, the vast majority of species for which data are available were consumed in greater proportion than their abundance would suggest if all species were eaten at random.

Species-specific plant part overlap also varied among groups. The mean monthly dietary overlap between Ujamaa and Ufalme was 17.0% (range = 4.0 - 26.8%; n = 18 months). Dietary overlap between Ujamaa and Nyumbani was 26.0% (range = 16.8 - 47.4%; n = 12 months). Finally, dietary overlap between Ufalme and Nyumbani was 30.7% (range = 17.8 - 51.8%; n = 12 months). Combing data for all three groups, dietary overlap averaged 10.4% (range = 1.6 - 16.6%; n = 12 months).

Spearman rank-order correlation coefficients were also used to compare monthly availability scores and consumption for the top 10 ranking species-specific plant parts for each group (Tables 2.12 – 2.14). For Ujamaa, the availability of *Milettia usamarensis* FL ($r_s = 0.49$; $p = 0.04$) and *Lepisanthes senegalensis* RFR ($r_s = 0.99$; $p < 0.01$) correlated with monthly consumption. For Ufalme, *Lecaniodiscus fraxinifolius* UFR ($r_s = 0.91$; $p < 0.01$) and *Gliricidia sepium* FL ($r_s = 0.83$; $p < 0.01$) availability correlated with monthly intake. For Nyumbani, the availability of *Ficus exasperata* UFR ($r_s = 0.59$; $p = 0.04$), *Zanthoxylum chalybeum* YL ($r_s = 0.90$; $p < 0.01$), and *Adenanthera pavonina* UFR ($r_s = 0.75$; $p < 0.01$) correlated with monthly consumption. Lastly, the availability of *Delonix regia* FL correlated with monthly consumption in all three groups (Ujamaa: $r_s = 0.81$; $p < 0.01$; Ufalme: $r_s = 0.70$; $p < 0.01$; Nyumbani: $r_s = 0.76$; $p < 0.01$).

Dietary Diversity

The three study groups consumed a total of 110 different plant species. Ujamaa fed from 73 species, Ufalme from 63 species, and Nyumbani from 76 species. The top 10 plant species made up 64.3% of the Ujamaa diet, 73.6% of the Ufalme diet, and 62.4% of the Nyumbani diet.

Lianas

The groups foraged on a total of 25 liana species during the study period. Ujamaa consumed 18 species of lianas, representing 30.3% of the total diet and five of the top 20 plant species consumed. Ufalme fed on 18 species of lianas, constituting 20.8% of the diet and five of the top 20 plant species consumed. Nyumbani ate 24 species of lianas, accounting for 38.4% of the diet and five of the top 20 species consumed.

Exotic Plant Species

Exotic plant species also contributed significantly to the diets of all three groups: Ujamaa- 10 species, 30.1% of the total diet; Ufalme- 13 species, 31.2% of the total diet; Nyumbani- 11 species, 40.3% of the total diet. For Ujamaa, three of the top 20 plant species consumed were exotic, including the top 2 species: *Pithecellobium dulce* and *Delonix regia*. For Ufalme, five of the top 20 plant species eaten were exotic, including the second and fourth ranking species: *Delonix regia* and *Bougainvillea spectabilis*. Lastly for Nyumbani, five of the top 20 ranking plant species consumed were exotic, including the top 3 ranking species: *Bougainvillea spectabilis*, *Delonix regia*, and *Adenanthera pavonina*.

DISCUSSION

Forest composition and food availability differed greatly among the home ranges of the three study groups. As predicted, the more disturbed ranges were characterized by a greater proportion of exotic tree species and lower food availability compared to the more intact home range. Diets differed significantly among groups; however, differences in tree species composition and food availability among home ranges did not readily explain these dietary differences because groups did not select plant species or plant parts in proportion to their availability. Contrary to my predictions, groups inhabiting the more disturbed areas did not exhibit greater dietary diversity or rely more heavily on lianas and exotic plants. Instead, all three groups consumed remarkably diverse diets, including several species of lianas and exotic plants.

The home ranges of the study groups differed spatially with regard to tree species composition. The Ujamaa range encompassed one of the most intact regions of the Diani Forest and was dominated by indigenous tall canopy (~20 - 25 m) trees (Dunham and McGraw 2014). The Ufalme range had a greater proportion of exotic tree species, including its two most abundant species: *Azadirachtar indica* and *Delonix regia*. The tall canopy *Combretum schumanni* trees characteristic of the Ujamaa range were largely absent and have been replaced by secondary growth of *Grewia plagiophylla*, *Lecaniodiscus fraxinifolius*, and *Zanthoxylum chalybeum* in the Ufalme range. Lastly, the Nyumbani range largely consisted of small private properties, many of which were significantly deforested beginning in the 1970s (Moreno-Black and Maples 1977). The exotic and invasive neem tree (*Azadirachta indica*) rapidly filled these forest openings. This single species represented nearly 40% of the tree biomass in the Nyumbani home range. Only six tree species were among the top 20 most abundant trees in all three home ranges including 4 indigenous species (*Adansonia digitata*, *Carpodiptera africana*, *Lecaniodiscus fraxinifolius*, and *Millettia usaramensis*) and 2 exotic species (*Delonix regia* and *Plumeria obtusa*).

Despite the spatial availability of potential food species differing significantly among home ranges, food selection did not readily correlate with spatial abundance for the majority of tree species. Instead, relatively rare plant species were selected disproportionately higher than their abundance would suggest if all plant species were eaten at random. That is, of the 41 species in which SR are available, thirty-seven of these species have SR > 1, while only 4 species have SR < 1. In contrast, some of the most abundant tree species were rarely eaten (e.g., *Carpodiptera africana*, *Lannea welwistchii*, *and Combretum schumanii*). Furthermore, the most abundant tree in both the Ufalme and Nyumbani ranges (*Azadirachta indica*), was never consumed by any of the three study groups over the entire 18 month study period. A propensity to select relatively rare plant species has been documented in other African colobine monkey studies (McKey et al. 1981; Dasilva 1992; Fashing 2001; Preece 2006). While spatial availability was not a strong predictor of food selection, it is worth emphasizing an obvious point: a plant species must be physically present in a home range to be selected. For instance, *Adenanthera pavonina* ranked third among plant species in the Nyumbani diet, and all of these feeding records came from a single *A. pavonina* tree within their range. In contrast, *A. pavonina* was never consumed by the Ufalme group because it was not found in their home range. Similarly, *Gliricidia sepium* ranked ninth overall in the Ufalme diet, but was absent from both Ujamaa and Nyumbani home ranges. Thus, only minor differences in forest composition among home ranges (e.g., the presence of a single tree) can significantly impact intergroup dietary differences.

In addition to differences in spatial availability of tree species, home ranges differed in their temporal availability of different plant parts. For example, the Ujamaa range had significantly greater availability of all plant parts compared to the Ufalme range and greater availability of YL and FR compared to the Nyumbani range. The

Nyumbani range also had significantly greater availability of YL and ML compared to the Ufalme range. As discussed earlier, groups did not differ in the proportion of plant parts in their overall diets, despite these differences in plant part availability among the home ranges. Furthermore, Spearman rank-order correlation coefficients found no significant relationships between monthly phenological availability of YL, ML, FR, or FL and monthly consumption for any of the three groups. Thus, the Diani colobus did not target any particular plant part, broadly speaking, in relation to its monthly availability.

Groups did not differ in the overall proportion of plant parts consumed, despite differences in plant part availability among the home ranges. Young leaves comprised the majority of all three groups' diets, ranging from 52.9 - 63.3% of the overall diet. Mature leaves (mean = 13.2%; range = 11.6 - 15.4%) constituted a considerably smaller proportion of the diet for all three groups. Total fruit consumption ranged from 11.8 - 16.4% of the diet and was dominated by unripe fruit (mean= 12.1%; range = 11.3 - 13.2%) with lesser amounts of ripe fruit (mean = 2.0%; range = 0.5 - 3.1%). Seeds comprised a larger percentage of the Ufalme diet (15.2%) compared to diets of Ujamaa (5.6%) and Nyumbani (7.9%). Overall, this result contrasts other studies of *Colobus angolensis* in which seeds constituted much larger proportions of the overall diet (Table 2.1). Seeds from the Leguminosae family were particularly important for *C. angolensis* at Ituri and Salonga (Bocian 1997; Maisels 1994). While seeds of the Leguminosae family were consumed by *C. a. palliatus* in this study, many of these species are exotic (e.g., *Adenanthera pavonina*, *Delonix regia*, *Gliricidium sepium*) and were not eaten frequently over the course of the study period. The seeds most frequently selected by the Diani colobus came from other plant families including: Lamiaceae (*Premna hildebrandti*), Sapindaceae (*Lecaniodiscus fraxinifolius*; *Lepisanthes senegalensis*), and Sapotaceae (*Sideroxylon inerme*). Lastly, flowers made up a considerably larger proportion of the diet (mean = 14.1%; range = 11.4 - 17.7%) than all previous studies of *Colobus* spp. (see Fashing 2011, p. 209). This is likely due, in part, to the prevalence of exotic/ornamental species in the Diani Forest that flower multiple times and for several months per year (e.g., *Delonix regia*, *Bougainvillea spectabilis*).

Despite the fact that the overall proportion of plant parts did not differ significantly among group diets, diets differed dramatically with regard to plant species and species-specific plant parts. Only three plant species ranked in the top 20 most frequently consumed for all three study groups: *Adansonia digitata, Bougainvillea spectabilis,* and *Delonix regia*. Dietary overlap was low among study groups with mean overlap ranging from 17.0% - 30.7% for pairwise comparisons of groups. Dietary overlap was just 10.4% among all three study groups for the 12 month period in which data were available for all groups. This intraspecific dietary overlap was considerably less than that reported in previous studies of African colobine monkeys: *Colobus guereza*, Kakamega, Kenya, neighboring groups, overlap = 54.4% (Fashing, 2001); *Piliocolobus badius*, neighboring groups, Kibale, Uganda, overlap = 37.3% (Chapman et al. 2002c). In fact, dietary overlap among all three Diani black and white colobus groups was on par or lower than interspecific dietary overlap between sympatric African colobines: *C. guereza* vs. *C. angolensis*, Ituri Forest, DRC., overlap = 28.5% (Bocian 1997); *C. angolensis* vs. *P. badius*, Salonga, DRC., overlap = 21.0% (Maisels et al. 1994).

Even though overall monthly plant part availability (i.e., pooling top 20 ranked species in each group's diet) did not correlate with monthly consumption, this may mask correlations between species-specific plant part availability and diet (Dasilva 1994). Of the top 10 ranking species-specific plant parts per group (i.e., n = 30 items), ten items showed positive correlations between monthly consumption and monthly availability. Of these ten items, four were fruits (*Adenanthera pavonina* UFR- Nyumbani, *Ficus exasperata* UFR- Nyumbani, *Lecaniodiscus fraxinifolius* UFR- Ufalme, *Lepisanthes senegalensis* RFR- Ujamaa), five were flowers (*Millettia usaramensis* FL- Ujamaa. *Gliricidia sepium* FL- Ufalme, *D. regia* FL- all three groups), and one was a YL (*Z. chalybeum*- Nyumbani). These results demonstrate that each group had one or two species of FR and one or two species of FL that it selected when available (Figure 2.4). It is likely that these species are particularly valuable and may have high concentrations of important nutrients.

The Diani *C. a. palliatus* exhibited remarkable dietary diversity, consuming at least 110 different plant species during the study, roughly two to three times the amount recorded in other studies of *C. angolensis* (Table 2.1). As a response to elevated habitat disturbance, I predicted that the Ufalme and Nyumbani groups would exhibit greater dietary diversity such that they would consume a greater number of plant species and that the top food items would make up a smaller proportion of the total diet compared to that of the Ujamaa group (Milich et al. 2014). Instead, the Ufalme group consumed the fewest number of species and their top 10 food items constituted the largest proportion of the overall diet.

Similarly, I predicted that the Ufalme and Nyumbani groups would expand their diets by consuming more lianas and exotic plant species in response to increased anthropogenic disturbance in their home ranges. These groups relied heavily on lianas as they consumed several species which represented large proportions of their overall diets (i.e., Ufalme: 20.8% of the diet; Nyumbani: 38.4% of the diet); however, the Ujamaa group also consumed a similar number of liana species which accounted for nearly a third of their total diet (i.e., 30.3%). Other studies have documented the dietary importance of lianas for primates inhabiting disturbed forest areas and fragments (Dunn et al. 2012; Martins et al. 2009; Passami and Rylands 2000; Wong et al. 2006). For example, lianas represented 1.6% of the total diet for *Colobus vellerosus* groups in the larger, more intact BFMS, but constituted between 9.3% and 26.3% of the diet for *C. vellerosus* groups inhabiting more disturbed forest fragments outside BFMS (Wong et al. 2006). Lianas are often more abundant in disturbed forests (DeWalt et al. 2000; Zhu et al. 2004), and this greater abundance likely correlates with their increased consumption; however, the spatial and temporary availability of lianas among the three study group home ranges was not recorded during this study.

The groups inhabiting the more degraded ranges consumed several exotic plant species (i.e., Ufalme: 13 species; Nyumbani: 11 species), and exotic plant species comprised substantial proportions of their total diets (i.e., Ufalme: 31.2%; Nyumbani: 40.3%). Contrary to my prediction, the Ujamaa group also relied heavily on exotic plants, consuming 10 species which constituted 30.1% of their total diet. In fact, the top two species in the Ujamaa diet were both exotic plants: *Pithecellobium dulce* and *Delonix* *regia*. Thus, even the group inhabiting the most intact forest area dominated by indigenous tree species, expanded their diet to include exotic plant species. Several studies have reported primates consuming exotic plant species (Anderson et al. 2007a; Bicca-Marques 2003; Bicca-Marques and Calegaro-Marques 1994; Eppley et al. 2015; Ganzhorn 1985; Grimes 2000; Ratsimbazafy 2002; Wong et al. 2006), and an ability to do so is likely a key variable in coping with habitat disturbance and fragmentation (Marsh et al. 2003).

Contrary to my predictions, the colobus group inhabiting the more intact forest area exhibited tremendous dietary diversity and consumed several species of exotic plants and lianas—a pattern generally consistent with groups inhabiting more degraded or fragmented forest areas (Dunn et al. 2012; Wong et al. 2006). This suggests that even the most intact areas of the Diani Forest are still characterized by significant anthropogenic disturbance. Thus, it may be better to describe the three study groups' ranges along a gradient of habitat perturbation rather than intact vs. degraded. Nonetheless, this study emphasizes that diets can vary considerably among groups living in the same forest (Chapman and Chapman 1999; Chapman et al. 2002c). Dietary variation reported here was related, only in small part, to differences in the spatial and temporal availability of food items among home ranges. That is, despite the fact that the availability of overall plant parts differed among home ranges, group diets did not differ in their proportions of different plant parts, nor did groups select overall plant parts in proportion to their availability. In terms of tree species, individuals from all groups selected spatially rare species in their home ranges (i.e., SR > 1 for most tree species). The Diani groups consumed 110 different plant species, which is two to three times the number recorded in other *C. angolensis* studies (Table 2.1). Lianas and exotic plant species constituted substantial proportions of the overall diet for all three groups. This degree of dietary flexibility likely enables *C. a. palliatus* to survive within increasingly fragmented and disturbed habitats such as the Diani Forest of Kenya (Silver and Marsh 2003).

Table 2.1. Percent plant parts in the diet of *C. angolensis* at different sites (6-month study minimum)

Subspecies	Study Site	Duration (months)	YL	ML	UL	TL	FL	FR	(SD)	OT	Species
C. a. cottoni	Ituri, DRC[1]	12	26	2	22	50	7	28	22	15	37
C. a. angolensis	Salonga DRC[2]	8	21	6	-	27	6	67	50	-	46
C. a. ruwenzorii	Nyungwe, Rwanda[3]	10	30	7	1	38	1	23	20	37	45+
C. a. ruwenzorii	Nyungwe, Rwanda[4]	12	25	40	7	72	5	17	-	6	59+
C. a. palliatus	Diani, Kenya[5]	6	-	-	-	57	11	32	11	-	24

[1] Bocian 1997; [2] Maisels et al. 1994; [3] Vedder and Fashing 2002; [4] Fimbel et al. 2001; [5] Moreno-Black and Maples 1977

YL = young leaf; ML = mature leaf; UL = unidentified leaf; TL = total leaf; FL = flower; FR = fruit including seeds; (SD) = seed; OT = other

Table 2.2. The 20 highest ranking trees in terms of biomass in the Ujamaa group home range

Rank	Species	Family	I/E	DBH/ha	% Biomass
1	*Combretum schumannii*	Combretaceae	I	660.2	17.0
2	*Fernandoa magnifica*	Bignoniaceae	I	314.0	8.1
3	*Adansonia digitata*	Malvaceae	I	308.4	8.0
4	*Lannea welwitschii*	Anacardiaceae	I	231.7	6.0
5	*Lecaniodiscus fraxinifolius*	Sapindaceae	I	218.6	5.6
6	*Sideroxylon inerme*	Sapotaceae	I	104.9	2.7
7	*Carpodiptera africana*	Malvaceae	I	96.7	2.5
8	*Hunteria zeylanica*	Apocynaceae	I	88.0	2.3
9	*Trichilia emetica*	Meliaceae	I	86.7	2.2
10	*Ficus lingua*	Moraceae	I	80.0	2.1
11	*Delonix regia*	Leguminosae	E	68.7	1.8
12	*Ficus polita*	Moraceae	I	60.9	1.6
13	*Pycnocoma littoralis*	Euphorbiaceae	I	54.1	1.4
14	*Ficus benjamina*	Moraceae	E	53.0	1.4
15	*Casuarina equisetifolia*	Casuarinaceae	E	51.6	1.3
16	*Millettia usaramensis*	Leguminosae	I	44.0	1.1
17	*Lannea schweinfurthii*	Anacardiaceae	I	41.6	1.1
18	*Plumeria obtusa*	Apocynaceae	E	37.1	1.0
19	*Xylopia parviflora*	Annonaceae	I	35.6	0.9
20	*Sesbania grandiflora*	Leguminosae	E	34.6	0.9

I = indigenous; E = exotic; DBH = diameter and breast height; ha = hectare

Table 2.3. The 20 highest ranking trees in terms of biomass in the Ufalme group home range

Rank	Species	Family	I/E	DBH/ha	% Biomass
1	*Azadirachta indica*	Meliaceae	E	403.0	15.9
2	*Delonix regia*	Leguminosae	E	306.1	12.1
3	*Grewia plagiophylla*	Malvaceae	I	266.2	10.5
4	*Lecaniodiscus fraxinifolius*	Sapindaceae	I	217.2	8.6
5	*Zanthoxylum chalybeum*	Rutaceae	I	192.6	7.6
6	*Adansonia digitata*	Malvaceae	I	125.9	5.0
7	*Diospyros squarrosa*	Ebenaceae	I	96.2	3.8
8	*Markhamia zanzibarica*	Bignoniaceae	I	63.4	2.5
9	*Carpodiptera africana*	Malvaceae	I	59.4	2.3
10	*Cussonia zimmermannii*	Araliaceae	I	56.8	2.2
11	*Plumeria obtusa*	Apocynaceae	E	53.9	2.1
12	*Cordia goetzei*	Boraginaceae	I	51.7	2.0
13	*Casuarina equisetifolia*	Casuarinaceae	E	50.6	2.0
14	*Euphorbia wakefieldii*	Euphorbiaceae	I	40.0	1.6
15	*Ficus zanzibarica*	Moraceae	I	39.7	1.6
16	*Euphorbia nyikae*	Euphorbiaceae	I	36.0	1.4
17	*Bourreria petiolaris*	Boraginaceae	I	34.5	1.4
18	*Hunteria zeylanica*	Apocynaceae	I	30.9	1.2
19	*Oncoba spinosa*	Salicaceae	I	28.9	1.1
20	*Millettia usaramensis*	Leguminosae	I	28.5	1.1

I = indigenous; E = exotic; DBH = diameter and breast height; ha = hectare

Table 2.4. The 20 highest ranking trees in terms of biomass in the Nyumbani group home range

Rank	Species	Family	I/E	DBH/ha	% Biomass
1	*Azadirachta indica*	Meliaceae	E	1346.3	39.4
2	*Delonix regia*	Leguminosae	E	480.9	14.1
3	*Lannea welwitschii*	Anacardiaceae	I	239.7	7.0
4	*Fernandoa magnifica*	Bignoniaceae	I	201.8	5.9
5	*Adansonia digitata*	Malvaceae	I	166.1	4.9
6	*Zanthoxylum chalybeum*	Rutaceae	I	96.0	2.8
7	*Plumeria obtusa*	Apocynaceae	E	54.5	1.6
8	*Balanites maughamii*	Zygophyllaceae	I	44.5	1.3
9	*Mangifera indica*	Anacardiaceae	E	39.0	1.1
10	*Carpodiptera africana*	Malvaceae	I	32.5	1.0
11	*Millettia usaramensis*	Leguminosae	I	28.1	0.8
12	*Combretum schumannii*	Combretaceae	I	22.9	0.7
13	*Lecaniodiscus fraxinifolius*	Sapindaceae	I	22.5	0.7
14	*Croton megalocarpus*	Euphorbiaceae	I	22.2	0.7
15	*Ficus benjamina*	Moraceae	E	22.2	0.6
16	*Ficus bubu*	Moraceae	I	17.8	0.5
17	*Grewia vaughanii*	Malvaceae	I	17.2	0.5
18	*Ficus sycamorus*	Moraceae	I	16.3	0.5
19	*Ficus lingua*	Moraceae	I	16.1	0.5
20	*Pycnocoma littoralis*	Euphorbiaceae	I	15.8	0.5

I = indigenous; E = exotic; DBH = diameter and breast height; ha = hectare

Table 2.5. Monthly food availability scores by plant part for Ujamaa home range

Month	ML FAI/ha	YL FAI/ha	FL FAI/ha	FR FAI/ha
Jul '14	15625973.0	6289328.3	448367.5	1253320.9
Aug '14	15825046.5	6090254.7	2152158.6	982801.3
Sep '14	16288090.6	5627210.6	517050.6	4781466.6
Oct '14	16850934.0	5064367.3	618717.1	4611707.5
Nov '14	17129655.9	4785645.4	504656.9	1068005.4
Dec '14	17033059.0	4882242.2	644387.1	680714.3
Jan '15	16945191.8	4970109.4	342818.4	7208288.0
Feb '15	17970549.6	3944751.7	1066167.8	5414084.1
Mar '15	18963024.0	2952277.3	1973925.0	4584158.7
Apr '15	1866920.2	20048381.1	783890.2	544494.7
May '15	2347898.4	19567402.9	379001.4	1189799.0
Jun '15	1952642.3	19962659.0	30334.9	815358.6
Jul '15	2560440.4	19354860.9	38811.7	2580361.2
Aug '15	4017009.9	17898291.3	48621.7	5133075.9
Sep '15	13022188.1	8893113.1	34207.6	5815896.3
Oct '15	18487601.8	3427699.5	129237.7	6737631.5
Nov '15	17127728.5	4787572.8	504656.9	1066078.0
Dec '15	17033059.0	4882242.2	644387.1	678786.9

ML = mature leaf; YL = young leaf; FL = flower; FR = fruit; FAI = food availability index; ha = hectare

Table 2.6. Monthly food availability scores by plant part for Ufalme home range

Month	ML FAI/ha	YL FAI/ha	FL FAI/ha	FR FAI/ha
Jul '14	2869159.3	1040120.5	220631.2	332320.8
Aug '14	2824672.8	1084606.9	107784.1	172842.3
Sep '14	2886286.8	1022993.0	213783.0	182812.9
Oct '14	2938603.2	970676.6	218305.8	87001.8
Nov '14	2981670.8	927609.0	218359.5	149780.8
Dec '14	2951908.7	957371.1	305752.6	54269.9
Jan '15	2491786.2	1417493.6	539174.3	150204.6
Feb '15	2387818.2	1521461.6	415893.0	184281.5
Mar '15	2827496.2	1081783.6	527173.5	249798.9
Apr '15	1206959.9	2702319.9	648947.1	141059.7
May '15	1404513.9	2504765.9	537732.0	380575.4
Jun '15	1514572.3	2394707.5	124741.7	658145.2
Jul '15	1778611.5	2130668.3	20993.4	590996.9
Aug '15	2336758.4	1572521.3	6622.6	441314.9
Sep '15	2865690.3	1043589.5	14862.2	409556.2
Oct '15	3534070.1	375209.7	62289.1	491530.8
Nov '15	2981670.8	927609.0	218359.5	149780.8
Dec '15	2951908.7	957371.1	305752.6	54269.9

ML = mature leaf; YL = young leaf; FL = flower; FR = fruit; FAI = food availability index; ha = hectare

Table 2.7. Monthly food availability scores by plant part for Nyumbani home range

Month	ML FAI/ha	YL FAI/ha	FL FAI/ha	FR FAI/ha
Jan '15	3865629.6	2704300.5	1674162.1	440715.6
Feb '15	2968948.4	3600981.6	1102445.9	309261.7
Mar '15	3664852.5	2905077.5	1389109.7	264803.0
Apr '15	2354476.7	4215453.3	1834428.6	25274.1
May '15	2243700.7	4326229.3	1537050.4	62360.9
Jun '15	2777002.9	3792927.1	373703.1	9.6
Jul '15	3023221.2	3546708.8	38561.4	113.4
Aug '15	4096909.3	2473020.7	2750.4	8494.9
Sep '15	4816756.1	1753173.9	2701.3	425144.9
Oct '15	5997131.6	572798.4	78836.9	1299902.0
Nov '15	5117592.1	1452337.9	5038.1	170225.2
Dec '15	5100717.6	1469212.4	34944.4	101912.8

ML = mature leaf; YL = young leaf; FL = flower; FR = fruit; FAI = food availability index; ha = hectare

Table 2.8. Percent plant part composition in the diets of three study groups

Plant Part	Ujamaa	Ufalme	Nyumbani
Young leaves	52.5	59.2	63.3
Mature leaves	15.4	12.6	11.6
Total leaves	68.0	71.8	74.9
Unripe fruit	11.8	13.2	11.3
Ripe fruit	2.5	3.1	0.5
Whole fruit	8.6	1.2	3.9
Seeds	5.6	15.2	7.9
Total fruit	14.2	16.4	11.8
Flowers	17.7	11.4	13.1
Other	0.1	0.4	0.3

Table 2.9. The top 20 ranking food species, plant parts, and selection ratios for Ujamaa group from July 2014 to December 2015

Ujamaa Group (n = 18 months)						
Rank	Plant Species	Family	I/E	Plant Parts Consumed	% of Diet	SR
1	*Pithecellobium dulce*	Leguminosae	E	YL, FL	13.2	660.0
2	*Delonix regia*	Leguminosae	E	YL, FL	9.4	15.2
3	*Premna hildebrandti* [1]	Lamiaceae	I	YL, ML, UFR-WF, FL	9.1	NA
4	*Adansonia digitata*	Malvaceae	I	YL, ML, FL	7.9	1.2
5	*Coccinia grandis* [1]	Cucurbitaceae	I	YL, ML, UFR-WF, FL	5.2	NA
6	*Berchemia discolor*	Rhamnaceae	I	YL, ML	5.0	1918.5
7	*Dalbergia vaccinifolia* [1]	Leguminosae	I	YL, ML, UFR-SD, FL	3.9	NA
8	*Trichilia emetica*	Meliaceae	I	ML	3.8	3.1
9	*Bougainvillea spectabilis* [1, 2]	Nyctaginaceae	E	YL, ML, FL	3.6	NA
10	*Hunteria zeylanica*	Apocynaceae	I	YL, ML, UFR-WF, FL	3.2	0.3
11	*Millettia usaramensis*	Leguminosae	I	YL, UFR-SD, FL	2.8	1.2
12	*Grewia holstii* [1]	Malvaceae	I	YL	2.4	NA
13	*Lecaniodiscus fraxinifolius*	Sapindaceae	I	YL, UFR-SD, RFR-SD, FL	1.9	0.2
14	*Antiaris toxicaria*	Moraceae	I	YL, UFR-SD	1.9	705.3
15	*Commiphora zanzibarica*	Burseraceae	I	YL, ML	1.9	47.5
16	*Sideroxylon inerme*	Sapotaceae	I	UFR-SD, RFR-SD	1.7	1.4
17	*Ziziphus mucronata*	Rhamnaceae	I	YL, ML	1.7	56.7
18	*Trema orientalis*	Cannabaceae	I	YL, UFR-WF	1.7	1.5
19	*Combretum schumannii*	Combretaceae	I	YL, ML	1.5	< 0.1
20	*Lepisanthes senegalensis*	Sapindaceae	I	YL, UFR-SD, RFR-SD	1.5	2.9

I = indigenous; E = exotic; SR = selection ratio; YL = young leaf; ML = mature leaf; FL = flower; UFR = unripe fruit; RFR = ripe fruit; WF = whole fruit; SD = seed; [1] = liana; [2] = shrub; all unmarked plants = trees

Table 2.10. The top 20 ranking food species, plant parts, and selection ratios for Ufalme group from July 2014 to December 2015

Ufalme Group (n = 18 months)						
Rank	Plant Species	Family	I/E	Plant Parts Consumed	% of Diet	SR
1	*Lecaniodiscus fraxinifolius*	Sapindaceae	I	YL, ML, UFR-SD, RFR-SD	14.4	1.4
2	*Delonix regia*	Leguminosae	E	YL, ML, UFR-SD, RFR-SD, FL	13.8	0.7
3	*Zanthoxylum chalybeum*	Rutaceae	I	YL, ML, FL	9.0	1.1
4	*Bougainvillea spectabilis* [1, 2]	Nyctaginaceae	E	YL, ML, FL	7.3	NA
5	*Markhamia zanzibarica*	Bignoniaceae	I	YL, ML, UFR-WF, FL	7.1	8.3
6	*Adansonia digitata*	Malvaceae	I	ML, FL	6.2	1.8
7	*Cordia goetzei*	Boraginaceae	I	YL	5.6	9.9
8	*Cissus integrifolia* [1]	Vitaceae	I	YL, ML, UFR-WF, FL	4.8	NA
9	*Gliricidia sepium*	Leguminosae	E	YL, UFR-SD, FL	3.0	NA
10	*Tinospora caffra* [1]	Menispermaceae	I	YL, ML	2.4	NA
11	*Coccinia grandis* [1]	Cucurbitaceae	I	YL, ML	2.1	NA
12	*Mangifera indica*	Anacardiaceae	E	YL, ML, FL	1.9	34.0
13	*Plumeria obtusa*	Apocynaceae	E	YL, ML, FL	1.6	2.6
14	*Haplocoelum inopleum*	Sapindaceae	I	YL, ML	1.5	236.8
15	*Flueggea virsoa* [2]	Phyllanthaceae	I	YL	1.5	NA
16	*Ziziphus mucronata*	Rhamnaceae	I	YL, ML	1.1	149.5
17	*Cassia abbreviata*	Leguminosae	I	YL, ML	1.0	116.3
18	*Cussonia zimmermannii*	Araliaceae	I	YL, ML, FL	1.0	1.5
19	*Flacourtia indica*	Salicaceae	I	YL, ML	1.0	7.6
20	*Premna hildebrandti* [1]	Lamiaceae	I	YL, ML, UFR-WF, FL	0.8	NA

I = indigenous; E = exotic; SR = selection ratio; YL = young leaf; ML = mature leaf; FL = flower; UFR = unripe fruit; RFR = ripe fruit; WF = whole fruit; SD = seed; [1] = liana; [2] = shrub; all unmarked plants = trees

Table 2.11. The top 20 ranking food species, plant parts, and selection ratios for Nyumbani group from January to December 2015

Nyumbani Group (n = 12 months)						
Rank	Plant Species	Family	I/E	Plant Parts Consumed	% of Diet	SR
1	*Bougainvillea spectabilis* [1, 2]	Nyctaginaceae	E	YL, ML, FL	15.3	NA
2	*Delonix regia*	Leguminosae	E	YL, ML, UFR-SD, FL	10.7	1.0
3	*Adenanthera pavonina*	Leguminosae	E	YL, ML, UFR-SD, RFR-SD	8.8	8657.6
4	*Cissus integrifolia* [1]	Vitaceae	I	YL, ML, UFR-WF	7.8	NA
5	*Sideroxylon inerme*	Sapotaceae	I	UFR-WF	4.8	1435.2
6	*Ficus exasperata*	Moraceae	I	YL, ML, UFR-WF	3.5	1982.7
7	*Zanthoxylum chalybeum*	Rutaceae	I	YL, ML	3.3	7.9
8	*Hunteria zeylanica*	Apocynaceae	I	YL, ML, UFR-WF	3.0	644.8
9	*Dalbergia vacciniifolia* [1]	Leguminosae	I	YL, ML	2.9	NA
10	*Maerua triphylla* [1]	Capparaceae	I	YL, ML	2.3	NA
11	*Cyphostemma adenocaule* [1]	Vitaceae	I	YL, ML, UFR-WF	2.2	NA
12	*Flueggea virsoa* [2]	Phyllanthaceae	I	YL, ML, UFR-WF	2.2	NA
13	*Pithecellobium dulce*	Leguminosae	E	YL, FL	2.0	5381.8
14	*Markhamia zanzibarica*	Bignoniaceae	I	YL, ML	1.8	247.6
15	*Commiphora zanzibarica*	Burseraceae	I	YL, ML	1.7	335.3
16	*Adansonia digitata*	Malvaceae	I	ML, FL	1.7	1.4
17	*Sterculia africana*	Malvaceae	I	YL	1.6	4305.5
18	*Millettia usaramensis*	Leguminosae	I	YL, ML, UFR-SD, FL	1.6	44.8
19	*Rauvolfia mombasiana*	Apocynaceae	I	YL, ML	1.4	251.3
20	*Hibiscus rosa-sinensis* [2]	Malvaceae	E	YL	1.3	NA

I = indigenous; E = exotic; SR = selection ratio; YL = young leaf; ML = mature leaf; FL = flower; UFR = unripe fruit; RFR = ripe fruit; WF = whole fruit; SD = seed; [1] = liana; [2] = shrub; all unmarked plants = trees

Table 2.12. The top 10 ranking species-specific plant parts for Ujamaa group from July 2014 - December 2015

Rank	Plant Species	PP	% of Diet
1	*Pithecellobium dulce*	YL	7.51
2	*Delonix regia*	FL	6.44
3	*Adansonia digitata*	ML	6.42
4	*Trichilia emetica*	ML	4.63
5	*Berchemia discolor*	YL	4.20
6	*Pithecellobium dulce*	FL	3.62
7	*Delonix regia*	YL	3.43
8	*Hunteria zeylanica*	YL	2.91
9	*Millettia usaramensis*	FL	1.84
10	*Lepisanthes senegalensis*	RFR	1.75

pp = plant part; ML = mature leaf; YL = young leaf; FL = flower; RFR = ripe fruit

Table 2.13. The top 10 ranking species-specific plant parts for Ufalme group from July 2014 - December 2015

Rank	Plant Species	PP	% of Diet
1	*Lecaniodiscus fraxinifolius*	UFR	7.26
2	*Zanthoxylum chalybeum*	YL	6.78
3	*Delonix regia*	YL	6.44
4	*Markhamia zanzibarica*	YL	6.33
5	*Cordia goetzei*	YL	5.66
6	*Delonix regia*	FL	3.76
7	*Lecaniodiscus fraxinifolius*	YL	3.45
8	*Delonix regia*	UFR	3.42
9	*Adansonia digitata*	ML	3.39
10	*Gliricidia sepium*	FL	2.87

pp = plant part; ML = mature leaf; YL = young leaf; FL = flower; UFR = unripe fruit

Table 2.14. The top 10 ranking species-specific plant parts for Nyumbani group from January - December 2015

Rank	Plant Species	PP	% of Diet
1	*Delonix regia*	FL	6.64
2	*Adenanthera pavonina*	YL	5.71
3	*Sideroxylon inerme*	UFR	4.21
4	*Delonix regia*	YL	4.05
5	*Ficus exasperata*	UFR	2.84
6	*Zanthoxylum chalybeum*	YL	2.47
7	*Hunteria zeylanica*	YL	2.41
8	*Adenanthera pavonina*	UFR	2.10
9	*Markhamia zanzibarica*	YL	1.66
10	*Pithecellobium dulce*	YL	1.56

pp = plant part; YL = young leaf; FL = flower; UFR = unripe fruit

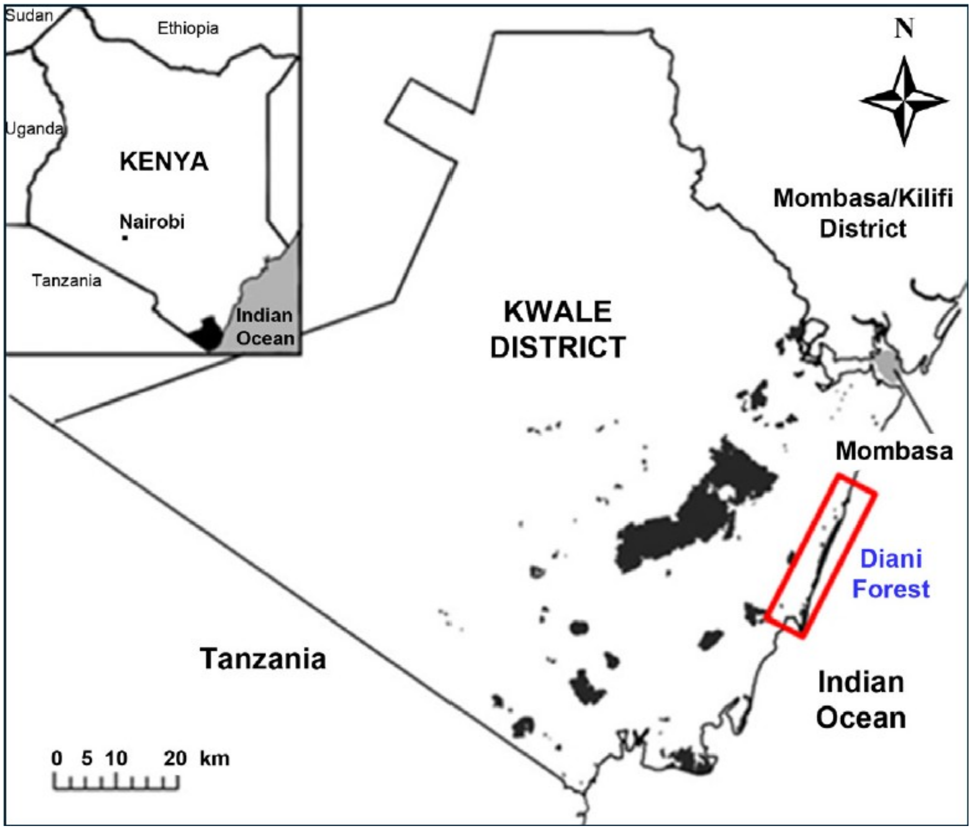

Figure 2.1. Map of south coastal Kenya forests with study site indicated

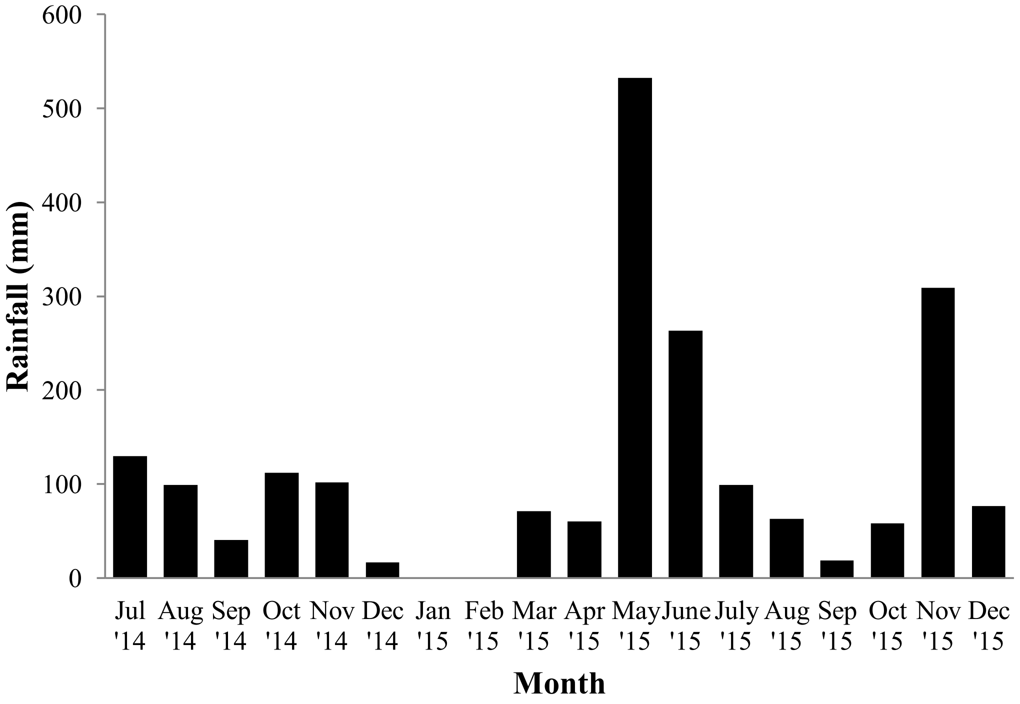

Figure 2.2. Rainfall pattern in the Diani Forest over the 18 month study period from July 2014 - December 2015

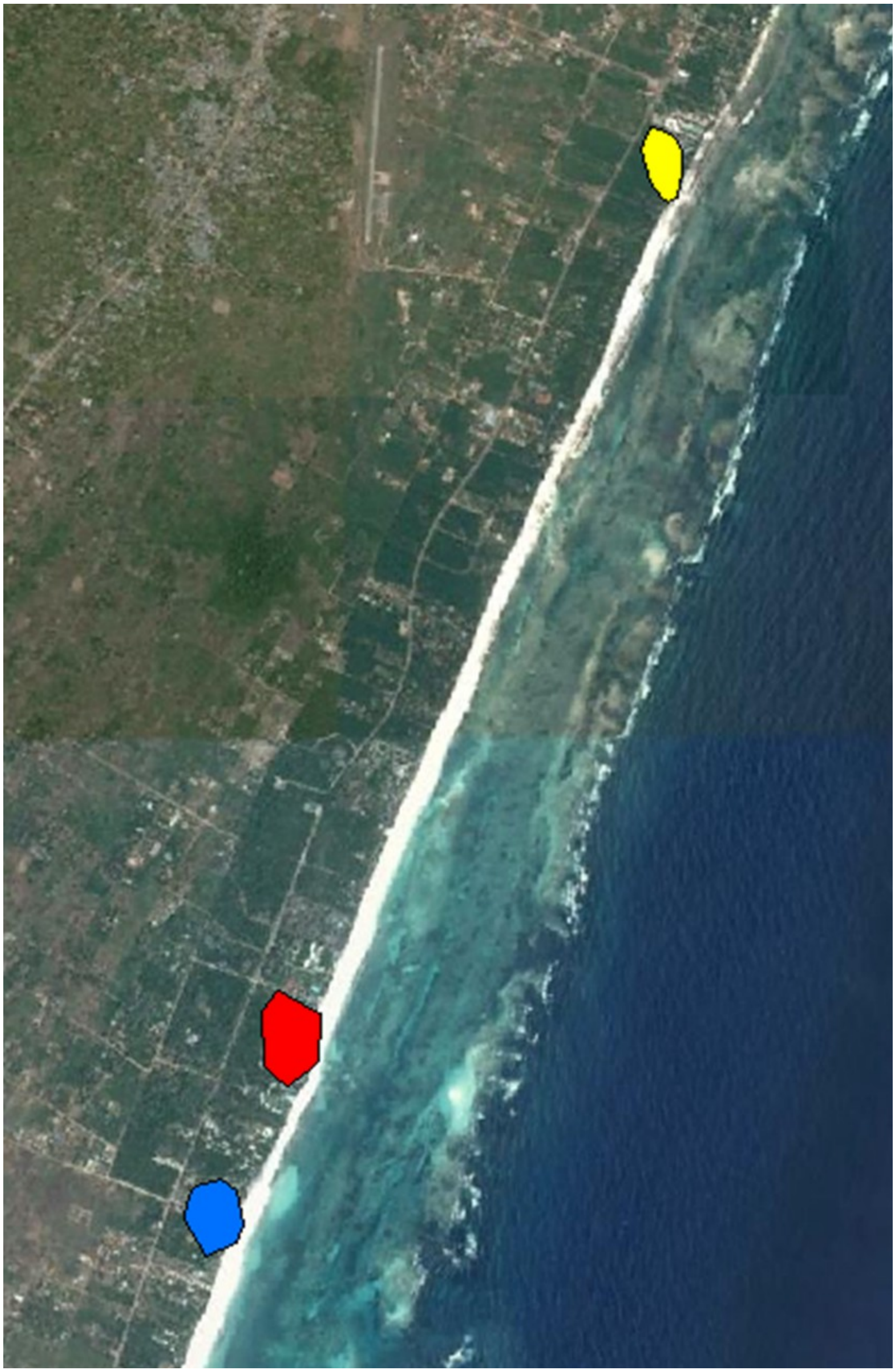

Figure 2.3. Map of Diani Forest with home ranges shown: Ujamaa (red), Ufalme (yellow), and Nyumbani (blue)

Figure 2.4. Adult male *C. a. palliatus* foraging on *Delonix regia* flowers

CHAPTER 3: FOOD SELECTION, FORAGING EFFICIENCY, AND MECHANICAL TOUGHNESS

INTRODUCTION

Behavioral ecologists and functional morphologists are increasingly interested in how food mechanical properties relate to food selection and oral processing behaviors as these relationships provide insight into the evolution of various craniofacial and dentognathic traits among living primates (Kinzey and Norconk 1990; Daegling and McGraw 2001; Lambert et al. 2004; Wright 2005; Norconk et al. 2009; Wright et al. 2009; Yamashita et al. 2009; Ross et al. 2012; Pampush et al. 2013; Vogel et al. 2014; McGraw et al. 2014, 2015). These endeavors, in turn, inform behavioral and dietary reconstructions of fossil forms (Strait et al. 2009, 2013; Daegling et al. 2011, 2013).

Compared to cercopithecines, colobines possess relatively larger bilophodont molars equipped with taller cusps (Lucas and Teaford 1994). It is well documented that these dental traits enhance the breakdown of mechanically tough foods such as leaves and seeds (Lucas and Teaford 1994). With that said, more nuanced studies examining diet and food mechanical properties in combination with idiosyncrasies in oral processing behaviors are required to interpret craniodental variation both among colobine species and among other primate taxa (Koyabu and Endo 2009; Norconk et al. 2009; McGraw and Daegling 2012; Ross et al. 2012; McGraw et al. 2015). Idiosyncrasies in oral processing behaviors include the frequency and manner in which various teeth (e.g., incisor vs. postcanine) are employed during ingestion (Yamashita 1998, 2003; Wright et al. 2008; Yamashita et al. 2009; McGraw et al. 2011, 2015). In fact, some fruits, nuts, and seed pods, require significant oral processing in order to remove outer casings prior to ingestion of internal elements (Kinzey and Norconk 1990; McGraw et al. 2014, 2015). Thus, pre-ingestive oral processing behaviors characterized by high bite forces, as well as the repetitive act of mastication, may significantly stress the jaw (Hylander 1979; Ravosa 1996; Ross et al. 2012).

Investigations of food mechanical properties often focus on the toughness of food items. Toughness is related to the amount and configuration of the cell wall in a given plant tissue and loosely correlates with its total fiber content (i.e., cellulose, hemicellulose, and lignin) (Dominy et al. 2001; Lucas et al. 1995). The role of fiber in colobine monkey diets has been studied extensively. For instance, fiber content is widely considered a strong predictor of colobine biomass as protein-to-fiber ratios of common leaf species positively correlate with colobine density at several sites (Waterman et al. 1988; Oates et al. 1990; Chapman et al. 2002a, 2004; Fashing et al. 2007a). Despite the fact that colobines have specialized digestive systems that aid in the breakdown of structural carbohydrates, fiber remains difficult to digest relative to other macronutrients (Lambert 1998). Consequently, many feeding ecology studies have found that folivorous primates, including colobines, tend to limit their fiber intake while maximizing the intake of protein or other macronutrients (Milton 1979; McKey et al. 1981; Oates 1988; Mowry et al. 1996; Bocian 1997; Rogers et al. 1990; Chapman et al. 2004).

Because fiber is largely undetectable during ingestion (i.e., fiber is tasteless, odorless, and colorless), it is likely that primates primarily gauge the digestibility of food items by assessing how difficult a given item is to chew (Hill and Lucas 1996; Teaford et al. 2006; Lucas et al. 2012). In other words, toughness values, and not fiber concentrations *per se*, likely influence food selection (Dominy et al. 2001). Despite this assertion, few studies have explicitly examined the relationship between toughness and food preference in free-ranging primates (Elgart-Berry 2004; Teaford et al. 2006; Wright et al. 2008; Yamashita et al. 2009; Vogel et al. 2014; McGraw et al. 2015).

If food toughness does influence food selection and act as a selective force for the evolution of specialized masticatory adaptations, it follows that tougher foods should be more costly to sufficiently break down through mastication (Marshall et al. 2009). This claim is largely supported or assumed in the literature, but it has gone virtually untested to date (Venkataraman et al. 2014). Furthermore, investigations of dietary toughness often examine differences in the average toughness values of foods consumed and/or the mean behavioral profiles of oral processing behaviors in order to explain behavioral and morphological differences among sympatric taxa (Wright et al. 2008; Yamashita et al. 2009; McGraw et al. 2015). While these types of studies are important, they potentially mask the capacity for oral processing behaviors to vary within a taxon and with regard to the range of toughness values of food items consumed.

The purpose of this study was to assess 1) the relationships between leaf toughness and food selection and 2) the relationships between leaf toughness and colobus foraging efficiency for several leaf species commonly eaten by a highly folivorous

African colobine monkey. It is hypothesized that colobus monkeys will select leaves with lower toughness values such that leaf toughness will negatively correlate with selection ratios. Furthermore, it is hypothesized that foraging efficiency will decrease as toughness values increase such that leaf toughness will 1) negatively correlate with ingestion rate in terms of grams consumed per minute (g/min), 2) positively correlate with masticatory investment (chewing investment: Shipley et al. 1994; Ross et al. 2012) in terms of the number of mastications per gram ingested (chews/g), and 3) positively correlate with masticatory rate measured in the number of mastications per minute (chews/min) during foraging.

METHODS

Study Site and Study Species

The Diani Forest is located in the Kwale District of south coastal Kenya and is one of the few remaining patches of biodiversity-rich coral rag forests in East Africa. East African coral rag forest is characterized by semideciduous, low canopy forest (i.e., usually ≤ 25 m tall) with soils composed largely of fossilized coral (Nowak and Lee 2011). Measuring approximately 4.6 km^2, the Diani Forest is comprised of patches of intact forest interspersed with degraded areas (Anderson et al. 2007; Dunham 2015). Several primate taxa inhabit the forest including small-eared galagos (*Otolemur garnettii*), Kenya coast galagos (*Galagoides cocos*), vervet monkeys (*Chlorocebus pygerythrus*), Sykes' monkeys (*Cercopithecus albogularis*), yellow baboons (*Papio* *cynocephalus*), and Peters' Angola black and white colobus monkeys (*Colobus angolensis palliatus*).

Throughout their ranges in eastern and central Africa, *Colobus angolensis* typically live in groups of 2-20 members. Group sizes have been documented to be up to 300+ members in Nyungwe, Rwanda (Fimbel et al. 2001; Fashing et al. 2007b). Group size in the Diani Forest ranged from approximately 2-13 individuals with groups typically consisting of one or two adult males, multiple adult females, and their offspring (Moreno-Black and Maples 1977; Dunham pers. observation). Like many other colobines, the Diani Angola colobus monkeys are highly arboreal and rarely venture to the ground (Dunham and McGraw 2014; Dunham 2015). Although largely folivorous throughout their ranges, research has shown that *Colobus angolensis* may also rely heavily on seeds and/or lichens at some sites (Bocian 1997; Maisels et al. 1994; Lowe and Sturrock 1998; Fimbel et al. 2001). In the Diani Forest, *C. a. palliatus* primarily feed on young and mature leaves along with a variety of whole fruits, seeds, and flowers (Moreno-Black and Maples 1977; Chapter 2).

Mechanical Toughness Measures

Toughness was measured on young leaves (YL) (n = 70 species) and mature leaves (ML) (n = 77 species) from May - July 2014 and January-November 2015. These samples represent leaves commonly consumed as well as leaves from the top 20 most abundant tree species in each colobus group's home range. YL and ML of a given species were differentiated based on a combination of factors including size, texture, color, and location within the canopy. YL were typically distinguishable from ML due to their smaller size, smoother texture, pale green or red coloration, and/or high concentrations at the terminal ends of branches (Dominy 2002). YL vs. ML is a false dichotomy since leaf maturation represents a continuum and can be divided into several stages (e.g., Lowman and Box 1983); however, I maintain YL and ML categories typically reported in primate feeding ecology studies. Leaf samples were collected from specific trees and canopy strata in which individuals fed. Colobus monkeys often broke terminal branches and dropped leaf clusters while foraging which facilitated leaf sample collection. In some cases researchers climbed into the lower strata and removed leaf samples manually. Leaves were collected when they were available and throughout the study period. While most species of ML were available year round, YL species were typically available and collected during and/or shortly after the rainy seasons (i.e., October-December and March-June). A minimum of six samples were used to create mean toughness values for each leaf species plant part. Only commonly consumed leaves were used in the analysis (i.e., leaf species in which behavioral data include at least 5 focal periods of ingestion rate and chewing cycles; YL = 27 species; ML = 13 species; n = 351 toughness tests).

Pooling the diets of the three colobus groups, YL and ML comprised 71.6% of the total diet during the study period (Chapter 2). Toughness values of the 40 leaf species included in this analysis represented the vast majority of this total, with the exception of a few commonly eaten leaf species (e.g., *Delonix regia* YL and ML and *Adenanthera pavonina* YL) that were too small to accurately assess in this toughness tester. All samples were tested within 24 hours of collection (Lucas and Teaford 1994). Non-leaf items are also thought to significantly load the jaws of *C. a. palliatus*. Flowers and flowers buds comprise 14.1% of the study groups' diet. Flowers were not tested because the majority of specimens were too small to accurately analyze with the tester. The combination of whole fruits and seeds likewise comprised 14.1% of the total diet. The majority of this fraction was made up of roughly pea-sized to marble-sized fruits. It is likely that hardness (i.e., force required to indent a material) is a more relevant mechanical property for assessing mechanical challenges imposed by these small fruits (Kinzey and Norconk 1990; Lambert et al. 2004). Only 2.8% of the overall diet was composed of leguminous seed pods in which the outer cover was first removed before consuming the seeds within. Seed casings have been found to have higher toughness values than leaves, and thus stripping/husking these casings likely significantly stresses the jaw (Vogel et al. 2014; McGraw et al. 2015). Husks and seeds were excluded from this study to prevent overloading the test instrument (load cell capacity: 110 N/ 25 lbs). Furthermore, because seeds constituted a small proportion of the overall diet, it is argued that analyses of leaves adequately reflect the vast majority of dietary challenges faced by *C. a. palliatus* with regard to toughness.

My colleague (Alexander Lambert) and I designed a leaf toughness tester for this study that functions similarly to the Darvell et al. (1996) universal tester commonly used in food mechanical properties studies in the primatology literature (e.g., Hill and Lucas 1996; Elgart-Berry 2004; Wright et al. 2008; Venkataraman et al. 2014). Rather than using scissors, the tester is equipped with a single razor blade mounted at 20° that was manually lowered at a rate of approximately 5 mm per second. The single razor blade design eliminated the need to sharpen scissor blades after a given number of tests (Ang et al. 2008). The razor blade was replaced (# 62-0165, American Safety Razor Company) after approximately 20 tests due to experimental data on copier paper in which toughness values began to increase after around 20 tests. Leaves were cut into 50 mm by 15 mm strips (with midrib running parallel to the long edge and through the center of strip) and clamped onto the baseplate of the instrument. The tester functioned by recording the force required to cut a specimen and distance the blade traveled using a load cell (Honeywell AL31) and linear transducer (Omega LD620-25), respectively. Force and displacement analog signals were sent to a data acquisition unit (Measurement Computing USB-204) and imported to a personal laptop computer equipped with National Instruments LabView 2013 software (Figure 3.1). Force and displacement values of this initial pass were multiplied to yield the work of the first pass. A second pass was then required with the blade lowered through the already cut sample. This value represents the work associated with the friction of cutting and was subtracted from the first pass to yield the work of fracturing the leaf (Lucas and Teaford 1994). Using digital calipers, the area of the leaf fracture was calculated by multiplying the length of the cut by the thickness of the leaf. Toughness (R: measured in J m^{-2}) was calculated by dividing the work of leaf fracture by the area of the cut (Lucas and Teaford 1994).

Because toughness values can vary depending on whether fractures are made with or against plant fiber orientation, all leaf samples were cut perpendicular to the leaf midrib to mimic how *C. a. palliatus* typically consumed leaves (Lucas et al. 1995) (Figure 3.2). The Diani colobus monkeys very rarely consumed just the leaf lamina or leaf tip but instead consumed the majority of the leaf body including the midrib. Because the midrib has been documented to be tougher than the lamina, all tests were made through a portion of the lamina and midrib to provide a maximum toughness value for the leaf samples (Choong 1996; Teaford et al. 2006).

Behavioral Methods

Behavioral data were collected on three habituated groups of *C. a. palliatus* from July 2014-December 2015 (n = 267 full day follows). Activity budget and feeding data, including plant species and part consumed (i.e., YL, ML, unripe fruit, ripe fruit, flower/ flower buds, and other), were collected during 5 minute group scans every 15 minutes. Group sizes ranged from 5-10 members. Individuals were easily identified by a combination of facial features and tail morphology. This individual recognition, in addition to the cohesiveness of the small groups, enabled me to account for all individuals on the vast majority of group scans. Only data of adult males and adult females were included in this study.

Ingestion and oral processing data were also collected opportunistically on individuals during three to five minute focal follows. Data collection was initiated after a particular individual had been actively foraging for at least one minute. Data recorded during focal follows included 1) ingestion events, defined as the number of food items of a given plant species introduced to the oral cavity, and 2) chewing cycles, defined as the number of postcanine mastication events during the focal period. Ingestion rates (i.e., grams consumed per minute) were then calculated by multiplying the ingestion events during a focal period by the average weight of a given plant species food item (n = 20 - 30 samples weighed per food item) measured with a portable balance (Nakagawa 2009). Depending on the size and nature of the plant part, a food item could be defined as a single leaf, strand of leaves, cluster of flower buds, whole fruit, etc. In order for a single researcher (NTD) to collect ingestion events and chewing cycles simultaneously, a handheld rotary counter was used to record ingestion events while chewing cycles were counted verbally. Both values were immediately recorded in a notebook at the conclusion of the focal period. Issues with visibility prevented accurate chewing cycle counts for some focal periods; therefore, there is a larger sample size for ingestion rates (n = 800) compared to chewing cycles (n = 586). I defined masticatory investment as the number of mastications per gram ingested and masticatory rate as the number of mastications per minute.

Statistical Methods

In order to test whether colobus monkeys were consistently selecting foods with lower toughness values, toughness values of commonly consumed leaves (i.e., leaves comprising at least 1% of a group's diet) were compared to those of the 20 most abundant YL and ML species in each group's home range (i.e., excluding those that constitute at least 1% of the group's diet). Nonparametric Mann Whitney *U* tests were used to compare toughness values of commonly consumed leaves to those of abundant leaves not consumed. Toughness values were also compared to selection ratios (SR) to determine if selection ratios correlated with leaf toughness. SR = [% of feeding time spent on species$_{(t)}$

/ % of total BA contributed by $\text{species}_{(t)}$] (Dasilva 1994). Selection ratios greater than 1 indicate that a given species was selected disproportionately higher than expected based on availability. Because selection ratios were not normally distributed, nonparametric Spearman rank-order coefficients were used to examine the relationship between selection ratios and leaf toughness.

Ingestion rates, masticatory investments, and masticatory rates of adult males and adult females were pooled by plant species and leaf type because these behaviors did not differ significantly between sexes using general linear models (ingestion rate: $F = 3.36$, $p = 0.07$; masticatory investment: $F = 0.49$, $p = 0.49$; masticatory rate: $F = 3.44$, $p = 0.06$). Ingestion rate, masticatory investment, and mastication rate followed normal distributions and their standard deviations were very similar when examining differences in YL vs. ML categories (Shapiro-Wilk test: $p > 0.05$ for all tests). Ingestion rates, masticatory investments, and masticatory rates were averaged across individuals for each plant species. Similarly, toughness values were averaged for each plant species. One-tailed student t-tests ($\alpha = 0.05$) were used to evaluate the hypothesis that ML will be characterized by higher mean toughness values compared to YL across all leaf species. Similarly, one-tailed student t-tests were used to test the hypotheses that across leaf species, ML will be associated with lower ingestion rates, higher masticatory investments, and higher masticatory rates compared to YL.

Linear regressions were used to test the hypotheses that leaf toughness will 1) negatively correlate with ingestion rate, 2) positively correlate with masticatory investment, and 3) positively correlate with masticatory rate. Each plant species item was assigned a mean toughness value, ingestion rate (g/min), masticatory investment (chews/g), and masticatory rate (chews/min). Scatter plots were constructed in which each data point represented the mean ingestive behavior (i.e., ingestion rate, masticatory investment, or masticatory rate) and mean toughness value for a particular plant species. One-tailed t-tests ($\alpha = 0.05$) were used to evaluate the correlations with the prediction that toughness will negatively influence foraging efficiency. That is, leaf toughness will negatively correlate with ingestion rate but positively correlate with both masticatory investment and masticatory rate. Statistical tests were performed using SPSS statistical software.

RESULTS

Mechanical Toughness

Results showed that the average toughness of the 40 leaf species included in the analysis (i.e., YL = 27 species ML = 13 species) was 183.4 ± 83.04 J m^{-2}. Each species was sampled 6 -18 times (i.e., cuts made to individual leaves) with an average of 8.8 samples per species. YL had significantly lower toughness values (155.3 ± 87.3 J m^{-2}) than ML (237.5 ± 64.3 J m^{-2}) ($p < 0.01$). Toughness values ranged from 71.4 J m^{-2} for *Antiaris toxicaria* YL to 388.5 J m^{-2} for *Mangifera indica* ML (Table 3.1).

Food Selection

Commonly consumed leaf items had significantly lower toughness values for the Ujamaa group ($p = 0.03$), but toughness values were not significantly different between commonly consumed leaf species and the most abundant leaf species for the Ufalme and Nyumbani groups. Species-specific plant part contributions to the overall diet and selection ratios are presented in Tables 3.2 – 3.4. Only YL and ML species that comprised at least 0.50% of a group's overall diet and had toughness data available were included in the analyses. Spearman rank-order correlation coefficients (r_s) were used to assess the relationship between leaf toughness and selection ratios for each group. There were no significant correlations between food selection and leaf toughness for any of the study groups: Ujamaa ($r_s = 0.19$; $p = 0.52$), Ufalme ($r_s = -0.18$; $p = 0.54$), Nyumbani ($r_s = 0.02$; $p = 0.93$).

Ingestion and Masticatory Behaviors

The ingestion rate of the 40 leaf species averaged 5.57 ± 1.64 g/min. YL were ingested at a significantly higher rate (5.98 ± 1.58 g/min) compared to ML (4.67 ± 1.46 g/min) ($p < 0.01$). Ingestion rates ranged considerably from 2.50 g/min for *Berchemia discolor* ML to 8.62 g/min for *Grewia holstii* YL (Table 3.5).

Of the 40 samples included in the ingestion rate analyses, three were omitted (*Balanites maughamii* YL, *Combretum schumannii* YL, and *Drypetes reticulata* YL) from analyses of masticatory investment (chews/g) and masticatory rate (chews/min) due to insufficient amounts of chewing data (i.e., less than 5 focal periods). When examining YL and ML of the remaining 37 samples, masticatory investment averaged 18.68 ± 7.00 chews/g. The mean masticatory investment was significantly higher for ML (23.83 ± 8.26 chews/g) compared to YL (15.92 ± 4.25 chews/g) ($p < 0.01$). Masticatory investment ranged considerably from 10.64 chews/g for *Cyphostemma adenocaule* YL to 38.05 chews/g for *Berchemia discolor* ML (Table 3.5).

Masticatory rate averaged 91.08 ± 7.17 chews/min across all leaf samples. Averages for YL (91.12 ± 6.91 chews/min) and ML (91.01 ± 7.46 chews/min) were not significantly different ($p = 0.48$). Chews per minute ranged from 74.32 for *Pithecellobium dulce* YL to 107.7 for *Bourreria petiolaris* YL (Table 3.5).

Regression Analyses

A strong negative correlation was found between the toughness of commonly consumed leaves and ingestion rate ($r^2 = 0.73$) (Figure 3.3). In other words, leaves with higher toughness values were consistent with lower ingestion rates and vice versa. This correlation was found to be significant using a one-tailed t-test ($p < 0.01$).

In contrast, a strong positive correlation was reported between leaf toughness and masticatory investment in terms of chews/g ($r^2 = 0.72$) (Figure 3.4). That is, leaves with higher toughness values were characterized by more chewing cycles per unit weight ingested compared to leaves with lower toughness values. A one-tailed t-test found this trend to be significant ($p < 0.01$).

When masticatory rate (chews/min) was plotted against toughness, however, no such correlation was found ($r^2 = 0.09$; $p = 0.07$) (Figure 3.5). Instead, chewing rate was consistent regardless of leaf type or toughness.

DISCUSSION

The aims of this study were to assess the hypotheses that mechanical toughness of food items significantly influences food selection and foraging efficiency (Pérez-Barbería and Gordon 1998; Venkataraman et al. 2014). One of the three study groups selected leaves with lower toughness values compared to those of abundant leaves not consumed. Leaf toughness did not correlate with selection scores in any of the three study groups. Ingestion rates (g/min) associated with different leaf species consumed by *C. a. palliatus* varied considerably and these rates showed a significant negative correlation with leaf toughness. Similarly, masticatory investment (chews/g) also varied widely, but was positively correlated with leaf toughness. While tougher leaves required significantly more chews/g in order to break down, chewing rate (chews/min) was highly consistent across leaf species and toughness values.

This analysis of 27 YL species and 13 ML species makes this one of largest sample sizes for examining leaf toughness in relation to primate foraging behavior. Toughness values varied considerably among leaf species consumed by *C. a. palliatus* (i.e., R = 71.4 - 388.5 J m^{-2}). The size of and variation among species in this dataset is significant given that previous investigations of leaf toughness typically sample a handful of leaf species and/or pool leaf species toughness values, reporting only averages for YL vs. ML. This underestimates the degree to which toughness values vary among leaves of different tree species, and, in turn, has the potential to blur important functional relationships between leaf material properties and foraging behavior.

The results of this study generally support the notion that ML (mean R = 237.5 J m^{-2}) are tougher than YL (mean R = 155.3 J m^{-2}) when all species are pooled together (Lowman and Box 1983). When comparing toughness within leaf species, YL had lower toughness values than ML in all eight species where data are available for both YL and ML (Table 3.1). This trend does not necessarily hold across species as ML of a given species may be considerably less tough than YL of other species. For instance, *Adansonia digitata* ML had a mean toughness value of 139.5 J m^{-2} which is less than 15 of the 27 YL species analyzed in this study. Finally, the toughness values reported in this study are not directly comparable to those of primate feeding ecology studies that use the Darvell et al. (1996) instrument equipped with scissors (e.g., Hill and Lucas 1996; Elgart-Berry 2004; Wright et al. 2008; Yamashita et al. 2009; Venkataraman et al. 2014). Berthaume (2016) stresses that razor blade tests and scissors tests are not directly comparable as they record different modes of fracture (i.e., Mode I vs. Mode III). Toughness values generated with a single razor blade design, such as the one used in this study, consistently reported lower toughness values for materials than those recorded using the scissor method (Ang et al. 2008). Copier paper (Prairie Paper Inc., Vancouver, BC, Canada) had a toughness value of 804.7 ± 11.7 J m^{-2} (Table 3.1). Ang and colleagues (2008), who also used a single razor blade tester, recorded a very similar mean toughness value of 799 ± 10 J m^{-2} for their A4 copier paper (Advance Paper Co. Ltd, Thailand). This suggests that toughness measurements from this study are directly comparable to those recorded with a single razor blade, such as the Ang et al. (2008) tester. Further testing of identical materials on both scissor testers and razor blade testers is required to generate better conversion equations between different fracture modes (Berthaume 2016).

Leaf toughness did not negatively correlate with selection ratios as hypothesized. Instead, there was no significant relationship between the two variables. While some leaves with high toughness values had low selection ratios (e.g., Ufalme- *Diospyros squarosa*: SR = 0.3; R = 352.5), other leaves with high toughness values were among the samples with the highest selection ratios (e.g., Nyumbani- *Sterculia africana* YL: SR = 4242.7; R = 325.2). Similarly, leaves with low toughness values (R < 150 J m^{-2}) had highly varying selection ratios. This suggests *C. a. palliatus* do not actively seek leaves specifically with regard to toughness values, but that other factors likely play a more important role.

Despite the nonsignificant relationship between leaf toughness and selection, toughness did correlate with foraging efficiency. As predicted, leaves with higher toughness values corresponded with lower ingestion rates and leaves with lower toughness values were consistent with higher ingestion rates. This trend was not unexpected; however, the extent to which foraging efficiency varied among leaves was noteworthy (i.e., 2.50 to 8.62 g/min). This range was similar to that reported in Dasilva's (1992) study of *Colobus polykomos* feeding behavior in which leaf ingestion rates varied from 1.71 to 6.43 g/min. During the study period, adult *C. a. palliatus* consumed approximately 840 g of plant material per day (Dunham, unpublished data). In a given feeding bout an adult might consume 200 g of a particular leaf species. Consuming leaves with a low toughness value, such as *Haplocoelum inopleum* YL (R = 88.5 J m^{-2}), would take an adult colobus monkey an estimated 23 minutes. In contrast, consuming 200 g of a tougher leaf species, such as *Cassia abbreviata* ML (R = 382.0 J m^{-2}), would take an individual approximately 80 minutes. Admittedly, these two leaf species are near the extremes for both toughness and ingestion rates among leaves eaten by *C. a. palliatus*; however, they showcase the dramatic variation in foraging efficiency associated with commonly consumed leaves. The necessity to spend more time feeding on tougher food items relative to less tough ones could be costly as primates are susceptible to predators while foraging (Fraser and Huntingford 1986; Cowlishaw 1997; Fichtel 2012). Furthermore, an increased time spent feeding on tougher foods limits the amount of time individuals can spend doing other important activities such as socializing and resting.

Even though foraging on tougher leaves may be inefficient in terms of initial ingestion (i.e., grams consumed per minute), foraging efficiency is ultimately dependent upon the amount and manner in which energy and various macro- and micronutrients are absorbed from a given food source (Lambert 1998). Similar to ruminants, colobine monkeys are foregut fermenters and possess gut microbiota that break down structural carbohydrates, converting them into useable energy (Kay and Davies 1994; Van Soest 1994). Additional research is required to elucidate the relationships among leaf toughness, digestibility, and nutrient absorption.

Tougher leaves are also potentially costly, not only in terms of time spent foraging but in relation to mastication. The number of chewing cycles per gram ingested also varied considerably among commonly consumed leaves. Tougher leaves were associated with significantly more chewing cycles per gram ingested. Data from this study includes estimates of the mass of leaves ingested and the number of mastication events during a given focal period, but the degree to which a food bolus is comminuted before swallowing remains unknown for *C. a. palliatus* (Hiiemae and Palmer 1999). It is assumed that different leaf species are comminuted to a relatively consistent threshold before swallowing and thus tougher leaves require significantly more chewing cycles per gram in order to effectively break down (Pérez-Barbería and Gordon 1998). Returning to the previous example, it would take an individual roughly 2,166 chewing cycles to process 200 g of *Haplocoelum inopleum* YL (R = 88.5 J m^{-2}) compared to an estimated 7,358 chewing cycles to comminute and ingest the same mass of *Cassia abbreviata* ML (R = 382.0 J m^{-2}). While the energy for a single mastication event may seem trivial, this example shows that mastication during a single feeding bout could realistically differ by thousands of chewing cycles depending on the toughness of the leaves consumed. Differences in the amount of chewing cycles on this scale certainly translate to appreciable differences in energy expenditure (Spencer 1998).

Venkataraman et al. (2014) found a similar relationship between increased dietary toughness and decreased chewing efficiency in geladas (*Theropithecus gelada*). Rather than estimating the mass of ingested food items and the number of chewing cycles, they examined foraging efficiency based on fecal particle size, under the premise that smaller fecal particle sizes were associated with more complete and efficient breakdown of food items. During the dry season, the gelada diet was composed of significantly tougher food items and this dietary shift corresponded with an increase in fecal particle size (Venkataraman et al. 2014). These findings, combined with those of this study of *C. a.*

palliatus, provide support for the idea that toughness significantly influences foraging and chewing efficiency in primates.

While leaf toughness positively correlated with masticatory investment (chews/g), there was no such pattern between leaf toughness and mastication rate (chews/min). Increasing chewing rate and/or bite forces during comminution of tougher leaves would increase the amount of work performed during a given feeding bout (Hylander 1979). Although increasing chewing power (i.e., power = work/time) would theoretically enhance the breakdown of tougher foods, anatomical constraints appear to prevent dramatic shifts in chewing rate in primates (Ross et al. 2009a). Within mammals, and within primates specifically, chewing rate is inversely proportional to body mass (Gerstner and Gerstein 2008). The relatively constant chewing rates within (but not among) mammalian species are likely an adaptation to minimize energy expenditure during mastication (Ross et al. 2007). Thus, these results refute the hypothesis that tougher leaves will be characterized by a faster chewing rate. Instead, mastication rate was remarkably consistent regardless of leaf toughness (mean for all leaves = 91.08 ± 7.17 chews/min). Furthermore, although data are unavailable for toughness values of non-leaf food items, the average number of chews/min was similar for flowers (91.16 ± 12.68 chews/min) and fruit (86.45 ± 15.47 chews/ min) consumed by *C. a. palliatus* (Dunham, unpublished data). This suggests that chewing rate in *C. a. palliatus* is highly consistent regardless of plant species and food item.

Given these results and the relatively constant chewing rates within many mammalian taxa (Ross et al. 2007), the amount of time spent feeding per day could be multiplied by chewing rates to yield an estimate of chewing cycles per day. For instance, adult *C. a. palliatus* individuals spent roughly 150 minutes actively feeding per day (Dunham, unpublished data) with an overall chewing rate of approximately 90 chews per minute for all food species and plant parts. Taken together this equals roughly 13,500 chewing cycles per day. Similar data on other taxa would allow researchers to test whether folivores actually do chew more than frugivores, and, if so, how differences in the amount of chewing relate to jaw morphology and microstructure (Hylander 1979). Careful consideration should be placed on estimating the amount of time spent feeding vs. time spent chewing. African colobines, including *C. a. palliatus*, are known to feed from seated postures, typically moving only after exhausting all food items within reach (McGraw 1998; Dunham and McGraw 2014). Thus, food intake and chewing remain fairly constant during a feeding bout. I argue that time spent feeding is roughly equivalent to time spent chewing in *C. a. palliatus*. It is likely that more mobile foragers (e.g., forest guenons) may spend a considerable portion of the day actively foraging/searching for food, but only a fraction of that time is actually spent chewing (McGraw 1998). This study is in agreement with Ross and colleagues (2009b, 2012) that behavioral data of this kind should help clarify relationships among body mass, mastication, and food mechanical properties.

Despite the efforts of many researchers, attempts to link mechanical and dietary profiles with a specific suite of morphological characteristics in primates have been met with limited success (McGraw and Daegling 2012; Ross et al. 2012). Several researchers have suggested that the deeper and more robust mandibles characteristic of colobines relative to cercopithecines is related to highly repetitive masticatory loading associated with a tough, folivorous/granivorous diet (Hylander 1979; Bouvier 1986; Ravosa 1996). While *C. a. palliatus* from this study and some populations of *Colobus* spp. are highly folivorous, other members of *Colobus* spp. rely heavily on whole fruits, leguminous seed pods, and lichens (see Fashing, 2011). For instance, some populations of *C. angolensis*, *C. polykomos* and *C. satanas*, face significant mechanical challenges from their habitual consumption of leguminous seed pods (Harrison 1986; Dasilva 1994; Maisels et al. 1994; Bocian 1997; McGraw et al. 2015). In particular, Koyabu and Endo (2009) argued that *C. angolensis* possess a variety of craniofacial features that enhance seed eating (i.e., relatively wider bigonial breadths, anteroposteriorly shorter faces, shorter postcanine tooth rows, wider bizygomatic arches, and anteroposteriorly longer zygomatic arches). McGraw and colleagues (2015) assert that the significant differences in oral processing behaviors among sympatric *C. polykomos* and red colobus (*Piliocolobus badius*) from the Taï Forest can be attributed almost entirely to the former's frequent consumption of *Pentaclethra macrophylla* seed pods which require aggressive incisal preparation to expose seeds from woody casings (McGraw et al. 2015). Despite *C. polykomos* having a more mechanically challenging diet, paradoxically, *P. badius* appears to have the more robust mandible (Daegling and McGraw 2001). Future research will examine the mandibular morphology of *C. angolensis palliatus* in relation to oral processing and mechanical properties data. This combined with studies examining the interactions of diet and oral processing behaviors in other colobines, as well as other types of data (e.g., histological analysis of secondary bone remodeling), may provide additional evidence for interpreting the functional significance of mandibular form (McGraw et al. 2015). Furthermore, it is paramount that morphological specimens come from the same population for which behavioral data are available (as in studies of the Taï Forest monkeys), and also that researchers identify the extent to which diet and oral processing behaviors vary among groups within a particular population (Chapman and Chapman 1999; Chapman et al. 2002b; Yamashita et al. 2015).

I analyzed the relationships among leaf toughness, selection ratios, ingestion rate, and mastication in Angola black and white colobus monkeys. In general, leaf toughness did not strongly correlate with food selection but significantly influenced foraging efficiency, such that leaf toughness negatively correlated with ingestion rate (g/min) and positively correlated with masticatory investment (chews/g). A handful of researchers have recently emphasized the importance of combining data on specific oral processing behaviors, in addition to food mechanical properties, to better interpret masticatory morphology (Norconk et al. 2009; Ross et al. 2012; McGraw et al. 2015). For example, recording the manner and frequency in which primates utilize their incisors, canines, and postcanines in relation to food items of varying mechanical properties is a promising research avenue (Yamashita 1998, 2003; Wright et al. 2008; Yamashita et al. 2009; McGraw et al. 2011, 2015). I strongly support such approaches and believe additional studies examining relationships among food mechanical properties, foraging efficiency, and oral processing behaviors will provide valuable context for interpreting masticatory morphology as it relates to a variety of topics including: dental microwear, occlusal topography, gross craniofacial and mandibular morphology, and bone remodeling patterns.

Table 3.1. Toughness values of leaves commonly consumed by *Colobus angolensis palliatus* in the Diani Forest, Kenya

				Toughness	
Plant Species	Family	Plant Type	Plant Part	Mean	Stdev
Adansonia digitata	Malvaceae	T	ML	139.5	14.9
Berchemia discolor	Rhamnaceae	T	ML	362.0	16.9
Bougainvillea spectabilis	Nyctaginaceae	L/S	ML	155.3	22.9
Cassia abbreviata	Leguminosae	T	ML	382.0	12.3
Cassia fistula	Leguminosae	T	ML	221.2	13.4
Commiphora zanzibarica	Burseraceae	T	ML	197.4	8.1
Cussonia zimmermannii	Araliaceae	T	ML	163.9	11.6
Hunteria zeylanica	Apocynaceae	T	ML	263.6	15.9
Lecaniodiscus fraxinifolius	Sapindaceae	T	ML	287.0	8.1
Mangifera indica	Anacardiaceae	T	ML	388.5	37.2
Premna hildebrandti	Lamiaceae	L	ML	195.7	23.6
Rauvolfia mombasiana	Apocynaceae	T	ML	172.7	10.6
Zanthoxylum chalybeum	Rutaceae	T	ML	235.3	12.0
All mature leaves	**NA**	**NA**	**ML**	**237.5**	**64.3**
Antiaris toxicaria	Moraceae	T	YL	71.4	13.2
Balanites maughamii	Zygophyllaceae	T	YL	209.9	14.0
Berchemia discolor	Rhamnaceae	T	YL	270.1	9.6
Bougainvillea spectabilis	Nyctaginaceae	L/S	YL	96.1	11.0
Bourreria petiolaris	Boraginaceae	T	YL	100.5	9.8
Cissus integrifolia	Vitaceae	L	YL	148.2	5.5
Coccinia grandis	Cucurbitaceae	L	YL	196.5	8.0
Combretum schumannii	Combretaceae	T	YL	142.6	9.8
Commiphora zanzibarica	Burseraceae	T	YL	172.3	9.0
Cyphostema spp.	Vitaceae	L	YL	101.0	12.2
Cyphostemma adenocaule	Vitaceae	L	YL	75.8	14.9
Diospyros squarrosa	Ebenaceae	T	YL	352.5	13.8
Drypetes reticulata	Putranjivaceae	T	YL	246.6	13.9
Feretia apodanthera	Rubiaceae	S/T	YL	172.8	13.6
Grewia holstii	Malvaceae	L/S	YL	138.6	25.3
Haplocoelum inopleum	Sapindaceae	T	YL	88.5	11.5
Hibiscus rosa-sinensis	Malvaceae	L/S	YL	163.8	20.4
Hunteria zeylanica	Apocynaceae	T	YL	137.8	29.6
Lecaniodiscus fraxinifolius	Sapindaceae	T	YL	178.6	8.2
Maerua triphylla	Capparaceae	L	YL	114.6	11.2
Markhamia zanzibarica	Bignoniaceae	T	YL	145.3	11.1
Millettia usaramensis	Leguminosae	T	YL	77.9	8.5
Pithecellobium dulce	Leguminosae	T	YL	149.4	8.4
Premna hildebrandti	Lamiaceae	L	YL	179.5	15.3
Rauvolfia mombasiana	Apocynaceae	T	YL	99.6	7.7
Tinospora caffra	Menispermaceae	L	YL	164.6	21.9

Continued

Table 3.1 Continued

Plant Species	Family	Plant Type	Plant Part	Toughness Mean	Stdev
Zanthoxylum chalybeum	Rutaceae	T	YL	113.4	17.1
All young leaves	**NA**	**NA**	**YL**	**155.3**	**87.3**
Copier paper	NA	NA	NA	804.7	11.7

Plant type: L = liana, S = shrub, T = tree; Plant part: ML = mature leaf, YL = young leaf
Each leaf species was sampled 6-18 times. Copier paper sampled 10 times.

Table 3.2. Top ranking leaves, selection ratios and toughness values for Ujamaa group from July 2014 to December 2015

Rank	Species	PP	% of Diet	SR	Toughness
1	*Pithecellobium dulce*	YL	7.51	338.5	149.4
2	*Adansonia digitata*	ML	6.42	1.0	139.5
3	*Trichilia emetica*	ML	4.63	3.7	405.4
4	*Berchermia discolor*	YL	4.20	1612.6	270.1
5	*Delonix regia*	YL	3.43	5.6	NA
6	*Hunteria zelyanica*	YL	2.91	0.3	137.8
7	*Ziziphus mucronata*	YL	1.68	19.8	NA
8	*Commpihora zanzibarica*	YL	1.58	39.3	172.3
9	*Lecaniodiscus fraxinifolius*	YL	1.44	0.1	178.6
10	*Milettia usamarensis*	YL	1.01	0.4	77.9
11	*Combretum schumanii*	YL	1.01	0.1	142.6
12	*Antiaris toxicaria*	YL	0.88	325.6	71.4
13	*Berchermia discolor*	ML	0.82	314.6	362.0
14	*Trema orientalis*	YL	0.59	0.5	167.0
15	*Adansonia digitata*	YL	0.57	0.1	106.4
16	*Combretum schumanii*	ML	0.51	0.0	222.1

pp = plant part; YL = young leaf; ML = mature leaf; SR = selection ratio

Table 3.3. Top ranking leaves, selection ratios and toughness values for Ufalme group from July 2014 to December 2015

Rank	Species	PP	% of Diet	SR	Toughness
1	*Zanthoxylum chalybeum*	YL	6.78	0.9	113.4
2	*Markhamia zanzibarica*	YL	6.33	7.4	145.3
3	*Cordia goetzi*	YL	5.66	10.0	NA
4	*Lecaniodiscus fraxinifolius*	YL	3.45	0.3	178.6
5	*Adansonia digitata*	ML	3.39	1.0	139.5
6	*Zanthoxylum chalybeum*	ML	2.07	0.3	235.3
7	*Haplocoelum inopleum*	YL	1.44	227.1	88.5
8	*Ziziphus mucronata*	YL	1.39	189.2	NA
9	*Plumeria obtusa*	YL	1.38	2.2	196.3
10	*Adansonia digitata*	YL	1.30	0.4	106.4
11	*Mangifera indica*	YL	1.16	20.8	NA
12	*Lecaniodiscus fraxinifolius*	ML	0.97	0.1	287
13	*Hunteria zeylanica*	YL	0.76	3.8	137.8
14	*Flacourtia indica*	YL	0.75	5.7	NA
15	*Cassia abbreviata*	ML	0.60	69.3	382
16	*Diospyros squarosa*	YL	0.55	0.3	352.5
17	*Bridelia cathatica*	YL	0.52	39.3	106.9
18	*Cassia abbreviata*	YL	0.52	59.9	382

pp = plant part; YL = young leaf; ML = mature leaf; SR = selection ratio

Table 3.4. Top ranking leaves, selection ratios and toughness values for Nyumbani group from January to December 2015

Rank	Species	PP	% of Diet	SR	Toughness
1	*Zanthoxylum chalybeum*	YL	2.47	5.9	113.4
2	*Hunteria zeylanica*	YL	2.41	518.5	137.8
3	*Markhamia zanzibarica*	YL	1.66	228.9	145.3
4	*Sterculia africana*	YL	1.58	4242.7	325.2
5	*Pithecellobium dulce*	YL	1.56	11536.9	149.4
6	*Commpihora zanzibarica*	YL	1.28	253.3	172.3
7	*Rauvolfia mombasiana*	YL	1.23	221.2	99.6
8	*Adansonia digitata*	ML	1.18	0.9	139.5
9	*Balanites maughamii*	YL	1.10	12.2	209.9
10	*Grewia vaughanii*	YL	0.85	63.6	213.8
11	*Onocoba spinosa*	YL	0.75	42628.1	127.2
12	*Zanthoxylum chalybeum*	ML	0.68	1.6	235.3
13	*Milletia usamarensis*	YL	0.59	16.6	77.9
14	*Hunteria zelyanica*	ML	0.50	107.8	263.6

pp = plant part; YL = young leaf; ML = mature leaf; SR = selection ratio

Table 3.5. Ingestion rate, masticatory frequency, and masticatory rate of leaves commonly consumed by *Colobus angolensis palliatus* in the Diani Forest, Kenya

		Ingestion Rate (g/min)			Masticatory Investment (chews/g)			Masticatory Rate (chews/min)		
Plant Species	PP	Mean	Stdev	N	Mean	Stdev	N	Mean	Stdev	N
Adansonia digitata	ML	5.53	1.19	90	18.54	3.98	55	102.4	13.31	55
Berchemia discolor	ML	2.50	0.40	11	38.05	4.73	7	93.20	10.15	7
Bougainvillea spectabilis	ML	6.43	2.32	13	17.32	8.33	11	96.93	19.24	11
Cassia abbreviata	ML	2.53	0.36	13	36.79	4.62	13	91.92	6.37	13
Cassia fistula	ML	4.48	0.88	5	18.49	5.50	5	79.13	4.84	5
Commiphora zanzibarica	ML	4.40	0.84	7	22.43	5.27	7	95.32	6.38	7
Cussonia zimmermannii	ML	5.82	1.84	8	17.25	5.49	8	91.78	5.99	8
Hunteria zeylanica	ML	4.74	1.36	12	18.40	4.98	12	82.60	15.11	12
Lecaniodiscus fraxinifolius	ML	2.54	0.36	13	34.14	2.20	10	83.21	7.59	10
Mangifera indica	ML	3.01	1.20	14	30.12	6.74	13	85.09	8.56	13
Premna hildebrandti	ML	3.37	0.45	8	26.35	3.39	8	88.12	10.86	8
Rauvolfia mombasiana	ML	6.05	1.48	7	16.22	4.42	6	96.37	13.96	6
Zanthoxylum chalybeum	ML	5.09	1.19	46	15.74	1.57	41	97.08	10.25	41
All mature leaves	**ML**	**4.67**	**1.46**	**247**	**23.83**	**8.26**	**196**	**91.01**	**7.46**	**196**
Antiaris toxicaria	YL	7.40	1.02	9	16.54	2.14	7	95.20	9.22	7
Balanites maughamii	YL	4.83	1.07	5	NA	NA	NA	NA	NA	NA
Berchemia discolor	YL	3.46	0.91	17	26.11	11.66	9	82.64	15.23	9
Bougainvillea spectabilis	YL	7.77	1.83	47	13.05	2.82	45	98.27	13.18	45
Bourreria petiolaris	YL	8.56	1.79	8	13.27	3.94	8	107.70	8.89	8
Cissus integrifolia	YL	4.82	0.77	50	19.43	4.18	24	95.18	18.70	24
Coccinia grandis	YL	6.46	1.31	18	12.43	1.88	15	89.73	11.70	15
Combretum schumannii	YL	4.62	1.55	5	NA	NA	NA	NA	NA	NA
Commiphora zanzibarica	YL	5.15	0.97	17	19.81	3.88	12	99.68	10.41	12
Cyphostema spp.	YL	6.77	2.42	10	17.16	6.54	9	101.34	5.82	9
Cyphostemma adenocaule	YL	8.58	3.43	15	10.64	2.84	12	83.48	22.05	12
Diospyros squarrosa	YL	3.66	0.27	9	27.23	2.40	6	80.87	8.50	6

Continued

Table 3.5
Continued

Plant Species	PP	Ingestion Rate (g/min) Mean	Stdev	N	Masticatory Investment (chews/g) Mean	Stdev	N	Masticatory Rate (chews/min) Mean	Stdev	N
Drypetes reticulata	YL	4.88	1.52	7	NA	NA	NA	NA	NA	NA
Feretia apodanthera	YL	5.45	0.84	11	16.98	2.83	5	93.44	7.77	5
Grewia holstii	YL	6.40	0.83	26	13.73	1.83	20	88.71	8.83	20
Haplocoelum inopleum	YL	8.62	1.39	9	10.83	1.21	7	94.21	9.09	7
Hibiscus rosa-sinensis	YL	6.78	2.46	29	16.93	6.61	28	100.31	11.05	28
Hunteria zeylanica	YL	7.13	1.31	42	12.59	5.77	41	89.49	10.56	41
Lecaniodiscus fraxinifolius	YL	5.04	1.46	9	17.76	5.51	6	90.68	15.14	6
Maerua triphylla	YL	6.80	1.39	24	12.68	3.30	17	85.06	9.70	17
Markhamia zanzibarica	YL	6.78	1.18	27	13.68	2.82	17	93.29	9.84	17
Millettia usaramensis	YL	6.68	1.28	8	17.45	4.20	11	87.92	12.74	11
Pithecellobium dulce	YL	4.51	1.07	40	16.49	3.05	21	74.32	18.79	21
Premna hildebrandti	YL	5.24	1.04	22	17.52	2.95	17	90.60	19.63	17
Rauvolfia mombasiana	YL	6.76	1.89	10	12.00	3.39	8	83.41	10.31	8
Tinospora caffra	YL	6.39	1.36	23	14.89	5.02	16	92.08	12.79	16
Zanthoxylum chalybeum	YL	6.78	2.93	56	12.15	6.47	29	89.20	10.82	29
All young leaves	**YL**	**5.98**	**1.58**	**553**	**15.92**	**4.25**	**390**	**91.12**	**6.91**	**390**

pp = plant part: ML = mature leaf, YL = young leaf; N = number of focal periods observed

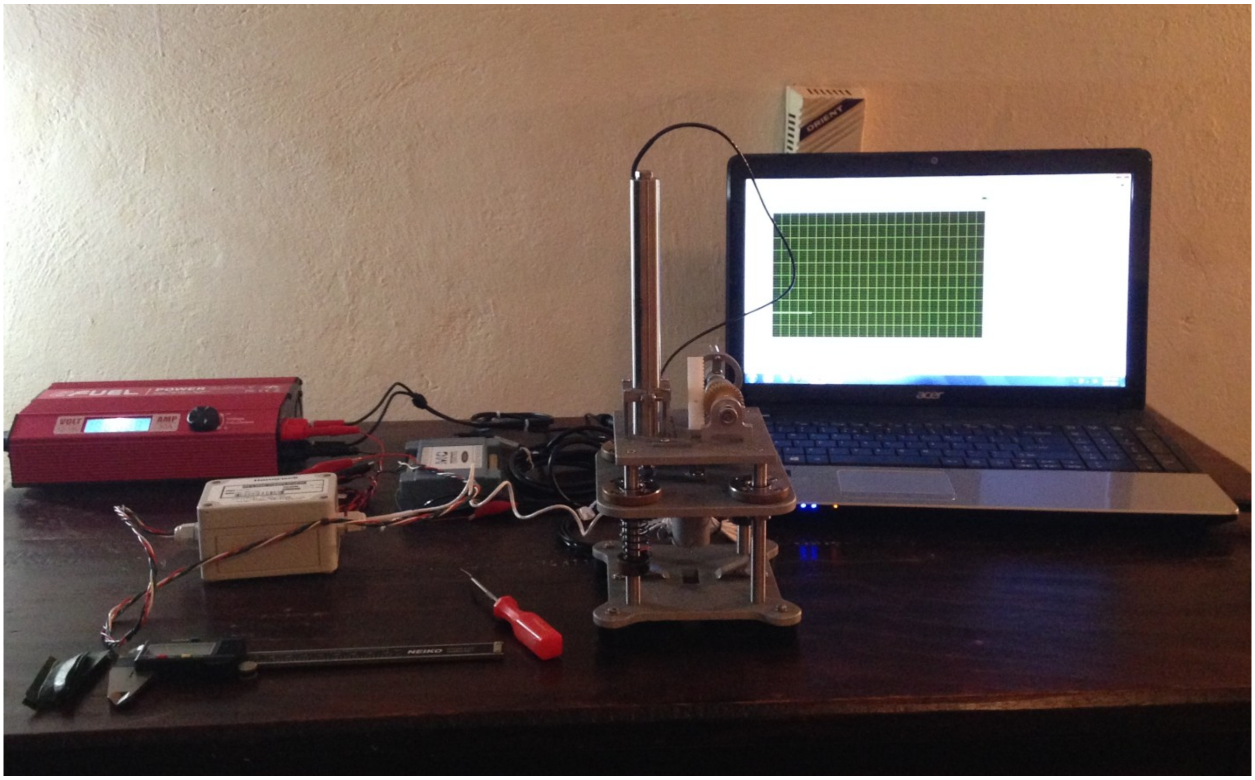

Figure 3.1. Mechanical toughness apparatus including: test stand equipped with load cell and linear transducer, signal amplifier, data acquisition unit, power supply, and laptop computer.

Figure 3.2. A juvenile male *Colobus angolensis palliatus* consuming *Thevetia peruviana* young leaves. Note that the midrib is running approximately perpendicular to the molar row during ingestion.

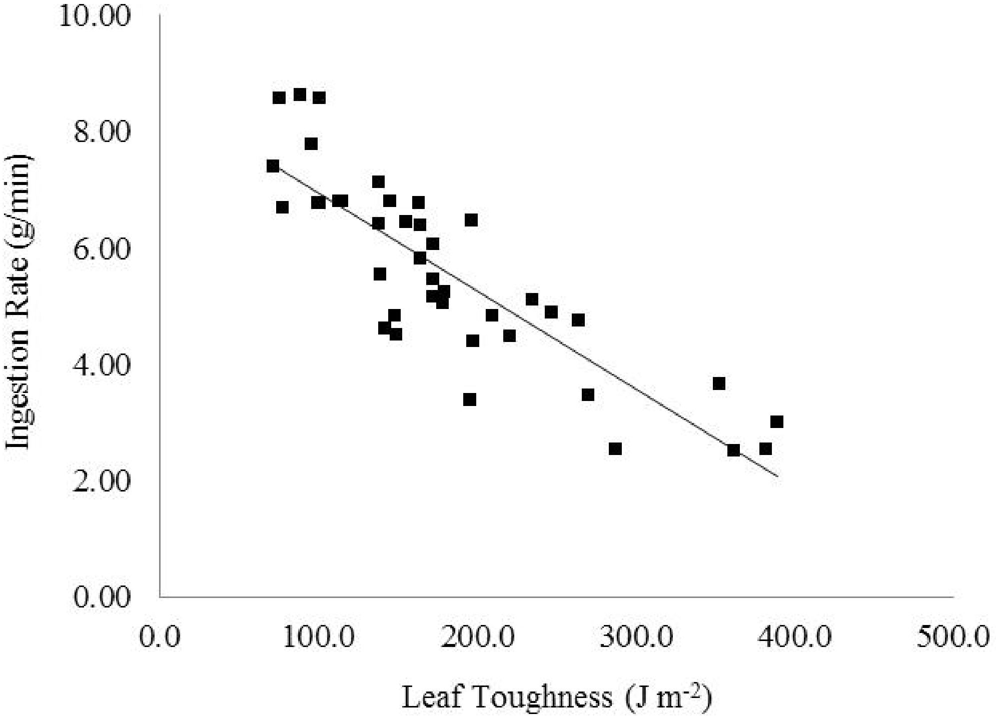

Figure 3.3. The relationship between leaf toughness and ingestion rate in *Colobus angolensis palliatus*. This negative correlation is significant ($r^2 = 0.73$; $p < 0.01$).

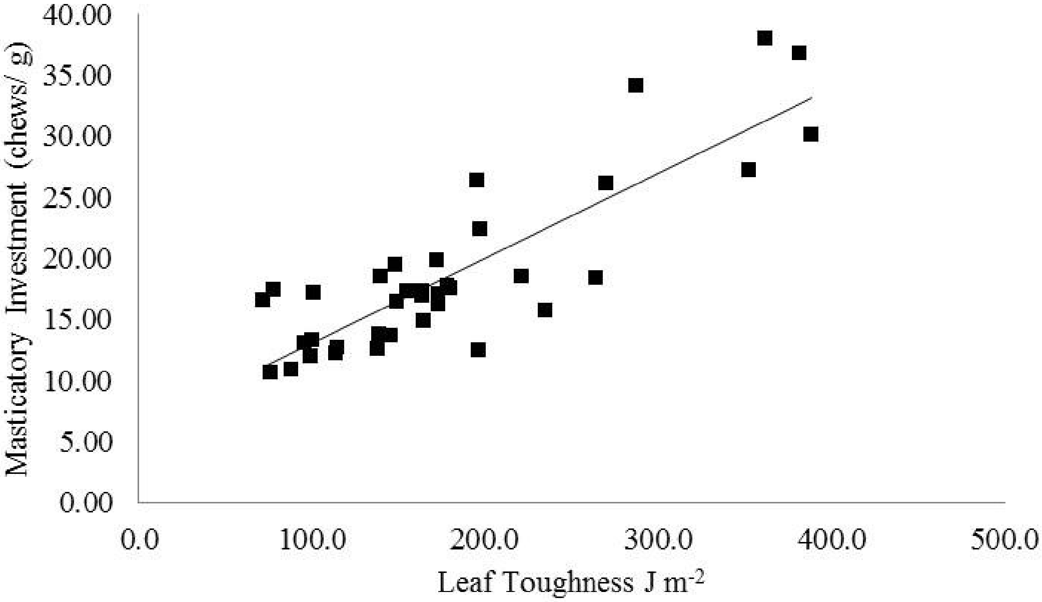

Figure 3.4. The relationship between leaf toughness and masticatory investment in *Colobus angolensis palliatus*. This positive correlation is significant ($r^2 = 0.72$; $p < 0.01$).

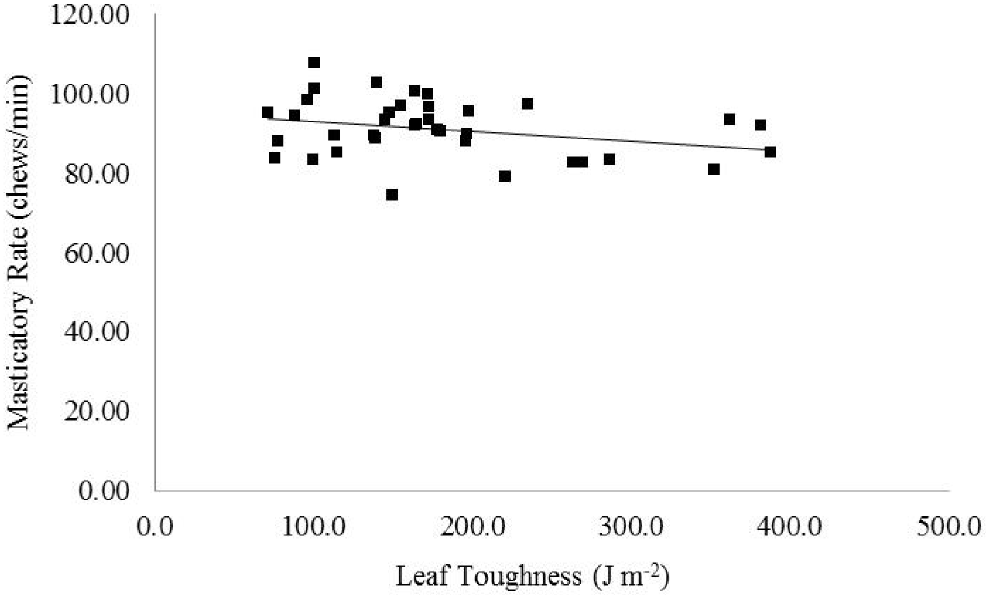

Figure 3.5. The relationship between leaf toughness and masticatory rate in *Colobus angolensis palliatus*. There is no significant correlation ($r^2 = 0.09$; $p = 0.07$).

CHAPTER 4: MACRONUTRIENT QUANTIFCATION USING CONVENTIONAL WET CHEMISTRY ASSAYS AND NEAR-INFRARED REFLECTANCE SPECTROSCOPY

INTRODUCTION

Quantifying the nutritional and chemical composition of plant materials is extremely useful for ecological studies that examine the foraging behavior and nutritional intake of animals (Foley et al. 1998; Ortmann et al. 2006; Rothman et al. 2012). Conventional wet chemistry approaches to nutrient quantification are often labor and time intensive, expensive, require hazardous chemicals, and/or utilize difficult methodological techniques. These challenges serve as significant barriers for analyzing large sample sets such as those required to adequately assess the composition of plant materials on broad spatial and temporal scales (Chapman et al. 2003; Rothman et al. 2015). These restrictions also inhibit studies examining the nutritional intake of animals with highly diverse diets, such as primates.

In order to circumvent these obstacles, ecologists have increasingly utilized near-infrared reflectance spectroscopy (NIRS) to provide more rapid, efficient, and reliable analyses of nutritional components (Foley et al. 1998; Rothman et al. 2009; Vance et al. 2016). Initially developed in the food and agricultural sciences, infrared spectroscopy (IR) uses infrared light to irradiate samples which, in turn, yield reflectance spectra. These spectra display peaks associated with particular molecular bonds (e.g., C─H, C─O, N─H, etc.) which can be linked to different macro- and micronutrients. After calibrating sample spectra to nutritional compositions determined via conventional wet chemistry methods, the nutritional composition of future samples can be predicted rapidly (i.e., < 1 minute) using only IR statistical models. IR spectroscopy has been successfully utilized in the analysis of dietary proteins, fats, water soluble carbohydrates, fiber, organic matter, and *in vitro* dry matter digestibility in a variety of free-ranging animal taxa (e.g., giraffe: Woolnough and du Toit 2001; wombats: Woolnough and Foley 2002; dugongs: Lawler et al. 2006; scarlet macaws: Cornejo et al. 2012), including several primate taxa (e.g., bamboo lemurs: Ortmann et al. 2006; colobus monkeys: Johnson et al. 2015, Dunham et al. 2016; mountain gorillas: Rothman et al. 2009, 2011; spider monkeys: Felton et al. 2009a, b).

The goal of this study is to develop a simple and rapid method for the quantification of six nutritional components (ash, crude protein, fat, water soluble carbohydrate, neutral detergent fiber, and acid detergent fiber) of leaves, fruits, and flowers from the Diani Forest, Kenya. Because this study is part of a larger research project examining the nutritional composition of ~ 400 species-specific plant parts in relation to nutritional intake strategies among Angola black and white colobus monkeys (*Colobus angolensis palliatus*), the primary goal is to determine if a subset of these samples (n = 138 samples) can be used to predict the nutritional composition of the remaining samples and future samples.

METHODS

Samples of young leaves, mature leaves, unripe fruit, ripe fruit, flowers and flower buds were collected from the Diani Forest, Kenya, from June - July 2014 and from January - November 2015. The Diani Forest is a coral rag forest located in the Kwale District of southern Kenya, measures roughly 455 ha in area, and is characterized by significant anthropogenic disturbance (Anderson et al. 2007; Dunham and McGraw 2014). Samples were dried in the field using an Excalibur food dehydrator to prevent molding. Upon returning to the laboratory in Columbus, OH, USA, samples were dried again in a vacuum oven at 105°C for 8 hr to remove residual moisture. Samples were then homogenized using a commercial blender and sieved through a 1 mm mesh. A total of 85 leaf samples, 30 fruit samples, and 23 flower samples were analyzed.

All samples were first analyzed in duplicate using wet chemistry reference methods. Ash content was quantified by heating samples at 600°C for 4 hours. Total nitrogen content was calculated via Dumas combustion. Crude protein was then calculated by multiplying total nitrogen by a factor of 6.25 (Maynard and Loosli 1969). It is recognized that this factor likely over estimates crude protein content in leaves, but it is nonetheless used in order to remain comparable with other studies (Milton and Dintzis 1981; Conklin-Brittain et al. 1999). Fat was quantified using a modified Bligh-Dyer (Bligh and Dyer 1959) technique in which ~0.1 g of sample was placed in a microcentrifuge tube and immersed in 1.0 mL of hexanes and 1.0 mL of water. Samples were then vortexed and centrifuged at 10,000 rpm for 5 minutes. The top layer of fat-containing hexanes was then removed and samples were washed two additional times in the same manner. Fat content was then quantified by evaporating hexanes via nitrogen gas. Water soluble carbohydrate (WSC) concentrations were calculated using the phenol–sulfuric acid method (Dubois et al. 1956; BeMiller and Low 2010) with modifications to accommodate WSC quantification from solid substances (Dunham et al. 2016). Finally, neutral detergent fiber (NDF: lignin, cellulose, and hemicellulose content) and acid detergent fiber (ADF: lignin and cellulose content) were analyzed sequentially following Van Soest et al. (1991). Ash, fat, and WSC analyses were conducted by the author in the Department of Food Science and Technology at The Ohio State University Columbus campus. Crude protein, NDF, and ADF analyses were conducted by trained technicians at the Service Testing and Research (STAR) Laboratory at The Ohio State University Wooster campus.

Infrared spectral data were collected using a Varian Excalibur 3100 benchtop instrument equipped with an Integrating Sphere accessory (PIKE Technology, Madison, Wisconsin) collecting spectra in the 10,000 – 4000 cm^{-1} region at 4 cm^{-1} resolution (Figure 4.1). Background spectra were taken on a standard gold-coated layer. Sixty-four scans were co-added per sample and each sample was measured in duplicate. Spectral data were analyzed using partial least squares regression (PLSR) to generate multivariate statistical models in Pirouette 4.5 software. By combining aspects of principal component analysis and multiple linear regression, PLSR reduces a large number of independent variables into a few latent variables (i.e., PLS factors). This is particularly useful when the number of spectral variables (i.e., independent variables) is much larger than the number of samples (i.e., dependent variables). PLSR is also an advantageous technique because it does not assume that conventional wet chemistry references methods are error free. For instance, errors may arise in sample preparation, dilution, and weighing (Brereton 2000). Cross-validated (leave-one-out approach) calibration models were generated by using mathematical normalization pre-processing. The cross validation procedure calibrates a model based on N - 1 samples with the remaining sample used as an independent validation set. This procedure is repeated until all samples have been cross-validated. The performance of the calibration models was evaluated in terms of loading vectors, standard error of cross validation (SECV = magnitude of error expected when independent samples are predicted using the model), and coefficient of determination (r^2 = proportion of variability described by the model), for the calibration models. Two sets of models were generated: one to predict leaf nutritional content and one to predict fruit and flower nutritional content. Leaves were not combined with fruits and flowers into a single predictive model due to inherent differences in spectral form between leaves vs. fruits and flowers.

RESULTS

Results from wet chemistry reference methods and NIRS predictive equations were remarkably similar (Appendix A). All values are presented as percentages of dry weight. Metrics for the calibration equations for leaves are presented in Table 4.1 and metrics for the calibration equations for fruits and flowers are presented in Table 4.2. Overall, calibration equations had strong predictive power for leaf components (i.e., r^2 =

0.90 – 0.95) and fruit and flower components (i.e., $r^2 = 0.90 – 0.95$) and are on par with those reported in agricultural and food sciences studies (Figure 4.2 and Figure 4.3) (Williams and Norris 1987; Rodriguez-Saona and Allendorf 2011).

For each macronutrient component, only specific wavenumber regions were used to create predictive equations. All other spectral regions were removed from statistical models in order to improve the predictions by eliminating irrelevant, noisy, and unreliable variables. Ash content ranged from 3.6% - 16.2% in leaves and from 2.6% - 10.9% in fruits and flowers. The wavenumber regions from 4150-6100 cm^{-1} (2410-1639 nm) best explained the variation among the samples (Figure 4.2A and Figure 4.3A). Crude protein ranged from 9.0% - 32.6% in leaves and from 6.7% - 27.5% in fruits and flowers. The wavenumber ranges from 4600-4900 cm^{-1} (2174-2041 nm) and 6900-7200 cm^{-1} (1449- 1389 nm) were used to construct predictive equations as these spectral ranges correspond with nitrogen content (Figure 4.2B and Figure 4.3B). Fat content varied from 1.9% - 6.1% in leaves and from 0.5% - 12.1% in fruits and flowers. Spectral regions from 4000-4500 cm^{-1} (2500 – 2222 nm) and 5500-6000 cm^{-1} (1818 – 1667 nm) were used to predict fat content (Figure 4.2C and Figure 4.3C). WSC concentrations varied considerably from 1.1% - 6.7% in leaves and from 1.4% - 34.0% in fruits and flowers. Wavenumber regions from 4900-5500 cm^{-1} (2041-1818 nm) and from 6700-7600 cm^{-1} (1493-1316 nm) best explained variation in WSC content among the samples (Figure 4.2D and Figure 4.3D). NDF content ranged from 28.6% - 78.9% in leaves and from 25.0% - 81.9% in fruits and flowers. Finally, ADF content ranged from 12.1% - 48.2% in leaves and from 10.1% - 57.4% in fruits and flowers. The spectral regions from 4200-

6000 cm^{-1} (2381-1667 nm) were used to construct predictive equations for both NDF and ADF (Figures 4.2E, 4.2F, 4.3E and 4.3F).

DISCUSSION

While most studies from the agricultural and food sciences use NIRS models for monitoring nutritional and chemical composition of a single crop or variations of similar consumer food items, this study highlights the fact that NIRS predictive models can accommodate highly diverse sample sets covering a multitude of plant species. Previous ecological research has demonstrated that NIRS models can accurately predict a variety of macronutrient concentrations from sample sets containing multiple plant species. For instance, Woolnough and Foley (2002) created a NIRS model based on 25 species of grasses and sedges common in the habitat of northern hairy-nosed wombats. In their model, Lawler et al. (2006) incorporated 10 species of sea grasses consumed by dugongs. Finally, Rothman et al. (2009) utilized 14 plant species regularly eaten by mountain gorillas to generate predictive models for macronutrients in leaves and stems. The sample set presented in this study was considerably more diverse. The leaf models contained 85 species-specific plant parts, including 55 plant species from 27 plant families. The fruit and flower models contained 23 species-specific flower parts, including 21 species from 12 plant families and 30 species-specific fruit parts, including 27 species from 15 plant families. These samples were not only diverse in terms of taxonomy, but also with regard to macronutrient composition. For example, CP ranged from 9.0% - 32.6% and NDF ranged from 28.6% - 78.9% in the leaf sample while WSC content ranged from 1.4% -

34.0% in fruits and flowers. Despite sample breadth and diversity, the power of the predictive models was on par with those reported in agricultural and food science studies of more homogenous data sets (i.e., $r^2 = 0.90$-0.95).

The predictive power of NIRS equations is primarily determined by the accuracy and precision of conventional wet chemistry methods used to generate the predictive models. Thus, researchers should be particularly meticulous when performing these wet chemistry techniques. It is best to use the Association of Official Analytical Chemists (AOAC) reference methods when possible, such as the methods used for quantification of ash, total nitrogen, NDF, and ADF in this study. For fat analysis, poor reproducibility was initially achieved when using official reference methods including the Soxhlet extraction method and the Bligh-Dyer method. This poor reproducibility was likely because fat concentrations were low in many of the samples (i.e., range = 1.9% - 6.1% of dry weight for leaves) (Soxhlet, 1879; Bligh and Dyer, 1959). Instead, this study recommends the procedure outlined in the Methods section of this paper in which powdered plant samples were immersed in a water-hexanes solution instead of the chloroform-methanol solution used in the Bligh-Dyer method. This modification allows the fat to be easily removed within the top hexanes layer after centrifuging instead of having to pipette fat from the bottom layer of chloroform in the Bligh-Dyer method. For WSC quantification, this study recommends a modified phenol sulfuric acid assay for WSC quantification from solid powders as described in detail in Dunham et al. (2016).

The validity of NIRS predictive equations is also influenced by parameters used in multivariate statistical modeling. Only specific wavenumber regions were included for generating predictive equations, rather than using the entire range of spectral data (Table 4.1 and Table 4.2). These regions included in the models corresponded with absorption bands of functional groups associated with a particular macronutrient or compound and also best explained the variation among the samples. Eliminating spectral regions that did not correspond with functional groups associated with a given macronutrient, and thus did not explain variation among samples, reduced dimensionality and noisy variables, resulting in more accurate and reproducible calibration models (Martens and Naes 1987).

With that said, there is often considerable overlap in near-infrared absorbance spectra between different components of interest (Osborne and Fearn, 1986). For example, the spectral regions used to predict fat content (4000-4500 cm^{-1}; 5500-6000 cm^{-1}) overlapped considerably with the spectral regions used to predict NDF and ADF (4200-6000 cm^{-1}). Multivariate PLSR analyses largely account for this spectral overlap by reducing the number of spectral bands to a few latent factors that best predict the concentration of a particular analyte.

This study demonstrated that NIRS equations can accurately quantify ash, CP, fat, WSC, NDF, and ADF in leaves, fruits, and flowers. Most notably, these results demonstrated that highly diverse sample sets, incorporating plant parts from dozens of plant families, can be combined into a single predictive equation that maintains the high predictive power (i.e., $r^2 = 0.90 - 0.95$) characteristic of equations based on more homogeneous data sets in the agricultural and food sciences (Landau et al. 2006; Rodriguez and Allendorf 2011). The use of NIRS in ecological studies is strongly supported due to its many advantages over conventional wet chemistry analyses including minimal sample preparation, rapid sample throughput (i.e., > 100 samples can be analyzed per day), absence of harsh chemicals, and sample preservation (Foley et al. 1998; Rothman et al. 2012; Vance et al. 2016). These advantages are particularly significant for ecological studies tasked with analyzing large data sets such as those used to evaluate the composition of different plant materials over large spatial and temporal dimensions (Chapman et al. 2003; Rothman et al. 2015). Finally, recognizing the ability of NIRS to incorporate dozens of plant species into a single predictive model also has major ramifications for examining the nutritional intake of animals with highly diverse diets such as primates.

Table 4.1. Performance of the PLSR models based on NIRS estimations of components in leaves

Component	Region Used (cm^{-1})	Mean	Slope	Intercept	Factors	r^2	SECV
Ash	4150-6100	8.98 (± 2.51)	0.88	1.04	6	0.92	1.05
CP	4600-4900; 6900-7200	18.39 (± 4.88)	0.91	1.60	6	0.93	1.90
Fat	4000-4500; 5500-6000	3.66 (± 0.94)	0.92	0.29	6	0.95	0.30
WSC	4900-5500; 6700-7600	3.87 (± 1.49)	0.91	0.33	4	0.95	0.48
NDF	4200-6000	47.29 (± 10.32)	0.86	6.78	6	0.90	4.95
ADF	4200-6000	28.43 (± 9.17)	0.96	1.17	6	0.95	2.92

CP = crude protein; WSC = water soluble carbohydrate; NDF = neutral detergent fiber; ADF = acid detergent fiber; SECV = standard error of cross-validation

Table 4.2. Performance of the PLSR models based on NIRS estimations of components in flowers and fruit

Component	Region Used (cm^{-1})	Mean	Slope	Intercept	Factors	r^2	SECV
Ash	4150-6100	5.65 (± 0.55)	0.90	0.55	6	0.94	0.71
CP	4600-4900; 6900-7200	14.06 (± 5.63)	0.91	1.20	5	0.93	2.17
Fat	4000-4500; 5500-6000	3.63 (± 2.46)	0.91	0.32	6	0.95	0.85
WSC	4900-5500; 6700-7600	9.07 (± 5.66)	0.90	0.79	6	0.93	2.10
NDF	4200-6000	50.41 (± 12.67)	0.86	6.57	6	0.90	5.89
ADF	4200-6000	30.44 (± 10.13)	0.85	4.59	6	0.91	4.46

CP = crude protein; WSC = water soluble carbohydrate; NDF = neutral detergent fiber; ADF = acid detergent fiber; SECV = standard error of cross-validation

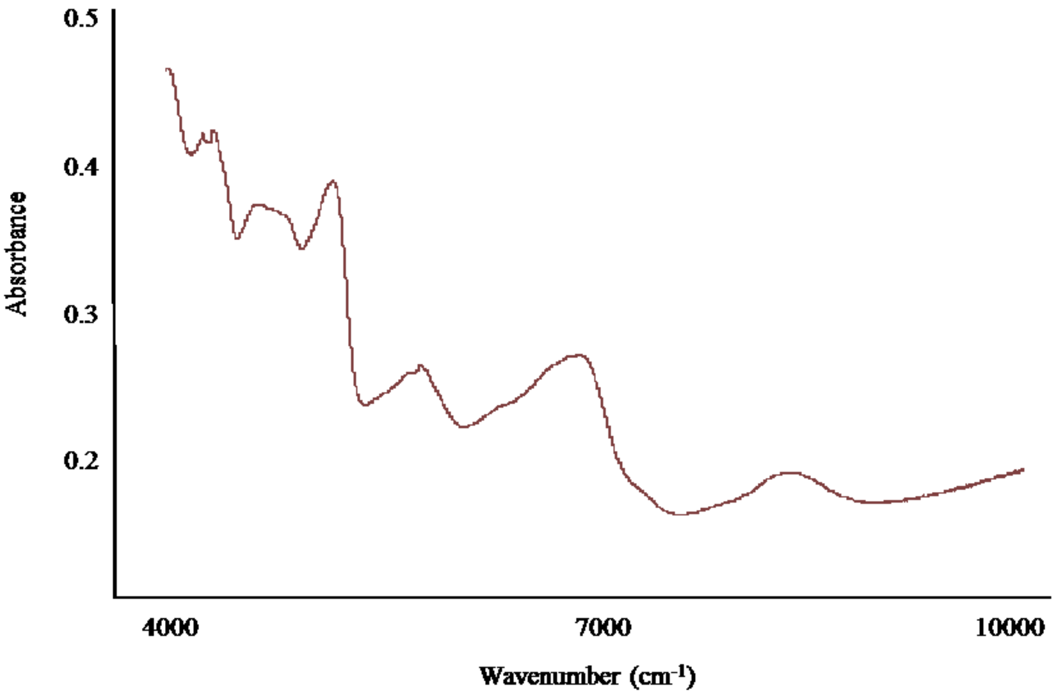

Figure 4.1. Representative NIRS spectrum of *Adansonia digitata* mature leaves

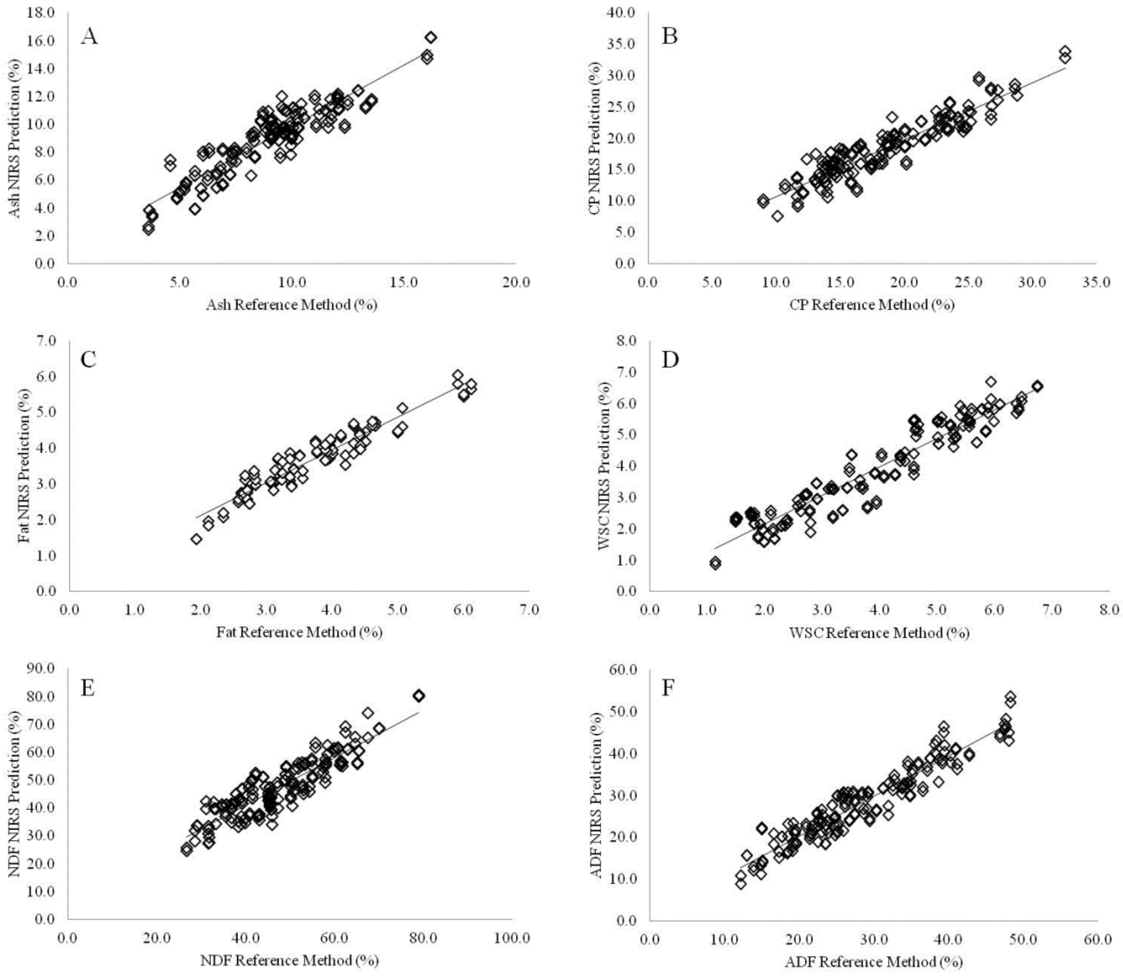

Figure 4.2. Cross validated (leave-one-out) partial least squares regression plots for ash, crude protein, fat, WSC, NDF, and ADF content in leaves from the Diani Forest, Kenya. Second derivatives spectral transformations were used for multivariate analyses.

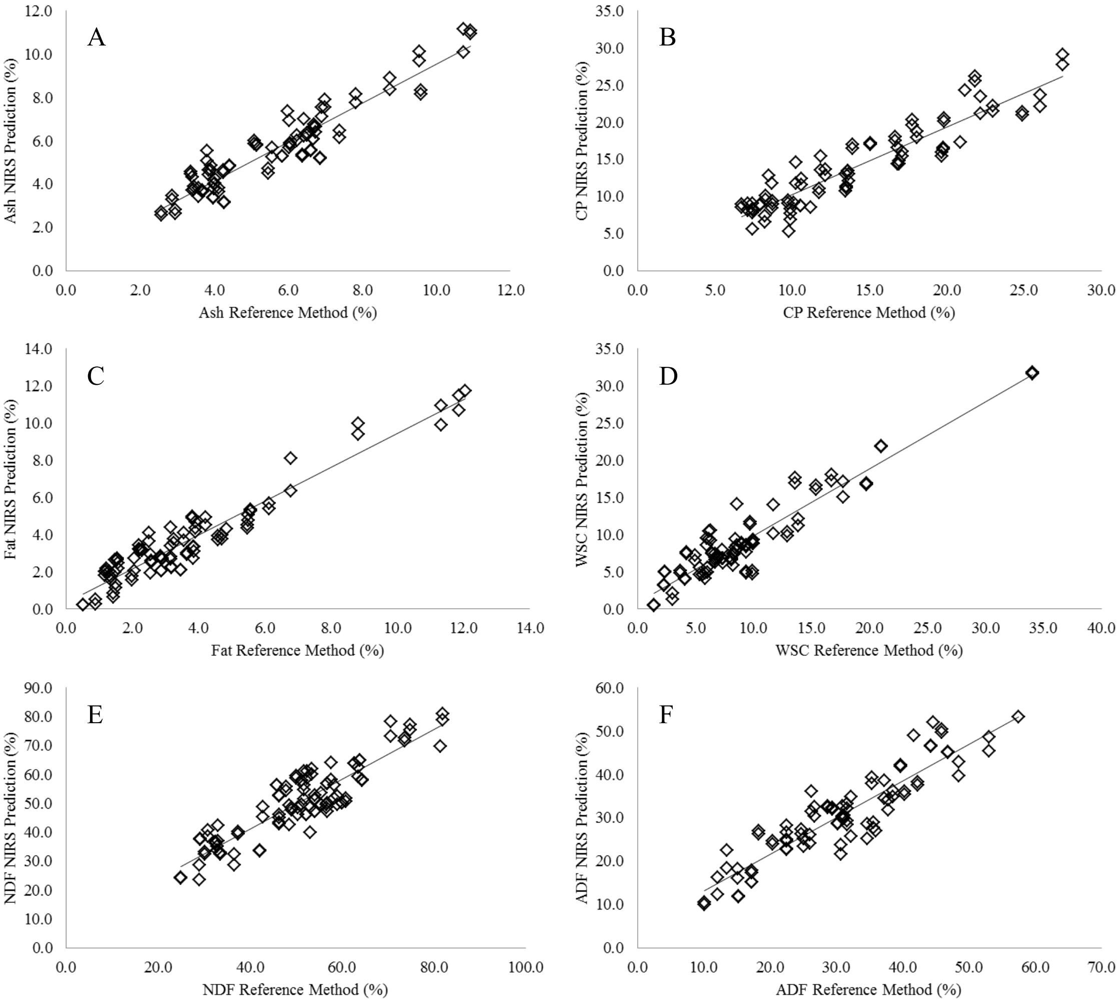

Figure 4.3. Cross validated (leave-one-out) partial least squares regression plots for ash, crude protein, fat, WSC, NDF, and ADF content in fruits and flowers from the Diani Forest, Kenya. Second derivatives spectral transformations were used for multivariate analyses.

CHAPTER 5: FOOD SELECTION IN RELATION TO NUTRITIONAL INTAKE STRATEGIES AND NUTRITIONAL BALANCING

INTRODUCTION

Primate dietary selection is typically examined in relation to energy maximization, protein maximization, fiber limitation, or plant secondary metabolite (PSM) minimization (Felton et al. 2009a). For colobine monkeys, food selection is usually discussed in relation to the latter three models due to the high concentrations of protein, fiber, and PSMs in leaves which often constitute a significant proportion of the diet for many populations. Several studies have shown that colobine monkey leaf selection positively correlates with protein content (Davies et al. 1988; Mowry et al. 1996; Koenig et al. 1998; Waterman et al. 1988; Yeager et al. 1997); however, many other studies did not find a positive relationship between protein content and leaf selection (Chapman et al. 2002; Dasilva 1994; Kool 1992; McKey et al. 1981; Oates et al. 1980; Waterman et al. 1988). Similarly, several studies have documented that colobine monkeys select leaves with low fiber content or high protein to fiber ratios (Davies et al. 1988; Waterman et al. 1988; Mowry et al. 1996; Chapman and Chapman 2002; Chapman et al. 2004; Fashing et al. 2007a), but these trends do not apply to all colobine species and populations (Ganzhorn et al. 2016). In addition to protein and fiber, researchers have examined the influence of plant PSMs on food selection. PSMs are a broad class of compounds that act as chemical defenses against insects and herbivores (Glander 1982; Burgess and Chapman 2005). While there are thought to be hundreds of thousands of unique PSMs, they are often grouped into large categories based on chemical structure including: tannins, lignins, saponins, and cyanogenic glycosides (Freeland and Janzen 1974; Glander 1982). PSMs are sometimes inversely related to food selection (Oates et al. 1980; Dasilva 1994; Fashing et al. 2007a) and in other cases appear to have no effect on food selection in colobines (Bocian 1997; Maisels et al. 1994; Mowry et al. 1996; Chapman and Chapman 2002).

While protein maximization, fiber limitation, and PSM minimization models explain dietary selection for various species and populations, it is clear that none of these models provide a strong overarching theoretical framework since they cannot be applied universally. The Geometric Framework (GF) goes beyond explaining food selection based on a single macronutrient or food component and instead examines the interactive effects of multiple nutrients (Raubenheimer and Simpson 1993; Simpson and Raubenheimer 1993; Simpson and Raunbenheimer 2012). Under this theory, animals require sufficient amounts of particular nutrients, but rather than maximizing one nutrient in particular, food selection and dietary intake should achieve an optimal balance among nutrients. When individuals are constrained from obtaining a nutritionally balanced diet, they must cope by over-ingesting or under-ingesting some nutrients. First developed and applied in laboratory studies of insects, the GF has demonstrated that 1) individuals do regulate to a nutritional intake target, 2) maintaining a target yields fitness benefits, and

3) individuals adopt different strategies to mitigate the deleterious effects of nutritional imbalance (i.e., “rules of compromise”) (Simpson and Raubenheimer 2012, p. 17).

The GF has since been applied to a variety of free-ranging animals including several primate species (Felton et al. 2009b, c; Rothman et al. 2011; Johnson et al. 2013, 2015; Irwin et al. 2015). From these studies it is clear that primate species balance their intake of non-protein energy (i.e., carbohydrate and fat) (NPE) and protein energy (AP-available protein) at different ratios. For example, sifakas maintained a NPE to PE ratio of approximately 9.5:1, spider monkeys- 8:1, a single female chacma baboon- 5:1, howler monkeys between 5.5:1 and 4:1 (NPE content includes digestible fiber), and mountain gorillas between 3:1 and 2:1 (Felton et al. 2009b, c; Rothman et al. 2011; Johnson et al. 2013; Righini 2014; Irwin et al. 2015). These ratios of NPE to AP differ among species in relation to species’ unique basal metabolic requirements and digestive physiology. Additionally, these studies have demonstrated that primate species utilize different rules of compromise to cope with nutritional imbalance. In order to achieve a threshold protein intake, spider monkeys were found to overeat fats and carbohydrates—a pattern very similar to that of protein leveraging in modern humans (Felton et al. 2009b; Gosby et al. 2011; Martinez-Cordero et al. 2012; Simpson et al. 2003; Simpson and Raubenheimer 2005). Mountain gorillas demonstrated the opposite pattern by prioritizing NPE and overconsuming PE, particularly during months when fruit availability was low (Rothman et al. 2011).

According to the the GF, tightly regulating nutritional intake ratios of NPE to AP is thought to be an adaptive strategy; however, the exent to which nutritional intake targets vary intraspecifically remains largely unstudied. This study examines dietary selection of three groups of Angola black and white colobus monkeys inhabiting structurally distinct forest areas and characterized by diets that differ dramatically with regard to species-specific plant parts (Chapter 2). The primary aims of this study are to first assess colobus food selection in relation to more conventional nutritrional models. Following conventional nutronal models, I predict individuals from the three study groups will select foods that maximize protein intake, limit fiber intake, and maximize protein to fiber intake ratios. Second, I apply the GF to analyze dietary intake and nutrient balancing among the three colobus groups. Based on the premises of the GF, I predict that individuals from the three groups will balance their intake of NPE to AP to a common target.

METHODS

Study Site and Study Species

This study was conducted in the coral rag Diani Forest of southeastern Kenya. Measuring approximately 4.6 km^2, the forest is characterized by patches of intact forest interspersed with highly degraded areas (Anderson et al. 2007; Dunham 2015; Dunham and McGraw 2014). There are two rainy seasons: October – December and March – June. Annual rainfall during this study was 1550 mm; however, this was markedly higher than the mean annual rainfall of 744 mm over a seven year period (Mwamachi et al. 1995).

Colobus angolensis typically live in small groups (i.e., ~2 – 20 members) throughout most of their ranges in eastern and central Africa. One subspecies, *C. a. ruwenzorii*, from Nyungwe, Rwanda, and Lake Nabugabo, Uganda, has been documented in groups of 200 – 300+ members (Bridgett et al. 2016; Fashing et al. 2007b; Fimbel et al. 2001). For this study, *C. a. palliatus* study group sizes ranged from 5 - 10 individuals. Group size and composition fluctuated during the study but all groups contained of one or two adult males, multiple adult females, and their offspring. The three study groups (i.e., Ujamaa, Ufalme, and Nyumbani) inhabited non-adjacent ranges, with several colobus groups ranging between the three study group ranges. The first group, Ujamaa, inhabited one of the most intact sections of the Diani Forest that is dominated by indigenous trees. Ufalme inhabited a more degraded forest area. Lastly, Nyumbani ranged through another degraded forest area dominated by exotic *Azadirachta indica* trees. See Chapter 2 for more extensive description of the study site and study species.

Behavioral Methods

With the help of a trained field assistant (Paul Opere), behavioral data were collected on individuals from Ujamaa, Ufalme, and Nyumbani groups (n = 267 full day follows). Behavioral data were recorded on Ujamaa and Ufalme from July 2014 - December 2015 and on Nyumbani from January - December 2015. Groups were followed on a weekly rotational basis such that each group was followed for 5 - 7 days per month. Activity budget and feeding data, including plant species and part consumed (i.e., young leaves, mature leaves, unripe fruit, ripe fruit, flower/ flower buds, and other), during 5 minute group scans at 15 minute intervals. I recorded each individual's behavior (i.e., resting, moving, feeding, socializing, other) instantaneously before rotating to another group member. A scan was completed after a maximum of 5 minutes or after the behavior of all individuals was recorded. Individuals were easily identified by a combination of facial features and tail morphology. Only data for adult males and adult females are included in these analyses.

Feeding data were also collected opportunistically on individuals during 5-minute focal follows. Data collection was initiated after a particular individual had been actively foraging for at least one minute. During these focal follows, the number of food items of a given plant species introduced to the oral cavity was counted (Nakagawa 2009). Ingestion rates (n = 800) were then calculated by multiplying the number of food items consumed during a focal period by the average weight of a given plant species food item (n = 20 - 30 samples weighed per food item) measured with a portable balance (Nakagawa 2009). Depending on the size and nature of the plant part, a food item could be defined as a single leaf, strand of leaves, cluster of flower buds, whole fruit, etc. A handheld rotary counter was used to record ingestion events.

Estimates of daily nutritional intake were then calculated by combining 1) data on time spent feeding on a given plant part (i.e., captured during behavioral scans), 2) the intake rate associated with a given plant part (i.e., captured during individual focal follows), and 3) the mean nutritional composition of the food item (Rothman et al. 2012). While all day focal follows of a single individual likely provide more accurate estimates of nutritional intake, it was not possible to maintain constant visibility of an individual, particularly when they occupied high and thick canopy positions. Only days in which individuals were accounted for on at least 80% of behavioral scans were included in the analysis. This reduces the likelihood of underestimating nutritional intake as individuals may have been foraging while out of sight. After excluding these cases, a total of 773 individual estimates of daily nutritional intake were used for analyses.

Nutritional Analyses

Samples (n = 382) of young leaves, mature leaves, unripe fruit, ripe fruit, and flowers were collected from the Diani Forest, Kenya, from June - July 2014 and from January - November 2015. Samples were dried in the field using an Excalibur food dehydrator to prevent molding. Upon returning to the laboratory in Columbus, OH, USA, samples were dried again in a vacuum oven at 105°C for 8 hours to remove residual moisture. Samples were then homogenized using a commercial blender and sieved through a 1 mm mesh.

Samples were analyzed in duplicate using wet chemistry reference methods and near-infrared spectral models (see Chapter 4 for more information on predictive equations). Ash content was quantified by heating samples at 600°C for 4 hours. Total nitrogen content was calculated via Dumas combustion. Crude protein was then calculated by multiplying total nitrogen by a factor of 6.25 (Maynard and Loosli 1969). Fat was quantified using a modified Bligh-Dyer (Bligh and Dyer 1959) technique (see Chapter 4). Water soluble carbohydrate (WSC) concentrations were calculated using the phenol–sulfuric acid method (Dubois et al. 1956; BeMiller and Low 2010) with modifications to accommodate WSC quantification from solid substances (Dunham et al. 2015). Finally, neutral detergent fiber (NDF), acid detergent fiber (ADF), and fiber bound protein were analyzed sequentially following Van Soest et al. (1991). Available protein was calculated by subtracting fiber bound protein from crude protein content. Total nonstructural carbohydrate (TNC) was calculated via subtraction: TNC = 100 – (ash + AP + fat + NDF) (Irwin et al. 2015). Nutritional compositions for all samples appear in Appendix B.

Statistical Analyses

In order to test whether colobus monkeys were selecting leaves with 1) higher protein content, 2) lower fiber content, and/or 3) higher protein to fiber ratios, the nutritional composition of commonly consumed leaves (i.e., leaves comprising at least 1% of a group's diet) was compared to that of the 20 most abundant young and mature leaf species (for which nutritional composition data are available) in each group's home range (i.e., excluding those that constitute at least 1% of the group's diet). Nonparametric Mann Whitney *U* tests were used to compare AP concentration, ADF concentration, NDF concentration, and protein to fiber ratios (i.e., CP:ADF) of commonly consumed leaves to those of abundant leaves not consumed.

The GF was used to plot the daily intake of macronutrients with each axis representing a different nutrient. Patterns of nutrient prioritization and nutrient balancing were determined by plotting NPE in relation to AP. Linear regression and coefficient of determination (R^2) with line of best fit forced through the origin was used to calculate the nutritional rail (i.e., the line representing the ratio of NPE to AP consumed) for each group and the strength of the correlation. The slope of these nutritional rails is equal to the ratio of NPE to AP consumed. Coefficient of variation (CV) was calculated for NPE and AP. CV values closer to zero indicate that a particular nutrient is more constrained or tightly regulated. Right-angled mixture triangles (RMTs) were used to plot and analyze the relative daily energy contribution of AP, TNC, fat, and digestible fiber (Raubenheimer 2011; Raubenheimer et al. 2015; Johnson et al. 2015). Linear regression and coefficient of determination were used to assess the extent to which the daily intake of individual macronutrients (i.e., on the implicit (I) axis) was regulated. Regression lines with R^2 closer to one indicate a strict regulation of the macronutrient on the I-axis.

RESULTS

Comparisons of nutritional contents among commonly consumed leaves and abundant leaves not consumed differed among study groups (Tables 5.1 – 5.3). The leaves commonly consumed by individuals of the Ujamaa group had significantly lower ADF content ($p = 0.002$) and significantly greater protein to fiber ratios ($p = 0.017$) compared to abundant leaves not consumed. AP and NDF contents did not differ significantly. For the Ufalme group, there were no significant differences for AP, ADF, NDF, or protein to fiber ratios. Lastly, leaves consumed by individuals of the Nyumbani group had a significantly lower ADF content ($p = 0.003$) than abundant leaves not consumed. None of the other comparisons were significant.

The mean daily energy take was 525.1 ± 184.9 kcal for all individuals. Of this total metabolizable energy, AP constituted 22.4 ± 5.0% , fat made up 12.5 ± 2.1%, TNC comprised 36.0 ± 6.3%, and digestible fiber amounted to 29.1 ± 4.4% for all individuals. Table 5.4 shows the intake values for males and females from the different study groups.

Using Kruskal-Wallis tests, adult female daily intakes differed significantly among study groups with regard to total kcal, NPE kcal, fat kcal, TNC kcal, digestible fiber kcal, and NPE:AP ($p < 0.001$ for all tests) (Table 5.5). Only AP kcal did not differ significantly among females of different groups. Ujamaa females consumed more total kcal than females from the other two groups ($p < 0.001$ for both comparisons). Ufalme females consumed less NPE kcal than Ujamaa females ($p < 0.001$) and Nyumbani females ($p = 0.005$). Ujamaa females took in more fat kcal than Ufalme females ($p < 0.001$) and Nyumbani females ($p = 0.013$). Nyumbani females consumed less TNC kcal than females from the other two groups ($p < 0.001$ for both comparisons). Ujamaa females took in more digestible fiber kcal than females from the other two groups ($p < 0.001$ for both comparisons). Finally, Nyumbani females had a significantly lower NPE to AP ratio compared to females from the two groups ($p < 0.001$ for both comparisons).

Adult male daily intakes differed significantly among study groups with regard to AP kcal ($p < 0.001$), fat kcal ($p < 0.001$), digestible fiber kcal ($p = 0.002$), and NPE:AP ($p < 0.001$) (Table 5.6). Total kcal, NPE kcal, and TNC kcal did not differ significantly among groups. The Ufalme male consumed less AP kcal than the males from Ujamaa ($p = 0.007$) and Nyumbani ($p < 0.001$). The same relationships were found for fat kcal ($p < 0.001$ for both comparisons). The Ufalme male also took in less digestible fiber kcal than the Nyumbani male ($p = 0.001$). With regard to NPE:AP, the Nyumbani male had a significantly lower ratio than males from the other groups ($p < 0.001$ for both comparisons), and the Ufalme male had a significantly greater ratio compared to the Ujamaa male ($p = 0.011$).

Males and females belonging to the same study group did not differ significantly in their ratio of NPE to AP consumed. Thus, NPE to AP results are plotted as three figures—one for each study group. Individuals from the Ujamaa group maintained a balance of NPE to AP ratio of 2.2:1 ($R^2 = 0.44$) (Figure 5.1). Individuals from the Ufalme group had a NPE to AP ratio of 2.1:1 ($R^2 = 0.17$) (Figure 5.2). Finally, individuals from the Nyumbani group consumed NPE to AP at a ratio of 1.7:1 ($R^2 = 0.27$) (Figure 5.3). CV for AP kcal was 33.4% for Ujamaa, 45.5% for Ufalme, and 42.0 for Nyumbani. For NPE kcal, CV was 35.1% for Ujamaa, 33.3% for Ufalme, and 36.3% for Nyumbani.

Right-angled mixture triangles depict the relative contribution of AP, fat, TNC, and digestible fiber to total metabolizable energy. In all three groups, fat kcal was the most tightly regulated nutritional component. Individuals from the Ujamaa group (Figure 5.4) showed a consistent contribution from AP kcal while individuals from the Ufalme (Figure 5.5) and Nyumbani (Figure 5.6) groups displayed more consistent contributions from digestible fiber kcal.

DISCUSSION

This study 1) assessed the extent to which conventional food selection models could be used to explain dietary selection and 2) utilized the GF to examine the interactive effects of macronutrients to identify intake targets and rules of compromise for three groups of Angola black and white colobus monkeys inhabiting structurally distinct forest areas. Commonly consumed leaves had lower ADF content than abundant leaves not consumed for two of the three groups, and commonly consumed leaves had greater protein to fiber ratios than those of abundant leaves not consumed for one out of the three groups. Thus, protein maximization, fiber limitation, and protein to fiber maximization models failed to explain food selection in all three study groups. Despite dramatic differences in diets in terms of species-specific plant parts (Chapter 2) and significant differences in the quantities of various macronutrients consumed per day, NPE to AP ratios were largely consistent among individuals of different groups. Furthermore, rather than prioritizing AP over NPE or vice versa, *C. a. palliatus* maintained a consistent balance of NPE to AP.

Protein maximization, fiber limitation, and protein to fiber maximization models have been used to explain dietary selection in several colobine monkey populations (Davies et al. 1988; Mowry et al. 1996; Koenig et al. 1998; Waterman et al. 1988; Yeager et al. 1997; Chapman and Chapman 2002; Chapman et al. 2004; Fashing et al. 2007a); however, these trends do not hold for all colobine monkey populations (Ganzhorn et al. 2016). In this study, there were a few significant differences in the nutritional composition of leaves commonly consumed compared to abundant leaves not consumed. That is, individuals from the Ujamaa group selected leaves with lower ADF content and greater protein to fiber ratios. Individuals from the Nyumbani group also selected leaves with lower ADF content compared to abundant leaves not consumed. The fact that commonly consumed leaves did not contain greater protein content, lower fiber content, and greater protein to fiber ratios (compared to abundant leaves not consumed) for all three study groups further demonstrates that these models cannot be applied universally to explain food selection in colobine monkeys. In their recent meta-analysis, Ganzhorn and colleagues (2016) found that these models typically only explained food selection in colobines and other folivorous primates inhabiting forests with low quality foliage. In forests with high quality foliage, there was often no difference in protein and fiber content of leaves consumed vs. those not consumed (Ganzhorn et al. 2016). Protein to fiber ratios of the most abundant mature leaves at a site are often used as a measure of overall leaf quality. Larger protein to fiber ratios are consistent with better leaf quality and greater colobine biomass (Chapman et al. 2002, 2004; Fashing et al. 2007a; Oates et al. 1990). Preliminary results suggest that, among mature leaves from the 20 most abundant tree species in each of the Diani study groups' home ranges, protein to fiber ratios averaged 0.595—a ratio greater than most published values from other sites (Chapman et al. 2002; Dunham unpublished data; Fashing et al. 2007a; Oates et al. 1990). Therefore, it is likely protein maximization and fiber limitation food selection models do not apply to all of the study groups because many of the abundant species not consumed by *C. a. palliatus* have protein and fiber contents not significantly different from those of leaves that are regularly consumed.

Individuals from different groups differed significantly in their intake of several macronutrients. Among groups, adult females differed significantly in their daily intake of total kcal, NPE kcal, fat kcal, TNC kcal, and digestible fiber kcal. Most of these discrepancies were explained by Ujamaa females consuming more total kcal, fat kcal, TNC kcal, and NPE kcal than individuals from one or both of the other study groups. Adult males also differed significantly in their daily intake of several nutrients. Many of these differences were attributed to the Ufalme male consuming less AP kcal, fat kcal, and digestible fiber kcal than the Ujamaa and/or Nyumbani male. Because data were only available for one adult male per group (i.e., all three groups were unimale for the majority of the study period), it was difficult to determine the extent to which differences in daily macronutrient intake were related to differences in habitat.

Despite these differences in the quantity of various nutrients consumed on a daily basis among both females and males of different groups, ratios of NPE to AP were generally more consistent. Arriving at this nutritional target can be achieved by consistently consuming foods whose nutritional composition is close to or equal to that of the target or by consuming foods with complementary nutritional compositions that balance out to the nutritional target (Behmer and Joern 2008) (Figure 5.7). Combining data on females and males within a group, individuals from the Ujamaa and Ufalme groups were similar with NPE to AP ratio of 2.2 to 1 and 2.1 to 1, respectively. Individuals from the Nyumbani group had a lower NPE to AP ratio of 1.7 to 1. It is possible that the Nyumbani group, which inhabited a highly degraded portion of the Diani Forest, altered their nutritional intake resulting in a lower NPE to AP ratio. On the other hand, it is possible that this statistically significant difference in NPE to AP ratios is not biologically significant. Mountain gorillas were found to vary their intake of NPE to AP from 3 to 1 during seasons when fruit was readily available down to 2 to 1 when fruit was not available (Rothman et al. 2011). Thus, despite significant intergroup dietary differences with regard to species-specific plant part (Chapter 2), it is likely that *C. a. palliatus* individuals are flexible enough to cope with this degree of intake variation. Long-term studies are required to determine the degree to which changes in NPE to AP ratios negatively impact fitness (Lee et al. 2008).

Coefficients of variation were used to determine whether NPE or AP was more tightly regulated vs. which was eaten in excess when individuals were constrained from reaching their intake target. CV ranged from 33.4 – 45.5% for AP kcal and from 33.3 – 36.3% for NPE kcal. Thus, neither AP kcal nor NPE kcal was substantially more tightly regulated. Instead, the daily intake of AP kcal and NPE varied to similar degrees and individuals from all groups tended to maintain a balanced intake of NPE to AP. This strategy differs from the strict protein regulation characteristic of spider monkeys as well as the NPE prioritization documented in mountain gorillas (Felton et al. 2009b; Rothman et al. 2011). Maintaining a relatively balanced intake of NPE to AP is a strategy that has been shown in a female chacma baboon over a 30 day period, in howler monkeys, and in diademed sifakas which reduced the quantity of total kcal consumed during the lean season but maintained a balanced ratio of NPE to AP across all seasons (Johnson et al. 2013; Righini 2014; Irwin et al. 2015).

RMTs were also used to assess the relative contributions of AP, fat, TNC, and digestible fiber to daily energy intake. Fat was the most tightly regulated macronutrient for all groups (R^2 = 0.77 – 0.93), but also contributed the smallest proportion of total daily energy intake of all macronutrients (i.e., 11.7 – 13.4% of total daily kcal). Even though fat comprised a relatively smaller proportion of daily caloric intake, this tight regulation suggests maintaining a consistent intake may be important (Righini et al. 2015). Individuals from the Ujamaa group also showed a consistent contribution from AP ($R^2 = 0.55$) while individuals from the Ufalme and Nyumbani groups displayed consistent contributions from digestible fiber kcal ($R^2 = 0.66$ for both groups). The TNC contribution was the least regulated of all macronutrients for all three groups ($R^2 = 0.00 – 0.22$).

Despite the fact that AP intake was not tightly regulated among individuals of all groups, protein is often thought to be a limiting resource for folivores and herbivores (Milton 1979; White 1993). The mean protein to fiber ratio of mature leaves from the most abundant trees in a forest is a strong predictor of colobine biomass (Waterman et al. 1988; Oates et al. 1990; Chapman et al. 2002, 2004; Fashing et al. 2007a). It has been recommended that protein should comprise at least 4.0% - 7.5% of the daily total metabolizable energy or 15% - 22% of the daily dry matter intake for adult nonhuman primates (Oftedal 1991; NRC 2003). During the study period, AP constituted a mean of 22.4% of the total metabolizable energy and 16.2% of the dry matter intake. Thus, it seems *C. a. palliatus* received more than sufficient quantities of protein. In fact, colobus monkeys may over consume protein and excrete the excess, as do mountain gorillas (Rothman et al. 2011).

As researchers continue to utilize the GF for examining nonhuman primate intake targets and rules of compromise it is becoming possible to make interesting interspecific comparisons. For instance, it is clear that more frugivorous primates such as orangutans, sifakas, and spider monkeys have greater NPE to AP ratios due to their consumption of carbohydrate-rich and fat-rich foods (Felton et al. 2009b; Irwin et al. 2015; Vogel et al. 2016). On the other hand, more folivorous primates such as mountain gorillas, guerezas, and now *C. a. palliatus* display lower NPE to AP ratios due their frequent consumption of protein-rich leaves (Rothman et al. 2011; Johnson et al. 2015). Data from additional species will allow researchers to test whether intake targets are more tightly constrained by phylogeny (as the data from this study suggests) or are relatively flexible to local ecological conditions.

Conventional models of food selection (i.e., protein maximization, fiber limitation, and protein to fiber maximization) did not consistently explain food selection in three groups of *C. a. palliatus*. Daily intake of NPE to AP ratios were largely consistent among individuals of different groups despite significant differences in the quantities of various macronutrients consumed per day and dramatic differences in species-specific plant parts consumed among individuals of different groups. Individuals maintained a relatively balanced intake of NPE to AP rather than prioritizing AP or NPE more strictly.

Table 5.1. Nutritional comparison of leaves commonly consumed vs. not consumed by Ujamaa group. Values reported as mean % of dry weight with standard deviation in parentheses.

Leaf Type	N	AP	ADF	NDF	Protein:Fiber
Commonly Consumed	18	15.4 (3.22)	24.3 (7.65)	45.2 (8.88)	0.85 (0.388)
Not Consumed	21	16.1 (5.55)	32.5 (6.85)	48.4 (7.19)	0.59 (0.190)

AP = available protein; ADF = acid detergent fiver; NDF = neutral detergent fiber

Table 5.2. Nutritional comparison of leaves commonly consumed vs. not consumed by Ufalme group. Values reported as mean % of dry weight with standard deviation in parentheses.

Leaf Type	N	AP	ADF	NDF	Protein:Fiber
Commonly Consumed	17	15.9 (4.58)	24.2 (6.86)	48.0 (8.41)	0.87 (0.424)
Not Consumed	19	14.9 (5.66)	31.9 (8.00)	50.7 (8.78)	0.60 (0.246)

AP = available protein; ADF = acid detergent fiver; NDF = neutral detergent fiber

Table 5.3. Nutritional comparison of leaves commonly consumed vs. not consumed by Nyumbani group. Values reported as mean % of dry weight with standard deviation in parentheses.

Leaf Type	N	AP	ADF	NDF	Protein:Fiber
Commonly Consumed	19	13.6 (4.64)	23.6 (8.70)	46.9 (7.25)	0.81 (0.412)
Not Consumed	25	15.6 (5.57)	29.6 (5.82)	48.9 (8.14)	0.64 (0.190)

AP = available protein; ADF = acid detergent fiver; NDF = neutral detergent fiber

Table 5.4. Nutritional intake of adult females and adult males from different groups

	No. Individuals	kcal per day	% AP[1]	% Fat[1]	% TNC[1]	% Dig. Fiber[1]
Ujamaa Females	4	587.2 (202.2)	21.4 (4.0)	13.0 (2.1)	35.5 (6.4)	30.1 (5.3)
Ufalme Females	2	528.9 (172.4)	22.0 (4.9)	11.7 (1.4)	37.7 (5.7)	28.6 (3.3)
Nyumbani Females	2	502.5 (176.3)	25.1 (5.3)	13.4 (2.6)	33.4 (5.2)	28.1 (3.0)
Total Females	8	546.5 (188.8)	22.5 (4.8)	12.6 (2.1)	35.8 (6.1)	29.1 (4.2)
Ujamaa Male	1	501.8 (161.7)	21.9 (4.6)	13.2 (2.2)	34.4 (6.6)	30.6 (6.0)
Ufalme Male	1	439.3 (144.3)	20.8 (5.3)	11.2 (1.3)	40.3 (6.3)	27.8 (3.6)
Nyumbani Male	1	502.4 (173.6)	25.7 (5.0)	13.2 (2.2)	33.0 (4.6)	28.1 (3.3)
Total Males	3	478.7 (167.2)	22.4 (5.3)	12.4 (2.2)	36.2 (6.8)	28.9 (4.7)
Total All Individuals	11	525.1 (184.9)	22.4 (5.0)	12.5 (2.1)	36.0 (6.3)	29.1 (4.4)

[1] Reported as percentage of total kilocalories per day; kcal = kilocalories; AP = available protein; TNC = total nonstructural carbohydrate

Table 5.5. Comparison of daily intakes among adult females of the three study groups using Kruskal-Wallis Tests

Variable	*H*	p
Total kcal	16.99	< 0.001
AP kcal	5.76	NS
NPE kcal	20.89	< 0.001
Fat kcal	26.31	< 0.001
TNC kcal	27.89	< 0.001
Dig. Fiber kcal	25.32	< 0.001
NPE:AP	32.40	< 0.001

kcal = kilocalories; AP = available protein; NPE = non-protein energy; TNC = total nonstructural carbohydrate

Table 5.6. Comparison of daily intakes among adult males of the three study groups using Kruskal-Wallis Tests

Variable	*H*	p
Total kcal	7.70	NS
AP kcal	18.84	< 0.001
NPE kcal	0.98	NS
Fat kcal	29.76	< 0.001
TNC kcal	1.86	NS
Dig Fiber kcal	12.05	0.002
NPE:AP	31.14	< 0.001

kcal = kilocalories; AP = available protein; NPE = non-protein energy; TNC = total nonstructural carbohydrate

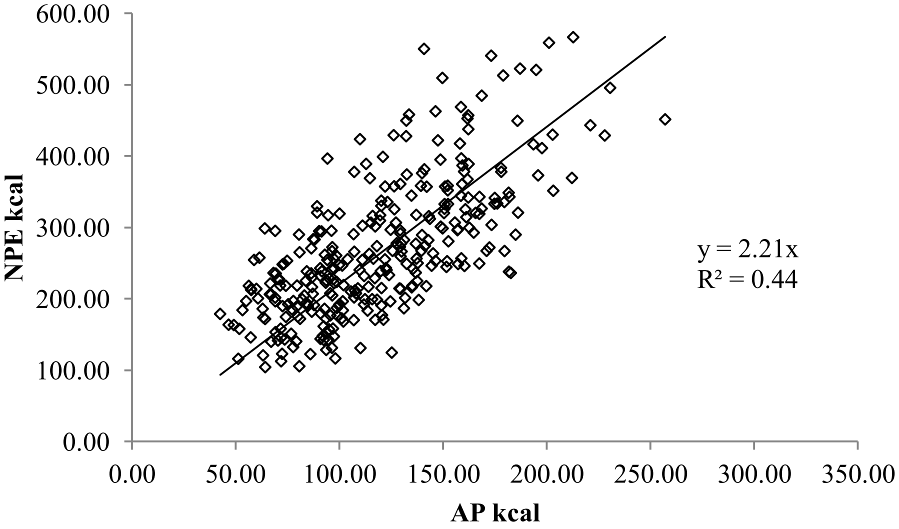

Figure 5.1. Daily intake of NPE vs. AP for all adults from the Ujamaa group

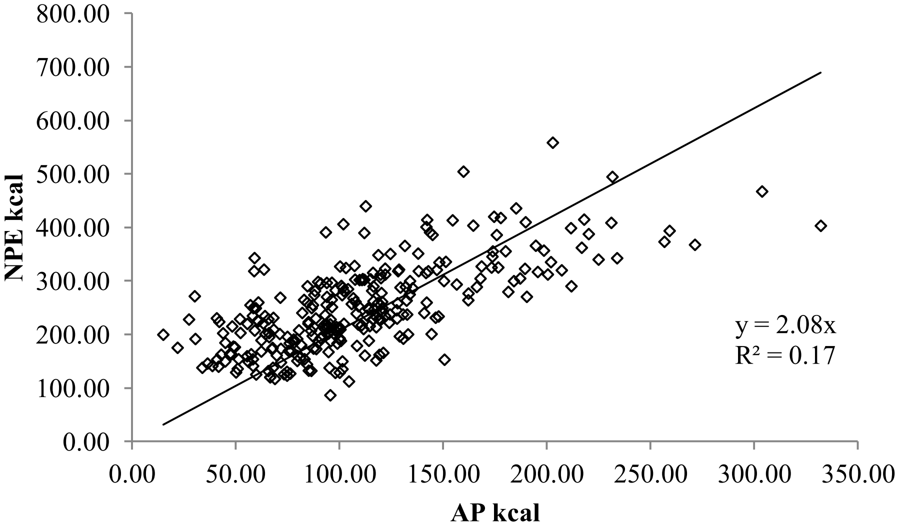

Figure 5.2. Daily intake of NPE vs. AP for all adults from the Ufalme group

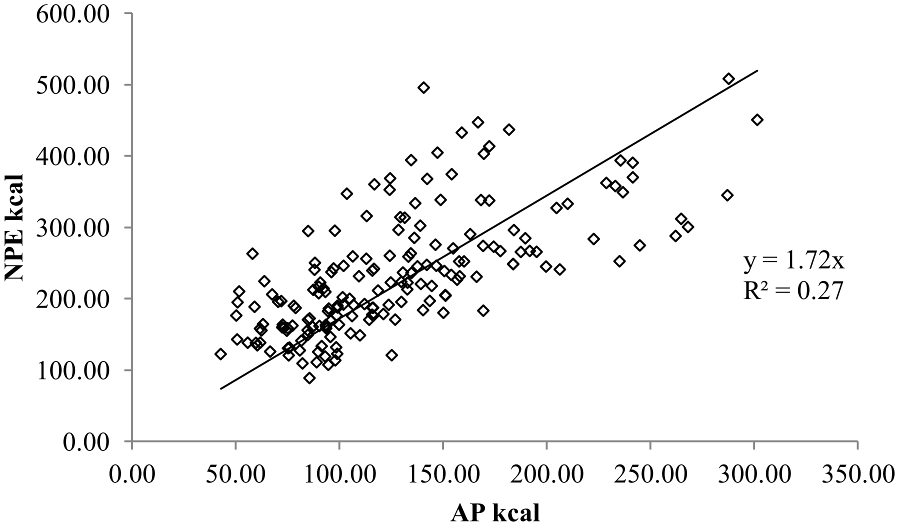

Figure 5.3. Daily intake of NPE vs. AP for all adults from the Nyumbani group

Figure 5.4. Right-angled mixture triangle (RMT) showing the relative contributions to daily total metabolizable energy (ME) for the Ujamaa group. **A:** Y-axis = %ME from NPE, X-axis = %ME from AP, I-axis = %ME from digestible fiber. Each point (diamond) represents a daily energy mixture intake that is equal to 100%. For example, the red triangle represents a daily intake with ME contributions of 48.5% NPE, 22.4% AP, and 29.1% dig. fiber. **B**: Y-axis = %ME from NPE, X-axis = %ME from dig. fiber, I-axis = %ME from AP. **C**: Y-axis = %ME from AP, X-axis = %ME from dig. Fiber + fat, I-axis = %ME from TNC. **D**: Y-axis = %ME from AP, X-axis = %ME from dig. Fiber + TNC, I-axis = %ME from fat. Regression equations with slope closer to one and with larger R^2 values indicate that the intake of the variable on the I-axis is more tightly regulated. Regression equations with slope closer to zero and with smaller R^2 values indicate that the intake of the variable on the I-axis is more variable.

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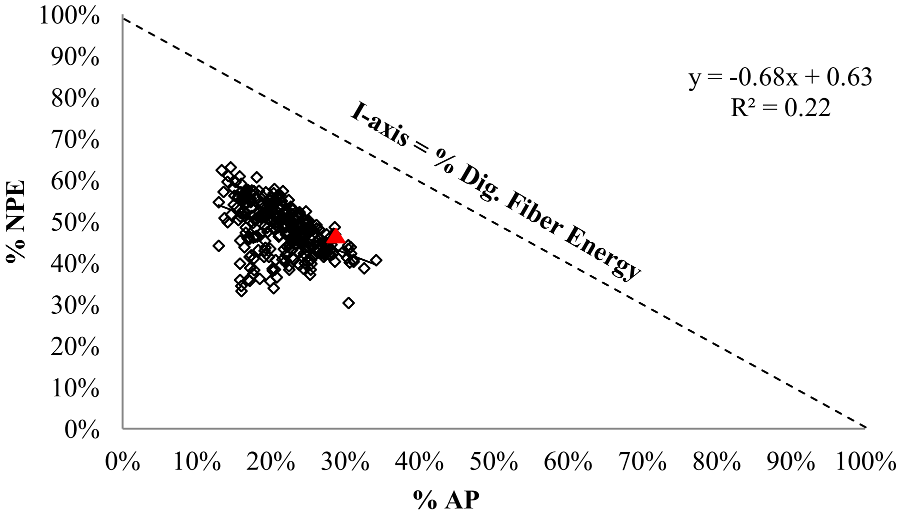
Figure 5.4 Continued



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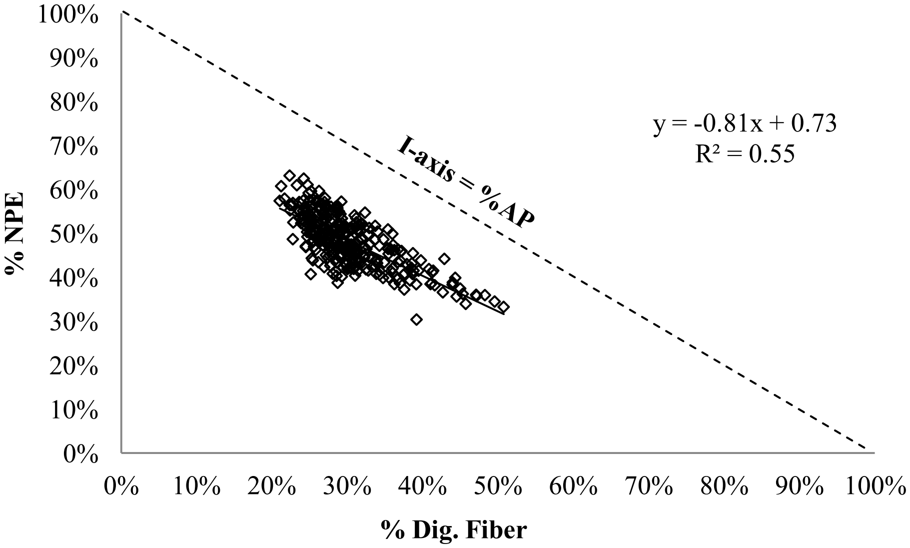

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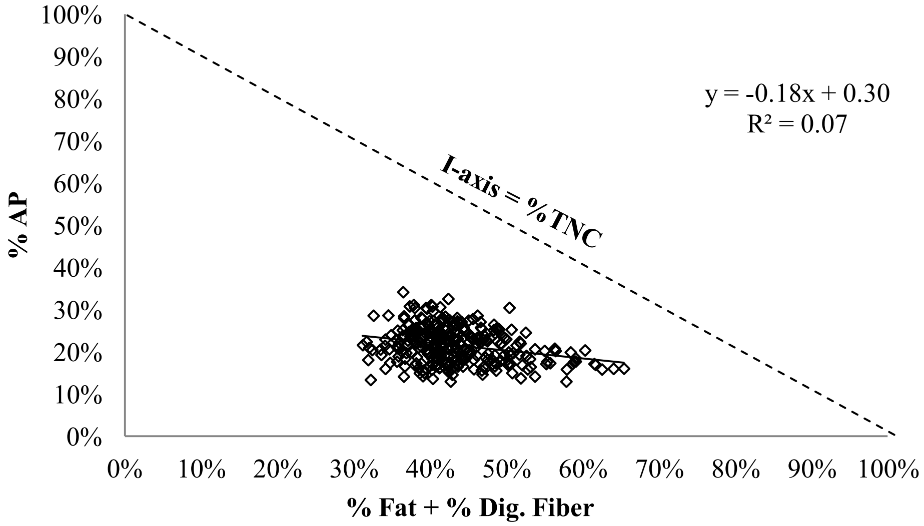
Figure 5.4 Continued



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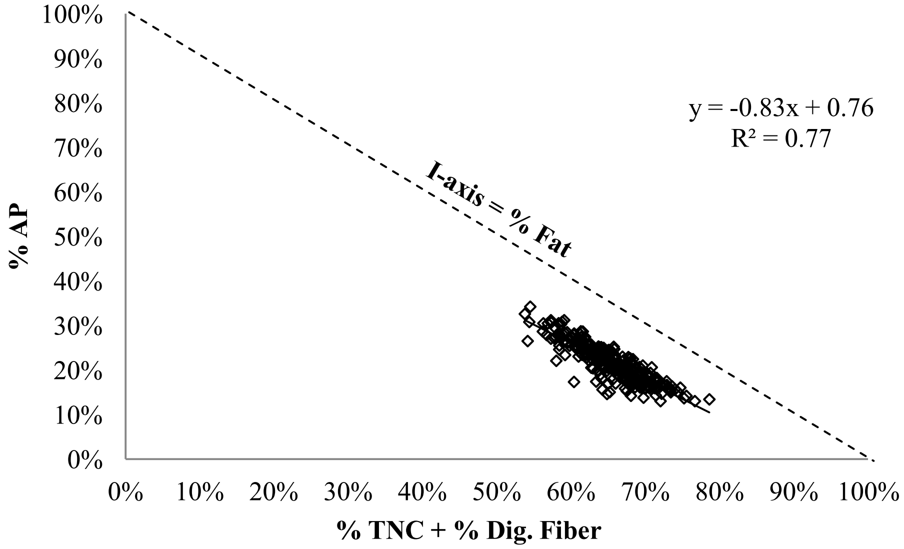

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Figure 5.5. Right-angled mixture triangle (RMT) showing the relative contributions to daily total metabolizable energy (ME) for the Ufalme group. **A:** Y-axis = %ME from NPE, X-axis = %ME from AP, I-axis = %ME from digestible fiber. Each point (diamond) represents a daily energy mixture intake that is equal to 100%. For example, the red triangle represents a daily intake with ME contributions of 48.5% NPE, 22.4% AP, and 29.1% dig. fiber. **B**: Y-axis = %ME from NPE, X-axis = %ME from dig. fiber, I-axis = %ME from AP. **C**: Y-axis = %ME from AP, X-axis = %ME from dig. Fiber + fat, I-axis = %ME from TNC. **D**: Y-axis = %ME from AP, X-axis = %ME from dig. Fiber + TNC, I-axis = %ME from fat. Regression equations with slope closer to one and with larger R^2 values indicate that the intake of the variable on the I-axis is more tightly regulated. Regression equations with slope closer to zero and with smaller R^2 values indicate that the intake of the variable on the I-axis is more variable.

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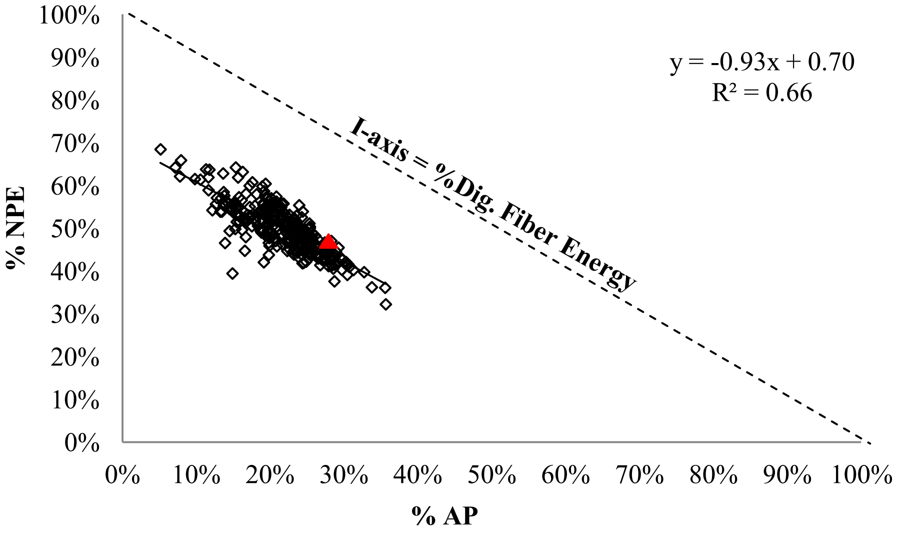
Figure 5.5 Continued



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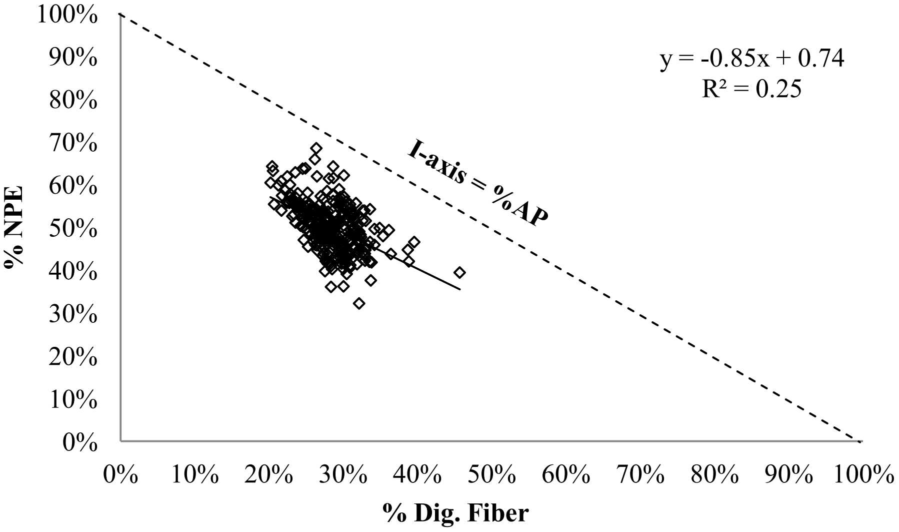

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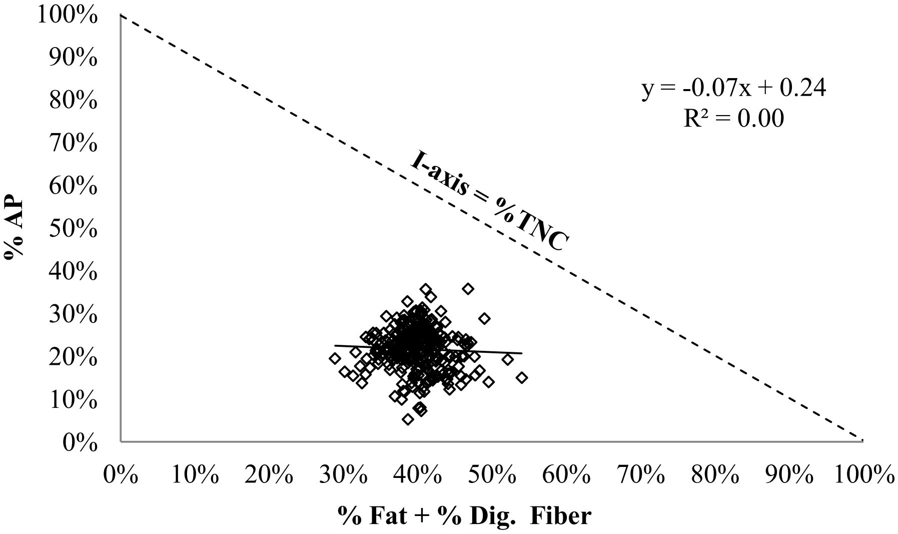

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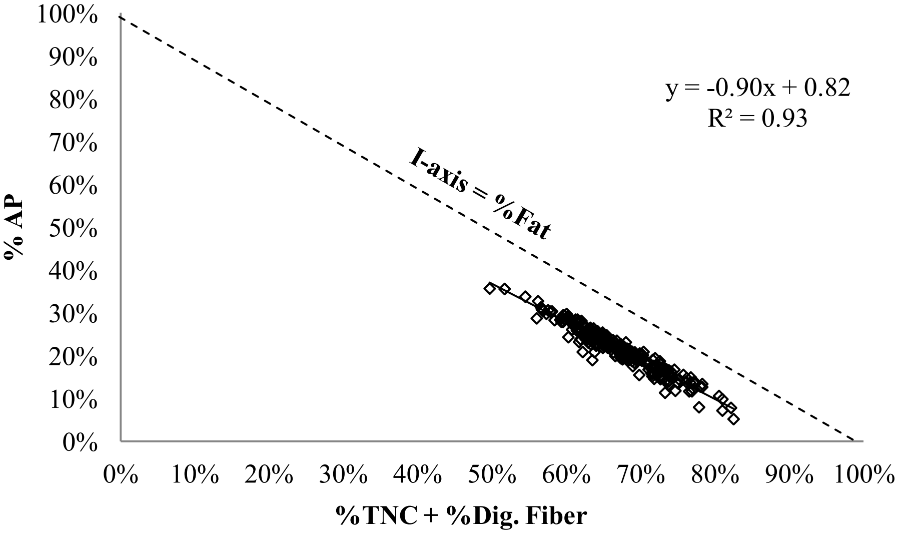

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Figure 5.6. Right-angled mixture triangle (RMT) showing the relative contributions to daily total metabolizable energy (ME) for the Nyumbani group. **A:** Y-axis = %ME from NPE, X-axis = %ME from AP, I-axis = %ME from digestible fiber. Each point (diamond) represents a daily energy mixture intake that is equal to 100%. For example, the red triangle represents a daily intake with ME contributions of 48.5% NPE, 22.4% AP, and 29.1% dig. fiber. **B**: Y-axis = %ME from NPE, X-axis = %ME from dig. fiber, I-axis = %ME from AP. **C**: Y-axis = %ME from AP, X-axis = %ME from dig. Fiber + fat, I-axis = %ME from TNC. **D**: Y-axis = %ME from AP, X-axis = %ME from dig. Fiber + TNC, I-axis = %ME from fat. Regression equations with slope closer to one and with larger R^2 values indicate that the intake of the variable on the I-axis is more tightly regulated. Regression equations with slope closer to zero and with smaller R^2 values indicate that the intake of the variable on the I-axis is more variable.

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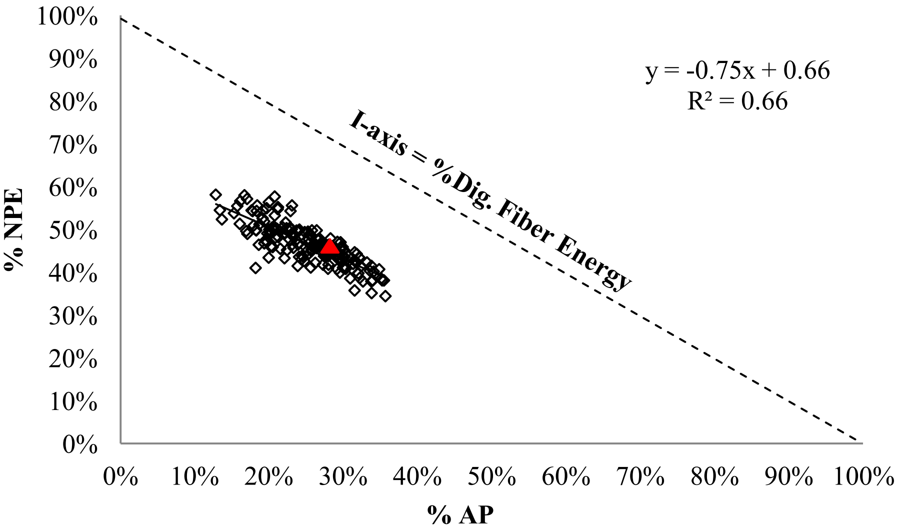
Figure 5.6 Continued



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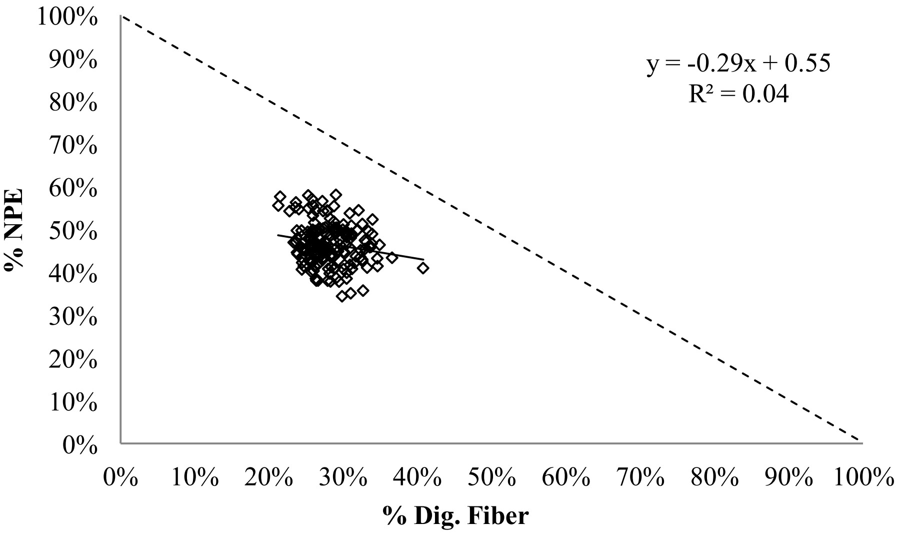

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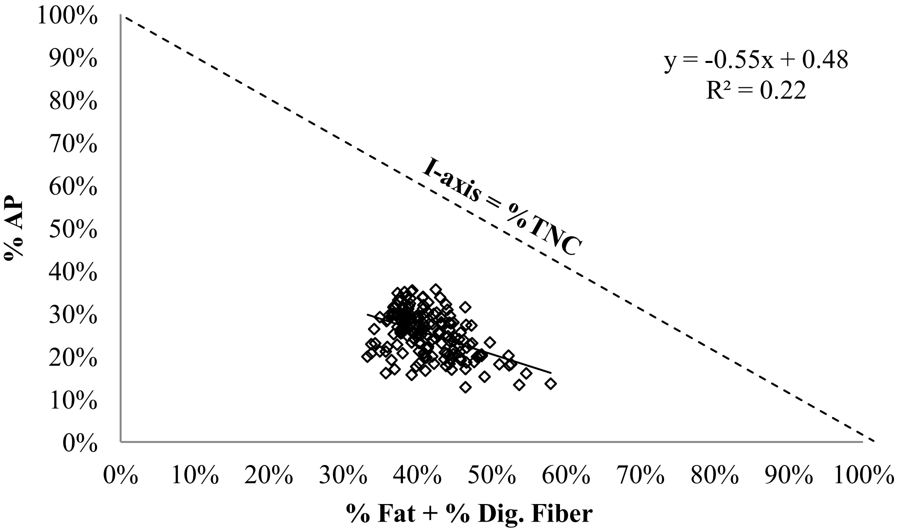

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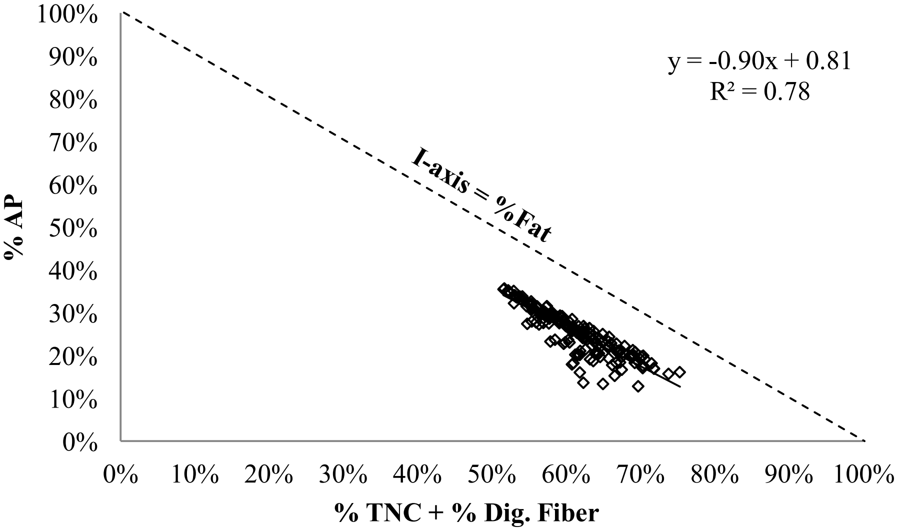

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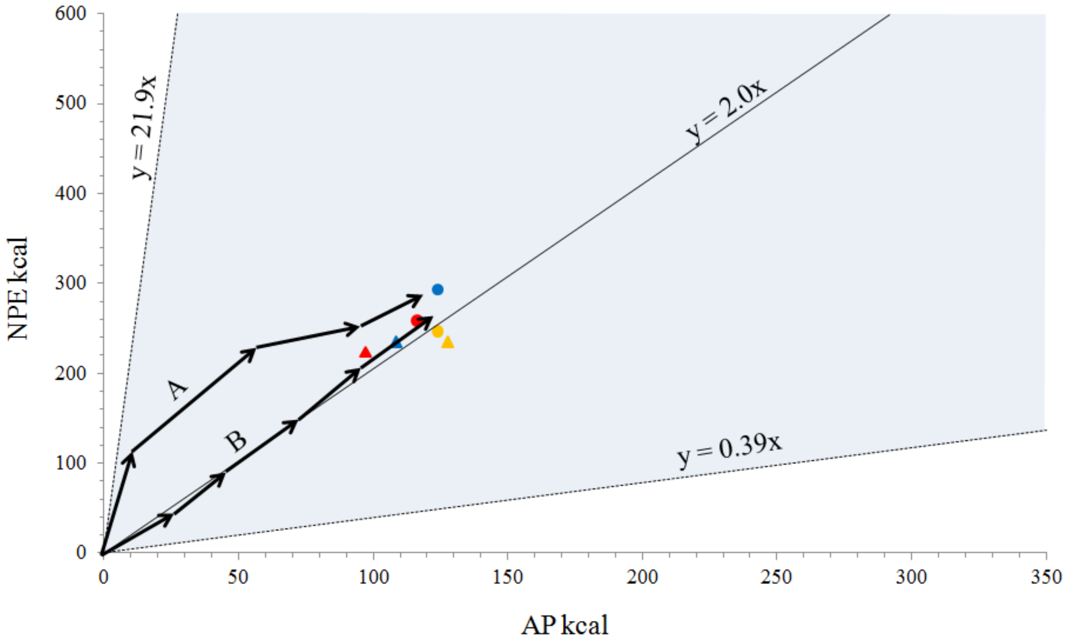

Figure 5.7. Different routes to achieving nutritional intake targets within nutritional space. Circles = adult female intakes, triangles = adult male intakes, blue = Ujamaa, red = Ufalme, orange = Nyumbani. Line with slope of 2.0 indicates the NPE to AP ratio for all individuals. Dotted line with slope of 21.9 represents the food consumed during study period with the largest NPE to AP ratio. Dotted line with the slope of 0.39 represents the food consumed during the study period with smallest NPE to AP ratio. Shaded area is equal to the nutritional space available to individuals during the study period. Arrowed lines represent different quantities of foods consumed characterized by a particular NPE to AP ratio. During the study period individuals consumed complimentary food items that balanced out to the intake target (A). Alternatively, individuals also reached their intake target by consuming foods that were inherently balanced at a ratio of approximately 2 NPE to 1 AP (B).

CHAPTER 6: MULTIVARIATE ANALYSIS OF LEAF SELECTION

INTRODUCTION

Researchers have long been interested in identifying characteristics that influence primate food selection (e.g., Milton 1979). Studies typically explain food selection in relation to availability, physical and mechanical properties, *or* nutritional composition of potential food items, but few studies simultaneously consider a combination of these variables and the interactions among these variables (see Leighton 1993).

Previous chapters examined the influence of spatial and temporal availability (Chapter 2), mechanical toughness (Chapter 3) and nutritional composition (Chapter 5) of potential food items on food selection among three groups of *Colobus angolensis palliatus*. In general, availability was not a strong predictor of food selection as groups did not select overall plant parts in proportion to their availability, nor did they select tree species in proportion to their abundance within a given home range. Leaf toughness was not a strong predictor of food selection because only one the three study groups consumed leaves with significantly lower toughness values compared to abundant leaves not consumed. Finally, conventional nutritional models explained food selection among two of the groups, but no model could be applied universally to all three groups. That is, commonly consumed leaves had lower acid detergent fiber (ADF) content and greater protein to fiber ratios for one group, commonly consumed leaves had lower ADF for another group, and there were no significant differences in protein content, fiber content, or protein to fiber ratios between commonly consumed leaves and the most abundant leaves not consumed for the third group.

Thus, when examined independently, availability, toughness, and nutritional composition had limited success in predicting food selection in *C. a. palliatus*; however, it is possible that interactive effects among these variables will yield a better model of food selection. The purpose of this study is to examine food selection as a multivariate phenomenon by combining availability, toughness, and nutritional variables into a multivariate statistical model. This study focuses exclusively on leaf selection because leaves are the only food items in which toughness data are available and because leaves constituted the majority of the diet for all three groups (range = 68.0% - 74.9% of the diet).

METHODS

Study Site and Study Species

This study was conducted in the Diani Forest of south coastal Kenya. This coral rag forest measures approximately 4.6 km^2 and is comprised of patches of intact forest interspersed with highly degraded areas (Anderson et al. 2007; Dunham and McGraw 2014; Dunham 2015). The climate is characterized by two rainy seasons (i.e., October – December; March – June) (Mwamachi et al. 1995). Annual rainfall during this study was 1550 mm (i.e., January-December 2015).

This study focuses on three groups of *C. a. palliatus* (Ujamaa, Ufalme, and Nyumbani) inhabiting non-adjacent ranges with several colobus groups ranging between the three study group ranges. Group sizes ranged from 5 - 10 individuals during the study period. The Ujamaa group ranged through one of the most intact areas of the Diani Forest that that is dominated by indigenous tree species. The Ufalme group inhabited a more degraded forest area approximately 4.9 km north of the Ujamaa range. The Nyumbani group occupied another degraded forest area roughly 1.0 km south of the Ujamaa range that was dominated by exotic tree species.

Behavioral Methods

Behavioral data were collected on the three *C. a. palliatus* study groups for 267 days. Behavioral data were recorded on Ujamaa and Ufalme from July 2014 - December 2015 and on Nyumbani from January - December 2015. Groups were studied on a rotational basis such that each group was followed for 5 - 7 consecutive days before rotating to the next group. Feeding data, including plant species and part consumed, were collected during 5 minute group scans at 15 minute intervals. Each individual's behavior was recorded instantaneously before rotating to another group member (Altmann 1974). Individuals were sampled in order based on proximity to the researcher beginning with the nearest individual. The cohesiveness of the small groups (i.e., 5 – 10 individuals), enabled recording of all members for the vast majority of group scans. Only data for adult males and adult females were included in this study. Dietary contributions were recorded using time-based estimates of food intake (i.e., instantaneous scan samples) rather than weight-based estimates of food intake.

Food Availability

A GPS waypoint was recorded using a portable Garmin 62s at the start of each behavioral scan (i.e., every 15 minutes). Each waypoint was marked at the approximate group center to estimate the group's overall position (Cords 1987). ArcGIS software was used to plot the waypoints, and the minimum convex polygon tool was used to create home range maps. Chapter 2 provides a more detailed description of the forest mapping methods. The basal area (BA) of each tree species was calculated using the formula: BA = $[(0.5 \text{ X DBH})^2 \text{ x } \pi]$ (Vandercone et al. 2012).

Phenology data were collected twice per month, on approximately the first and fifteenth day. Phenology data were collected from 407 trees dispersed along three trails, including one trail within each home range. The availability of young leaves, mature leaves, unripe fruit, ripe fruit, and flowers was scored on a whole number scale of 0 - 4. Scores were defined as: 0 = absent or 0% of tree canopy contains the particular plant item, 1 = ~1 - 25%, 2 = ~26 - 50%, 3 = ~51 - 75% and 4 = ~76 - 100% of the canopy was laden with a given plant part.

Data on forest composition and phenology were combined to create a food availability index (FAI) for each tree species: FAI = [mean phenological score X BA] (Dasilva 1994; Fashing 2001). Indices were generated for leaves that comprised at least 1% of a group's diet (i.e., based on time spent feeding).

Leaf Toughness

Toughness was measured on young leaves (YL) and mature leaves (ML) from May - July 2014 and January - November 2015. Chapter 3 provides more detail on how YL and ML were defined and distinguished from one another. When possible, leaf samples were collected from specific trees and canopy locations where individuals fed. Leaves were collected throughout the study period. Most species of ML were available year round; YL species were typically available and collected during and/or shortly after the rainy seasons (i.e., October-December and March-June). Mean toughness values were generated for each leaf species plant part.

Toughness was recorded using the leaf toughness tester described in detail in Chapter 3. The instrument functions similarly to the Darvell et al. (1996) universal tester commonly used in food mechanical properties studies in the primatology literature (e.g., Hill and Lucas 1996; Elgart-Berry 2004; Wright et al. 2008; Venkataraman et al. 2014). Toughness (measured in J m^{-2}) was calculated by dividing the work of leaf fracture by the area of the cut (Lucas and Teaford 1994). All leaf samples were cut perpendicular to the leaf midrib to simulate the manner in which *C. a. palliatus* typically consumed leaves (Lucas et al. 1995). Individuals rarely consumed just the leaf lamina or leaf tip but instead consumed the majority of the leaf body including the midrib. Thus, all tests were made through the lamina and midrib (Choong 1996; Teaford et al. 2006).

Nutritional Composition

Leaf samples were collected from the Diani Forest, Kenya, from June - July 2014 and from January - November 2015. Samples were initially dried in the field using an Excalibur food dehydrator to prevent molding. Upon returning to the laboratory in Columbus, OH, USA, samples were dried again in a vacuum oven at 105°C for 8 hr to remove residual moisture. Samples were then homogenized using a commercial blender and sieved through a 1 mm mesh.

All samples were analyzed in duplicate using a combination of traditional wet chemistry assays and near-infrared spectroscopy (NIRS) models (see Chapter 4 for more information on NIRs predictive equations). Ash content was quantified by heating samples at 600°C for 4 hours to remove all organic matter. Total nitrogen content was calculated via Dumas combustion. Crude protein was then calculated by multiplying total nitrogen by a factor of 6.25 (Maynard and Loosli 1969). Available protein was calculated by subtracting the fiber bound fraction from CP (Rothman et al. 2008). Fat was quantified using a modified Bligh-Dyer (Bligh and Dyer 1959) technique (see Chapter 4). Water soluble carbohydrate (WSC) concentrations were calculated using the phenol–sulfuric acid method (Dubois et al. 1956; BeMiller and Low 2010) with modifications to accommodate WSC quantification from solid substances (Dunham et al. 2015). Finally, neutral detergent fiber (NDF), acid detergent fiber (ADF), and fiber bound protein were analyzed sequentially following Van Soest et al. (1991). Available protein was calculated by subtracting fiber bound protein from crude protein content. Total nonstructural carbohydrate (TNC) was calculated via subtraction: TNC = 100 – (ash + AP + fat + NDF) (Irwin et al. 2015).

Statistical Methods

Binary logistic regression was used to simultaneously examine the effects of availability, toughness, and nutritional composition on leaf selection. The response variable (i.e., dependent variable) was defined as either zero (i.e., leaves not consumed: the 20 most abundant YL and ML per home range that were not consumed) or one (i.e., leaves consumed: leaves that comprised at least 1% of a group's diet). The predictors (i.e., independent variables) were availability (recorded as FAI score), leaf toughness, ash content, available protein content, fat content, ADF content, and NDF content. All nutritional variables were reported as percentage of dry weight. TNC content was excluded from the analysis because it was highly correlated with NDF content ($r = -0.88$; $p < 0.001$). FAI scores were log transformed in order to make the data normally distributed. A backward stepwise variable selection procedure was used to assess statistical models incorporating different combinations of predictors. All of the predictor variables were initially inputted into the statistical model. The variable with the lowest predictive power was then removed from the model and the analysis was run again. This procedure continued in a stepwise fashion until only independent variables with p-values < 0.05 remained. The model with the best predictive power (i.e., the model with the greatest Nagelkerke R^2 value) was selected and discussed (Nagelkerke 1991). Data from all three study groups were combined into a single statistical model.

RESULTS

The statistical model including log availability, toughness, fat content, and ADF content had the best predictive power (Nagelkerke $R^2 = 0.28$). Ash, available protein, and NDF were excluded from the model. The model correctly identified 76.5% of samples (N = 98 total samples) as either not consumed vs. consumed. This model provided a significantly more accurate prediction of whether leaves were not consumed vs. consumed compared to the null model which did not incorporate any predictor variables ($\chi^2 = 22.40$; df = 4; $P < 0.001$).

Table 6.1 shows the beta-coefficients, Wald statistics, and p-values for the predictor variables. In general, leaves with a combination of lower FAI scores, lower toughness values, lower fat content, and lower ADF content were selected; however, only ADF content had a significant effect when controlling for the other variables ($P < 0.007$).

DISCUSSION

The strongest predictive model of food selection incorporated availability, toughness, fat content and ADF content. All of these predictors had a negative relationship with leaf selection (i.e., negative beta-coefficients: Table 6.1). This result largely corroborates previous investigations in which the effects of availability, toughness, and nutritional composition on food selection were analyzed independently (Chapters 2, 3, and 5). That is, availability did not positively correlate with food selection. Instead, the majority of dietary items were selected disproportionately higher than their abundance would suggest if all plant species were eaten at random (Chapter 2).

In other words, availability had an inverse relationship with selection. In terms of toughness, only one of the three study groups was found to select leaves with significantly lower toughness values compared to those of leaves not consumed (Chapter 3). It is unclear why fat content had a negative relationship with leaf selection. This result may be an artifact of low fat content in the leaf samples: range = 1.89% - 5.54% of the dry weight. Finally, there was a significant negative relationship between ADF content and food selection in two of the three study groups (Chapter 5). This negative relationship between ADF content and leaf selection was the primary predictor in the multivariate statistical model as it was the only independent variable with a significant effect when controlling for all other predictors.

The multivariate model showed that the majority of the predictor variables did not have significant effects on leaf selection. It is possible that this study failed to account for better predictors of leaf selection. For instance, studies have documented that other plant item characteristics can influence food selection such as size, texture, color, and odor (Dominy and Lucas 2001; Dominy et al. 2001; Leighton 1993; Nevo and Heymann 2015). The majority of these studies have focused on the physical characteristics of fruits. Additional research is required to determine how these traits influence leaf selection; however, there is evidence that some primates may select leaves in relation to color-preferring young leaves with reddish hues over more greenish hues (Lucas et al. 1998; Dominy 2002; Rushmore et al. 2012).

Plant secondary metabolites (PSMs) are another variable that has frequently been examined in relation to leaf selection. PSMs serve as chemical defenses to folivory and primates have been found to avoid of limit their intake of leaves with high concentrations of certain PSMs including tannins, lignins, saponins, and cyanogenic glycosides (Oates et al. 1980; Dasilva, 1994; Fashing et al. 2007). Still, several other studies have found no relationship among PSM concentrations and leaf selection, so including PSMs among the predictor variables in this study may not have improved the food selection model (Bocian, 1997; Maisels et al. 1994; Mowry et al. 1996; Chapman and Chapman, 2002). Finally, there is evidence that colobine monkeys may select certain plant items and soils for their high concentrations of particular minerals (Oates 1978; Dunbar 1987; Fashing et al. 2007; Rode et al. 2003). Total ash content represented the combination of all mineral components and was not a strong predictor of food selection in this study. It is possible that individual minerals such as sodium, calcium, and zinc may have been better predictors of food selection (Oates 1978; Dunbar 1987; Fashing et al. 2007; Rode et al. 2003).

Alternatively, the fact that many of the independent variables were poor predictors of leaf selection suggests that *C. a. palliatus* have more complex food selection criteria. That is, models that emphasize a particular nutrient, physical trait, or combination of these factors, still over simply dietary selection. For example, individuals may select food A due to its high protein content, select food B due to its greater spatial availability and fat content, and select food C due to its lower fiber content and greater ash content. It is difficult to fit a statistical model to these circumstances.

Particularly with regard to nutritional components, models that emphasize maximizing or limiting the intake of particular macronutrients are restricted in their application. First, it is clear that protein maximization and fiber limitation models do not apply to all folivorous primates, but rather these models are dependent on the overall nutritional quality of the most abundant trees at a given site. That is, these models generally do not apply to sites with an abundance of high quality foliage (Ganzhorn et al. 2016). Second, these maximization and minimization models fail to account for the fact that individuals can suffer deleterious health outcomes if a particular nutrient is not consumed within a certain threshold. For example, both over consuming protein and under consuming dietary fiber can negatively impact an individual's health and fitness (Simpson and Raubenheimer 2012).

Examining food selection in relation to nutritional balancing (i.e., the Geometric Framework (GF)) resolves some of the shortcomings of the multivariate predictive model of this study (Simpson and Raubenheimer 2012). That is, the GF 1) considers that some foods may be incorporated into the diet based on different selection criteria and 2) records the quantities of different nutrients consumed per day. Rather than emphasizing the traits that predict whether a food will be eaten, the GF identifies nutritional intake targets. These targets can be achieved by consistently consuming foods whose nutritional composition is close to or equal to that of the target or by consuming foods with disparate nutritional compositions that balance out to the nutritional target (Behmer and Joern 2008). Because many of the nutritional variables did not predict leaf selection in this study, it is likely that *C. a. palliatus* utilize the latter strategy and consume leaves with varying but complementary nutritional compositions and toughness values.

Table 6.1. Variables included in the best predictive model of food selection

Predictor	*B*	Wald	P-value
log Availability	-0.265	1.555	0.212
Toughness	-0.004	1.972	0.160
Fat Content	-0.472	1.446	0.229
ADF Content	-0.113	7.156	0.007

ADF = acid detergent fiber

CHAPTER 7: SUMMARY, CONTRIBUTIONS, AND FUTURE DIRECTIONS

SUMMARY

This study examined the feeding ecology, dietary variation, and food selection of Angola black and white colobus monkeys (*Colobus angolensis palliatus*) in the Diani Forest, Kenya. Foraging behavior and food selection were influenced to varying degrees by 1) seasonal and spatial availability, 2) mechanical toughness, and 3) nutritional composition of food items. The diets of groups inhabiting structurally distinct forest areas differed significantly with regard to species-specific plant parts indicating that *C. a. palliatus* can adjust their diets to local ecological conditions. At the same time, nutritional balancing (i.e., intake of nonprotein energy to protein energy) among individuals of the three groups was remarkably consistent suggesting nutrient intake may be more tightly constrained.

Chapter 2 investigated the degree to which diets varied among three *C. a. palliatus* groups and whether differences in diet could be explained by differences in food availability and forest composition among the groups' home ranges. The home ranges differed considerably among the groups, with only six tree species among the 20 most abundant found in all three home ranges. The availability of overall plant parts (i.e., mature leaves, young leaves, fruits, and flowers) also differed significantly among the home ranges. The diets of the three groups did not differ significantly with regard to overall plant parts: young leaves made up the majority of the diet for all three groups, followed by fruit, mature leaves, and flowers. Diets did differ considerably with regard to plant species and species-specific plant parts: only three species ranked in the top 20 food species for all three groups and mean monthly dietary overlap was just 10.4% among all groups. However, these dietary differences were not readily explained by the documented differences in spatial and temporal availability of the most abundant tree species within the groups' home ranges. Instead, all groups selected relatively rare tree species and plant parts from their ranges (i.e., selection ratios > 1 for most tree species).

Chapter 3 assessed the relationships among leaf selection, foraging efficiency, and leaf toughness. Leaf toughness was not a strong predictor of food selection as only one of the three study groups selected leaves with lower toughness values compared to abundant leaves not consumed. Furthermore, leaf toughness did not correlate with selection scores for any of the three groups. Despite the weak relationship between toughness and leaf selection, toughness did significantly impact foraging efficiency. That is, leaf toughness negatively correlated with ingestion rate (i.e., g/min) and positively correlated with masticatory investment (i.e., chews/ g). In other words, tougher leaves required more time and chewing cycles to sufficiently comminute.

Chapter 4 outlined conventional wet chemistry methods used to quantify the nutritional composition of a subset of plants samples and assessed the efficacy of near-infrared reflectance spectroscopy (NIRS) models in predicting the nutritional composition of additional plant samples. A total of 85 leaf samples, 30 fruit samples, and 23 flower samples were analyzed in duplicate using conventional wet chemistry assays for ash, crude protein, fat, water soluble carbohydrates, neutral detergent fiber, and acid detergent fiber. Results from these samples, combined with their near-infrared spectra, were used to construct predictive models: one set of models for leaves and another set of models for fruits and flowers. Despite the highly diverse nature of the samples, NIRS models had excellent predictive power, on par with that of models used in the food and agricultural sciences based on more homogeneous data sets. These models were used to rapidly predict the nutritional composition of an additional 244 plant samples.

Chapter 5 examined food selection in relation to the nutritional composition of potential food items. This chapter first evaluated conventional models of food selection: protein maximization, fiber limitation, and protein to fiber ratio maximization that have often been applied to studies of colobine monkey feeding ecology. Commonly consumed leaves had lower acid detergent fiber (ADF) content than abundant leaves not consumed for two of the three groups, and commonly consumed leaves had greater protein to fiber ratios than those of abundant leaves not consumed for one out of the three study groups. Thus, none of the conventional models explained leaf selection in all three study groups. This chapter also quantified the nutritional intake of individuals from the three study groups and used the theoretical approach known as the Geometric Framework to analyze nutritional balancing. Despite dramatic differences in diets in terms of species-specific plant parts and significant differences in the quantities of various macronutrients consumed per day among individuals of different groups, the ratios of non-protein energy (NPE) consumed vs. available protein energy (AP) consumed were largely consistent among individuals of different groups. Rather than prioritizing AP over NPE (or vice versa) as demonstrated in other primate species, *C. a. palliatus* maintained a consistent balance of NPE to AP of approximately 2:1.

Chapter 6 combined aspects of Chapter 2, 3, and 5 with the aim of creating a multivariate statistical model to predict leaf selection based on availability, toughness, and nutritional composition. A binary logistic regression was used in which the dependent variable was defined as either zero (i.e., leaves not consumed) or one (i.e., leaves consumed). The independent variables were availability (recorded as FAI score), leaf toughness, ash content, available protein content, fat content, ADF content, and NDF content. The strongest predictive model of food selection incorporated availability, toughness, fat content and ADF content; however, ADF content was the only independent variable with a significant effect when controlling for all other predictors. These results largely corroborate previous investigations in which the effects of availability, toughness, and nutritional composition on food selection were analyzed independently: groups selected relatively rare plant species, toughness had an inverse relationship with food selection in one group, and ADF content had an inverse relationship with selection in two of the groups.

CONTRIBUTIONS

This study emphasizes that some aspects of behavior and diet can vary considerably among groups living in the same forest (Chapman and Chapman 1999; Chapman et al. 2002). Diets were highly variable among groups with regard to species-specific plant parts. All three study groups exhibited tremendous dietary diversity, consuming a total of 110 different plant species—two to three times the number recorded in other *C. angolensis* studies (Fashing 2011). All three groups relieved heavily on exotic plant species and lianas which tend to become more abundant with increasing forest disturbance and fragmentation (Lovejoy et al. 1986; DeWalt et al. 2000; Zhu et al. 2004). These results, in conjunction with other studies of *C. angolensis*, highlight the behavioral and dietary flexibility of this taxon: *C. angolensis* inhabit a variety of forest types (i.e., primary rainforest, dry lowland forest, gallery forest, coral rag forest, submontane and montane forest, swamp forest, and agricultural matrix habitat), exhibit remarkable variation in group size (range = 2 – 300+ individuals), home range size (range = <10 ha – 2440 ha), and social structure (i.e., one-male, multi-male, fission-fusion), and display variable diets, relying heavily on leaves, seeds, lichens, and/or flowers throughout their ranges (Anderson et al. 2007a, b, c; Bocian 1997; Bridgett et al. 2016; Dunham this study; Fashing et al. 2007; Fimbel et al. 2001; Maisels et al. 1994; Marshall et al. 2005; McGraw 1994; Moreno-Black and Maples 1977; Rodgers 1981; Rovero et al. 2009; Vedder and Fashing 2002). This degree of behavioral and dietary plasticity likely enables *C. a. palliatus* to survive within increasingly fragmented and disturbed habitats such as the Diani Forest of Kenya (Silver and Marsh 2003). Results from this study will be used to inform reforestation efforts ongoing in the Diani Forest.

In addition to the conservation implications, this research adds to the growing theoretical shift in primate feeding ecology studies by utilizing the Geometric Framework of nutrition to examine nutrient intakes and nutrient balancing (Felton et al. 2009a, b; Rothman et al. 2011; Johnson et al. 2013, 2015; Irwin et al. 2015; Righini 2014; Vogel et al. 2016). Despite significant dietary differences with regard to both species-specific plant parts consumed and the amount of kilocalories consumed per day among individuals of different groups, the ratios of NPE to AP consumed were remarkably consistent across individuals of different groups. This suggests that balancing the intake of different macronutrients to a specific target (and tightly regulating the intake target) is an adaptive strategy (Simpson and Raubenheimer 2012). While conventional models that emphasize energy maximization, protein maximization, and fiber limitation explain food selection in some primate populations and not others, the GF provides a theoretical approach that can be applied universally across all primates and animals (Simpson and Raunbenheimer 2012). This study provides the first published GF study of daily nutritional intake in a colobine monkey species. These results add to the increasing body of primate GF literature that includes studies of spider monkeys (*Ateles chamek*), mountain gorillas (*Gorilla beringei*), chacma baboons (*Papio ursinus*), sifakas (*Propithecus diadema*), howler monkeys (*Alouatta pigra*), and orangutans (*Pongo pygmaeus*) (Felton et al. 2009a, b; Rothman et al. 2011; Johnson et al. 2013; Irwin et al. 2015; Righini 2014; Vogel et al. 2016). Data from additional species and populations of *C. angolensis* will allow researchers to test whether intake targets are tightly constrained by phylogeny.

While it is largely assumed that consuming tougher foods is costly due to the greater peak forces, greater number of chewing cycles, and/or increased time required to sufficiently process them, this study clearly demonstrated that tougher leaves take significantly longer time to process and require more chewing cycles per unit mass ingested. In fact, leaves on the tougher end of the spectrum in this study required up to three and half times the number of minutes and chewing cycles to comminute a given mass compared leaves on the lower end of the toughness spectrum. These results also have implications for estimates of food and nutritional intake. Ingestion rates for commonly consumed leaves varied from 2.50 – 8.62 g/min. Thus, researchers should strive to identify species-specific plant part intake rates rather than taking the mean intake rate for all leaves or plant parts consumed (Nakagawa 2009).

This study also made significant methodological contributions with regard to quantifying the nutritional composition of plant materials. NIRS equations accurately quantified ash, crude protein, fat, water soluble carbohydrate, NDF, and ADF concentrations in leaves, fruits, and flowers from the Diani Forest. These results demonstrate that highly diverse sample sets, incorporating young and mature leaves representing 55 species and 27 families, can be combined into a single predictive equation. Similarly, fruits representing 27 species from 15 plant families and flowers representing 21 species from 12 plant families were combined into a single predictive model that maintains the high predictive power (i.e., $r^2 = 0.90 - 0.95$) characteristic of equations based on more homogeneous data sets in the agricultural and food sciences. NIRS is an excellent technique for ecological studies due to its many advantages over conventional wet chemistry analyses including minimal sample preparation, rapid sample throughput, absence of harsh chemicals, and sample preservation (Foley et al. 1998; Rothman et al. 2012; Vance et al. 2016). These advantages are particularly significant for primate feeding ecology studies that seek to analyze large data sets (Chapman et al. 2003; Rothman et al. 2015).

FUTURE DIRECTIONS

Future research will explore the relationship between mechanical toughness and nutritional/chemical composition of plant materials. Toughness is related to the configuration of the cell wall in a given plant tissue and loosely correlates with its total fiber content (Dominy et al. 2001; Lucas et al. 1995); however, this relationship remains murky. Building on the NIRS model used to predict the nutritional composition of plants items, future research will examine the near-infrared profiles of leaf samples to determine which spectral regions and chemical compounds best predict toughness. Assuming the model achieves strong predictive power, an equation could be generated to predict the toughness of future samples based on their spectral profiles. This would allow researchers to rapidly quantify toughness for large data sets and also enable researchers to quantify toughness at field sites that do not have access to mechanical properties testers.

In terms of the Geometric Framework and nutritional balancing, this study was primarily concerned with comparing intergroup differences and identifying intake targets over the course of the entire study period. Future research will deconstruct the data set and examine how a variety of other variables influence NPE to AP balancing and other nutritional intake patterns. For example, I plan to identify the extent to which intake patterns differ with seasonality (i.e., wet seasons vs. dry seasons) (Irwin et al. 2015). I also plan to examine how nutritional intake patterns differ in relation to ontogeny. Given that juveniles have greater protein demands necessary for growth and development compared to adults, it is reasonable to expect that juveniles may balance their nutritional intake differently and acquire a greater proportion of their energy from protein (Oftedal et al. 1991; Rothman et al. 2008). Just as nutritional demands change throughout an individual’s growth and development, nutritional and energetic demands vary with regard to reproductive state in adult females. In particular, lactating females incur greater energetic costs compared to cycling females (Altmann 1980; van Noordwijk 2012). Future research will examine the extent to which nutritional intake differs among females that are cycling, gestating, or nursing dependent offspring and whether intake targets differ or are conserved among the different reproductive states.

CHAPTER 1 REFERENCES

Bocian CM. 1997. Niche separation of black-and-white colobus (*Colobus angolensis* and *C. guereza*) in the Ituri forest. Ph.D.thesis, City University of New York.

Burgess MA, Chapman CA. 2005. Tree leaf chemical characters: selective pressures by folivorous primates and invertebrates. African Journal of Ecology 43:242-250.

Chapman CA, Chapman LJ. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates 40:215-231.

Chapman CA, Chapman LJ. 2002. Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. Computational Biochemistry and Physiology Part A 133:861–875.

Chapman CA, Wrangham RW, Chapman L, Kennard DK, Zanne AE. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. Journal of Tropical Ecology15:189-211.

Chapman CA, Chapman LJ, Gillespie TR. 2002a. Scale issues in the study of primate foraging: red colobus of Kibale National Park. American Journal of Physical Anthropology 117:349-363.

Chapman CA, Chapman LJ, Gautier-Hion A, Lambert JE, Rode K, Tutin CEG, White LJT. 2002b. Variation in the diet of *Cercopithecus* monkeys: differences within forests, among forests, and across species. In: Glenn M, Cords M, editors. The guenons: diversity and adaptation in African monkeys. New York: Kluwer Academic Press. pp. 303–317.

Chapman CA, Chapman LJ, Bjorndal KA, Onderdonk DA. 2002c. Application of protein to fiber ratios to predict colobine abundance on different spatial scales. International Journal of Primatology 23:283-310.

Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, McDowell LR. 2004. Predicting folivorous primate abundance: validation of a primate nutritional model. American Journal of Primatology 62:55-69.

Chapman CA, Chapman LJ, Zanne AE, Poulsen JR, and Clark CJ. 2005. A 12-year phenological record of fruiting: implications for frugivore populations and indicators of climate change. In: Dew JL, Boubli JP, editors. Tropical Fruits and Frugivores: The Search for Strong Interactors. The Netherlands, Springer. pp. 75-92.

Charnov EL. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129–136.

Chaves OM, Bicca-Marques JC. 2013. Dietary flexibility of the brown howler monkey throughout its geographic distribution. American Journal of Primatology 75:16–29.

Dasilva GL. 1994. Diet of *Colobus polykomos* on Tiwai Island: selection of food in relation to its seasonal abundance and nutritional quality. International Journal of Primatology 15:655-680.

Davies AG, Bennett EL, Waterman PG. 1988. Food selection by two south-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. Biological Journal of the Linnean Society 34:33-56.

Dominy NJ, Lucas PW, Osorio D, Yamashita N. 2001. The sensory ecology of primate food perception. Evolutionary Anthropology 10:171-186.

Elgart-Berry A. 2004. Fracture and toughness of mountain gorilla (*Gorilla gorilla beringei*) food plants. American Journal of Primatology 62:275-285.

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

Fashing PJ, Dierenfeld ES, Mowry CB. 2007. Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of *Colobus guereza* in Kakamega, Kenya. International Journal of Primatology 28:673-703.

Felton AM, Felton A, Lindenmayer DB, Foley WJ. 2009. Nutritional goals of wild primates. Functional Ecology 23:70-78.

Freeland WJ, Janzen DH. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. American Naturalist 108:269-289

Ganzhorn J, Arrigo-Nelson S, Carrai V, Chalise M, Donati G, et al. 2016. The importance of protein in leaf selection of folivorous primates. American Journal of Primatology: doi:10.1002/ajp.22550.

Garber PA. 1987. Foraging strategies among living primates. Annual Review of Anthropology 16:339-364.

Glander KE. 1982. The impact of plant secondary compounds on primate feeding behavior. American Journal of Physical Anthropology 25:1-18

Harris TR, Chapman CA. 2007. Variation in diet and ranging of black and white colobus monkey in Kibale National Park, Uganda. Primates 48:208-221.

Harris TR, Chapman CA, Monfort SL. 2010. Small folivorous primate groups exhibit behavioral and physiological effects of food scarcity. Behavioral Ecology 21:46–56.

Harrison MJS. 1986. Feeding ecology of black colobus, *Colobus satanas*, in Central Gabon. In Else JG, Lee PC, editors. Primate ecology and conservation. Cambridge University Press, Cambridge, pp. 31-38.

Hill DA, Lucas PW. 1996. Toughness and fiber content of major leaf foods of Japanese macaques (*Macaca fuscata yakui*) inYakushima. American Journal of Primatology 38:221–231.

Irwin MT, Raharison J-L, Raubenheimer DR, Chapman CA, Rothman JM. 2015. The nutritional geometry of resource scarcity: effects of lean seasons and habitat disturbance on nutrient intakes and balancing in wild sifakas. PLoS ONE 10:e0128046.

Johnson CA, Raubenheimer D, Rothman JM, Clarke D, Swedell L. 2013. 30 days in the life: daily nutrient balancing in a wild chacma baboon. PLoS ONE 8:e70383.

Jones CB. 2005. Behavioral flexibility in primates: causes and consequences. New York, Springer.

Kay RNB, Davies AG. 1994. Digestive physiology. In Davies AG, Oates JF, editors. Colobine monkeys: their behavior, ecology, and conservation. Cambridge, Cambridge University Press. pp. 229-250.

Koenig A, Beise J, Chalise MK, Ganzhorn JU. 1998. When females should contest for food-testing hypotheses about resource density, distribution, size and quality with Hanuman langurs (*Presbytis entellus*). Behavioral Ecology and Sociobiology 42:225–237.

Kool, K.1992. Food selection by the silver leaf monkey, *Trachypithecus auratus sondaicus*, in relation to plant chemistry. Oecologia 90:527-533.

Lambert JE. 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. Evolutionary Anthropology7:8-20.

Lambert JE. 2011. Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In: Campbell CH, Fuentes A, Mackinnon KC, Panger M, Bearder SK, editors. Primates in perspective. New York: Oxford University Press. pp. 512-522.

Lambert JE, Rothman JM. 2015. Fallback foods, optimal diets, and nutritional targets: primate responses to varying food availability and quality. Annual Review of Anthropology 44:493-512.

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

Lucas PW, Copes L, Constantino PJ, Vogel ER, et al. 2012. Measuring the toughness of primate foods and its ecological value. International Journal of Primatology 33:598-610.

Lucas PW, Darvell BW, Lee PC, Yuen TDB, Choong MF. 1995. The toughness of plant cell walls. Philosophical Transactions of the Royal Society of London B 348:363–372.

Lucas PW, Teaford MF. 1994. Functional morphology of colobine teeth. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour, and evolution. Cambridge: Cambridge University Press. pp. 173-204.

MacArthur RH, Pianka ER. 1966. On optimal use of a patchy environment. The American Naturalist 100:603-609.

Maisels F, Gautier-Hion A, Gautier JP. 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. International Journal of Primatology 15:681-701.

Marshall AJ, Boyko CM, Feilen K, Boyko Rh, Leighton M. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. American Journal of Physical Anthropology 140:603-614.

McGraw WS, Daegling DJ. 2012. Primate feeding and foraging: integrating studies of behavior and morphology. Annual Review of Anthropology 41:203–219.

McGraw WS, van Casteren A, Kane E, Geissler E, Burrows B, Daegling DJ. 2015. Feeding and oral processing behaviors of two colobine monkeys in Tai Forest, Ivory Coast. Journal of Human Evolution doi:10.1016/j.jhevol.2015.06.001.

McKey DB, Gartlan JS, Waterman PG, Choo GM. 1981. Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. Biological Journal of the Linnean Society 16:115-146.

Milich KM, Stumpf RM, Chambers JM, Chapman CA. 2014. Female red colobus monkeys maintain their densities through flexible feeding strategies in logged forests in Kibale National Park, Uganda. American Journal of Physical Anthropology 154:52–60.

Milton K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. American Naturalist 114:362–378.

Milton K. 1999. Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us? Nutrition 15:488-498.

Mowry CB, Decker BS, Shure DJ. 1996. The role of phytochemistry in dietary choices of Tana River red colobus monkeys (*Piliocolobus badius rufomitratus*). International Journal of Primatology 17:63-84

Oates JF, Waterman PG, Choo GM. 1980. Food selection by the South Indian leafmonkey, *Presbytis johnii*, in relation to leaf chemistry. Oecologia 45:45-56.

Onderdonk DA, Chapman CA. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. International Journal of Primatology 21:587–611.

Post DG. 1984. Is optimization the optimal approach to primate foraging? In Adaptations for foraging in nonhuman primates. New York: Columbia University Press. pp. 280-303.

Raubenheimer D, Simpson SJ. 1993. The geometry of compensatory feeding in the locust. Animal Behavior 45:953–964.

Reiner WB, Petzinger C, Power ML, Hyeroba D, Rothman JM. 2014. Fatty acids in mountain gorilla diets: implications for primate nutrition and health. American Journal of Primatology 76:281–288.

Righini N. 2014. Primate nutritional ecology: the role of food selection, energy intake, and nutrient balancing in Mexican black howler monkey (*Alouatta pigra*) foraging strategies. Ph.D. dissertation, Department of Anthropology, University of Illinois at Urbana-Champaign, Urbana.

Righini N, Garber PA, Rothman JM. 2015. The effects of plant nutritional chemistry on food selection of Mexican black howler monkeys (*Alouatta pigra*): The role of lipids. American Journal of Primatology DOI:10.1002/asp.22524.

Rothman JM, Chapman CA, Van Soest PJ. 2012. Methods in primate nutritional ecology: a user's guide. International Journal of Primatology 33:542-566.

Simpson SJ, Raubenheimer D. 1993. A multi-level analysis of feeding behaviour: the geometry of nutritional decisions. Philosophical Transactions of the Royal Society London B 342:381-402.

Rothman JM, Raubenheimer D, Chapman CA. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. Biology Letters 7:847-849.

Simpson SJ, Raubenheimer D. 2012. The Nature of nutrition: a unifying framework from animal adaptation to human obesity. Princeton: Princeton University Press.

Snaith TV, Chapman CA. 2007. Primate group size and interpreting socioecological models: do folivores really play by different rules? Evolutionary Anthropology 16:94-106.

Snaith TV, Chapman CA. 2008. Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. Behavioral Ecology 19:1289–1296.

Simmen B, Tarnaud L, Marez A, Hladik A. 2014. Leaf chemistry as a predictor of primate biomass and the mediating role of food selection: a case in a folivorous lemur (*Propithecus verreauxi*). American Journal of Primatology 76:563-575.

Simpson SJ, Raubenheimer D. 1993. A multi-level analysis of feeding behaviour: The geometry of nutritional decisions. Philosophical Transactions of the Royal Society London B 342:381-402.

Teaford MF, Lucas PW, Ungar PS, Glander KE. 2006. Mechanical defenses in leaves eaten by Costa Rican howling monkeys (*Alouatta palliata*). American Journal of Physical Anthropology 129:99–104.

van Schaik CP, Terborgh JW,Wright SJ. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annual Review of Ecology, Evolution, and Systematics 24:353–77.

Venkataraman VV, Glowacka H, Fritz J, Clauss M, Seyoum C, Nguyen N, Fashing PJ. 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). American Journal of Physical Anthropology 155:17-32.

Vogel ER, Zulfa A, Hardus M, Wich SA, Dominy NJ, Taylor AB. 2014. Food mechanical properties, feeding ecology, and the mandibular morphology of wild orangutans. Journal of Human Evolution 75:110–124.

Vogel ER, Rothman JM, Alavi SE, Bransford TD, Utami Atmoko SS, Erb WM, van Noorwwijk, Raubenheimer D. 2016. Different to be the same: individual variation in diet among wild Bornean orangutans (*Pongo pygmaeus wurmbii*) in a peatland habitat reflects regulation of macronutrient balance. Podium Presentation. International Primatological Society Congress, Chicago, IL.

Waterman PG, Ross JAM, Bennet EL, Davies AG. 1988. A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. Biological Journal of the Linnean Society 34:1-32.

Wong SNP, Saj TL, Sicotte P. 2006. Comparison of habitat quality and diet of *Colobus vellerosus* in forest fragments in Ghana. Primates 47:365-373.

Wright BW, Ulibarri L, O'Brien J, Sadler B, Prodham R, Covert HH, Nadler T. 2008. It's tough out there: variation in the toughness of ingested leaves and feeding behavior among four Colobinae in Vietnam. International Journal of Primatology 29:1455-1466.

Yamashita N, Vinyard CJ, Tan CL. 2009. Food mechanical properties in three sympatric species of *Hapalemur* in Ranomafana National Park, Madagascar. American Journal of Physical Anthropology 139:68–381.

Yeager CP, Silver SC, Dierenfeld ES. 1997. Mineral and phytochemical influences on foliage selection by the proboscis monkey (*Nasalis larvatus*). American Journal of Primatology 41:117-128.

CHAPTER 2 REFERENCES

Anderson J, Rowcliffe JM, Cowlishaw G. 2007. The Angola black and white colobus (*Colobus angolensis palliatus*) in Kenya: historical range contraction and current conservation status. American Journal of Primatology 69:664-680.

Bocian CM. 1997. Niche separation of black-and-white colobus (*Colobus angolensis* and *C. guereza*) in the Ituri forest. Ph.D.thesis, City University of New York.

Buzzard PJ. 2006. Ranging patterns in relation to seasonality and frugivory among *Cercopithecus campbelli, C. petaurista, and C. diana* in the Tai Forest. International Journal of Primatology 27:559-573.

Cords M. 1987. Mixed species association of *Cercopithecus* monkeys in the Kakamega Forest, Kenya. Univ. Calif. Publ. Zool. Berkeley, University of California Press 117:1–109.

Chapman CA, Chapman LJ. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates 40:215-231.

Chapman CA, Wrangham RW, Chapman LJ, Kennard DK, Zanne AE. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. Journal of Tropical Ecology 15:189–211.

Chapman CA, Chapman LJ, Gillespie TR. 2002a. Scale issues in the study of primate foraging: red colobus of Kibale National Park. American Journal of Physical Anthropology 117:349-363.

Chapman CA, Chapman LJ, Gautier-Hion A, Lambert JE, Rode K, Tutin CEG, White LJT. 2002b. Variation in the diet of *Cercopithecus* monkeys: differences within forests, among forests, and across species. In: Glenn M, Cords M, editors. The guenons: diversity and adaptation in African monkeys. New York: Kluwer Academic Press. pp. 303–317.

Dasilva GL. 1992. The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure, and energy intake. Journal of Animal Ecology 61:79-91.

Dasilva GL. 1994. Diet of *Colobus polykomos* on Tiwai Island: selection of food in relation to its seasonal abundance and nutritional quality. International Journal of

Primatology 15:655-680.

Dunham NT, McGraw WS. 2014. Positional behavior and habitat use of Peters' Angola black and white colobus monkey (*Colobus angolensis palliatus*) in structurally distinct areas of the Diani Forest, Kenya. African Primates 9:1-14.

Dunham NT. 2015. Ontogeny of positional behavior and support use among *Colobus angolensis palliatus* of the Diani Forest, Kenya. Primates 56:183-192.

Dunn JC, Asensio N, Arroyo-Rodríguez V, Schnitzer S, Cristóbal-Azkarate J. 2012. The ranging costs of a fallback food: liana consumption supplements diet but increases foraging effort in howler monkeys. Biotropica 44:704–714.

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

Fashing PJ, Mulindahabi F. Gakima J, Masozera M, Mununura I, Plumptre AJ, Nguyen N. 2007. Activity and ranging patterns of *Colobus angolensis ruwenzorii* in Nyungwe Forest, Rwanda: possible costs of large group size. International Journal of Primatology 28:529-550.

Fashing PJ. 2011. African colobine monkeys. In Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, editors. Primates in Perspective. Oxford University Press, Oxford. pp. 203-229.

Fimbel C, Vedder A, Dierenfeld E, Mulindahabi F. 2001. An ecological basis for large group size in *Colobus angolensis* in the Nyungwe Forest, Rwanda. African Journal of Ecology 39:83-92.

Gautier-Hion A. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. Journal of Animal Ecology 49:237-269.

Holmes RT, Pitelka FA. 1968. Food overlap among coexisting sandpipers on northern Alaskan tundra. Systematic Zoology 17:305–318.

Kay RNB, Davies AG. 1994. Digestive physiology. In Davies AG, Oates JF, editors. Colobine monkeys: their behavior, ecology, and conservation. Cambridge, Cambridge University Press. pp. 229-250.

Koyabu D, Endo H. 2009. Craniofacial variation and dietary adaptations of African colobines. Journal of Human Evolution 56:525-536.

Lambert JE. 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. Evolutionary Anthropology 7:8-20.

Lambert JE, Rothman JM. 2015. Fallback foods, optimal diets, and nutritional targets: primate responses to varying food availability and quality. Annual Review of Anthropology 44:493-512.

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

Maisels F, Gautier-Hion A, Gautier JP. 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. International Journal of Primatology 15:681-701.

McKey DB, Gartlan JS, Waterman PG, Choo GM. 1981. Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. Biological Journal of the Linnean Society 16:115-146.

Milton K. 1980. The foraging strategy of howler monkeys: a study in primate economics. New York: Columbia University Press.

Moreno-Black G, Maples MR. 1977. Differential habitat utilization of four Cercopithecoidea in a Kenyan forest. Folia Primatologica 27:85-107.

Mwamachi DM, Audho JO, Thorpe W, Baker RL. 1995. Evidence for multiple anthelmintic resistance in sheep and goats reared under the same management in coastal Kenya. Veterinary Parisitology 60:303–313.

Oates JF. 1977. The guereza and its food. In Clutton-Brock TH, editor. Primate Ecology. Academic Press, New York. pp. 275-321.

Okanga S, Muchemi G, Maingi N, Mogoa E, Munene E. 2006. Gastrointestinal parasite of free-ranging colobus monkeys (*Colobus angolensis palliatus*) in Kwale District, Kenya coast. African Journal of Ecology 44:410–412.

Onderdonk DA, Chapman CA. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. International Journal of Primatology 21:587-611.

Preece G. 2006. Factors influencing variation in the population densities of *Colobus guereza*, within selectively logged forest at the Budongo Forest Reserve. In Newton-Fisher NE, Nortman H, Paterson JD, Reynolds V, editors. Primates of Western Uganda. Springer, New York. pp. 23–43.

Rudran R. 1978. Socioecology of the blue monkeys (*Cercopithecus mitis stuhlmanii*) of the Kibale Forest, Uganda. Smithsonian Contributions to Zoology 249:1–83.

Struhsaker TT, Oates JF. 1975. Comparison of the behavior and ecology of red colobus and black-and-white colobus monkeys in Uganda: A summary. In Tuttle RH, editor. Socio-ecology and Psychology of Primates, Mouton, The Hague. pp. 103–123.

Struhsaker TT. 2010. The red colobus monkey: variation in demography, behavior, and ecology of an endangered species. Oxford University Press, Oxford.

Vandercone RP, Dinadh C, Wijethunga G, Ranawana K, Rasmussen T. 2012. Dietary diversity and food selection in Hanuman langurs (*Semnopithecus entellus*) and purple-faced langurs (*Trachypithecus vetulus*) in the Kaludiyapokuna Forest Reserve in the dry zone of Sri Lanka. International Journal of Primatology 33:1382–1405.

van Schaik CP, Terborgh JW,Wright SJ. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annual Review of Ecology, Evolution, and Systematics 24:353–77.

Vedder A, Fashing PJ. 2002. Diet of a 300-member Angolan colobus monkey (*Colobus angolensis*) supergroup in the Nyungwe Forest. Rwanda. American Journal of Physical Anthropology Supplement 34:159.

Wong SNP, Saj TL, Sicotte P. 2006. Comparison of habitat quality and diet of *Colobus vellerosus* in forest fragments in Ghana. Primates 47:365-373.

CHAPTER 3 REFERENCES

Anderson J, Cowlishaw G, Rowclifee JM. 2007. Effects of forest fragmentation on the abundance of *Colobus angolensis palliatus* in Kenya's coastal forests. International Journal of Primatology 28:637–655.

Ang KY, Lucas PW, Tan HTW. 2008. A novel way of measuring the fracture toughness of leaves and other thin films using a single inclined razor blade. New Phytologist 177:830–837.

Berthaume MA. 2016. Food mechanical properties and dietary ecology. American Journal of Physical Anthropology 159:79-104.

Bocian CM. 1997. Niche separation of black-and-white colobus (*Colobus angolensis* and *C. guereza*) in the Ituri forest. Ph.D.thesis, City University of New York.

Bouvier M. 1986. A biomechanical analysis of mandibular scaling in Old World monkeys. American Journal of Physical Anthropology 69:473-482.

Chapman CA, Chapman LJ. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates 40:215–232.

Chapman CA, Chapman LJ, Bjorndal KA, Onderdonk DA. 2002a. Application of protein to fiber ratios to predict colobine abundance on different spatial scales. International Journal of Primatology 23:283-310.

Chapman CA, Chapman LJ, Gautier-Hion A, Lambert JE, Rode K, Tutin CEG, White LJT. 2002b. Variation in the diet of *Cercopithecu*s monkeys: differences within forests, among forests, and across species. In: Glenn M, Cords M, editors. The guenons: diversity and adaptation in African monkeys. New York: Kluwer Academic Press. pp. 303–317.

Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, McDowell LR. 2004. Predicting folivorous primate abundance: validation of a primate nutritional model. American Journal of Primatology 62:55-69.

Choong MF. 1996. What makes a leaf tough and how this affects the pattern of *Castanopsis fissa* leaf consumption by caterpillars. Functional Ecology 10:668-674.

Cowlishaw G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Animal Behavior 53:667-686.

Daegling DJ, WS McGraw. 2001. Feeding, diet and jaw form in West African *Colobus* and *Procolobus*. International Journal of Primatology 22:1033-1055.

Daegling DJ, McGraw WS, Ungar PS, Pampush JD, Vick AE, Bitty EA. 2011. Hard object feeding in sooty mangabeys (*Cercocebus atys*) and the interpretation of early hominin feeding ecology. PLoS One 6:e23095.

Daegling, David J., Stefan Judex, Engin Ozcivici, Matthew J. Ravosa, Andrea B. Taylor, Frederick E. Grine, Mark F. Teaford, and Peter S. Ungar. 2013. Viewpoints: feeding mechanics, diet, and dietary adaptations in early hominins. American Journal of Physical Anthropology 151:356-371.

Darvell BW, Lee PKD, Yuen TD, Lucas PW. 1996. A portable fracture toughness tester for biological materials. Measurement Science and Technology 7:954–962.

Dasilva GL. 1992. The western black and white colobus as a low-energy strategist: activity budgets, energy expenditure, and energy intake. Journal of Animal Ecology 61:79-91.

Dasilva GL. 1994. Diet of *Colobus polykomos* on Tiwai Island: selection of food in relation to its seasonal abundance and nutritional quality. International Journal of Primatology 15:655-680.

Dominy NJ, Lucas PW, Osorio D, Yamashita N. 2001. The sensory ecology of primate food perception. Evolutionary Anthropology 10:171-186.

Dominy NJ. 2002. Incidence of red leaves in the rainforest of Kibale National Park, Uganda: shade tolerators and light-demanders compared. African Journal of Ecology 40:94-96.

Dunham NT, McGraw WS. 2014. Positional behavior and habitat use of Peters' Angola black and white colobus monkey (*Colobus angolensis palliatus*) in structurally distinct areas of the Diani Forest, Kenya. African Primates 9:1-14.

Dunham NT. 2015. Ontogeny of positional behavior and support use in *Colobus angolensis palliatus* of the Diani Forest, Kenya. Primates 56:183-192.

Elgart-Berry A. 2004. Fracture and toughness of mountain gorilla (*Gorilla gorilla beringei*) food plants. American Journal of Primatology 62:275-285.

Fashing PJ, Dierenfeld ES, Mowry CB. 2007a. Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of *Colobus guereza* in Kakamega, Kenya. International Journal of Primatology 28:673-703.

Fashing PJ, Mulindahabi F. Gakima J, Masozera M, Mununura I, Plumptre AJ, Nguyen N 2007b. Activity and ranging patterns of *Colobus angolensis ruwenzorii* in Nyungwe Forest, Rwanda: possible costs of large group size. International Journal of Primatology 28:529-550.

Fashing PJ. 2011. African colobine monkeys. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, editors. Primates in perspective. Oxford: Oxford University Press. pp. 203-229.

Fichtel C. 2012. Predation. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB, editors. The evolution of primate societies. Chicago: University of Chicago Press. pp. 169-194.

Fimbel C, Vedder A, Dierenfeld E, Mulindahabi F. 2001. An ecological basis for large group size in *Colobus angolensis* in the Nyungwe Forest, Rwanda. African Journal of Ecology 39:83-92.

Fraser DF, Huntingford FA. 1986. Feeding and avoiding predation hazard: the behavioural response of the prey. Ethology 73:56–68.

Gerstner GE, Gernstein JB. 2008. Chewing rate allometry among mammals. Journal of Mammalogy 89:1020-1030.

Harrison MJS. 1986. Feeding ecology of black colobus, *Colobus satanas*, in Central Gabon. In: Else JG, Lee PC, editors. Primate ecology and conservation. Cambridge: Cambridge University Press. pp. 31-38.

Hiiemae KM, Palmer JB. 1999. Food transport and bolus formation during complete feeding sequences on foods of different initial consistency. Dysphagia 14:31-42.

Hill DA, Lucas PW. 1996. Toughness and fiber content of major leaf foods of Japanese macaques (*Macaca fuscata yakui*) inYakushima. American Journal of Primatology 38:221–231.

Hylander WL. 1979. The functional significance of the primate mandibular form. Journal of Morphology 160:223-240.

Kay RNB, Davies AG. 1994. Digestive physiology. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour, and evolution. Cambridge: Cambridge University Press. pp. 229-250.

Kinzey WG, Norconk MA. 1990. Hardness as a basis of fruit choice in two sympatric primates. American Journal of Physical Anthropology 81:5-15.

Koyabu DB, Endo H. 2009. Craniofacial variation and dietary adaptations of African colobines. Journal of Human Evolution 56:525-536.

Lambert JE. 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. Evolutionary Anthropology 7:8-20.

Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain NL. 2004. Hardness of Cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. American Journal of Physical Anthropology 125:363-368.

Lowe AJ, Sturrock GA. 1998. Behaviour and diet of *Colobus angolensis palliatus* Peters 1868, in relation to seasonality in a Tanzanian dry coastal forest. Folia Primatologica 69:121-128.

Lowman MD, Box JD. 1983. Variation in leaf toughness and phenolic content among five species of Australian rain forest trees. Australian Journal of Ecology 8:17-25.

Lucas PW, Teaford MF. 1994. Functional morphology of colobine teeth. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour, and evolution. Cambridge: Cambridge University Press. pp. 173-204.

Lucas PW, Darvell BW, Lee PC, Yuen TDB, Choong MF. 1995. The toughness of plant cell walls. Philosophical Transactions of the Royal Society B 348:363–372.

Lucas PW, Copes L, Constantino PJ, Vogel ER, et al. 2012. Measuring the toughness of primate foods and its ecological value. International Journal of Primatology 33:598-610.

Maisels F, Gautier-Hion A, Gautier JP. 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. International Journal of Primatology 15:681-701.

Marshall AJ, Boyko CM, Feilen K, Boyko Rh, Leighton M. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. American Journal of Physical Anthropology 140:603-614.

McGraw WS. 1998. Posture and support use of Old World monkeys (Cercopithecidae): the influence of foraging strategies, activity patterns and the spatial distribution of preferred food items. American Journal of Primatology 46: 229–250.

McGraw WS, Vick AE, Daegling DJ. 2011. Sex and age differences in the diet and ingestive behaviors of sooty mangabeys (*Cercocebus atys*) in the Tai Forest, Ivory Coast. American Journal of Physical Anthropology 144:140-153.

McGraw WS, Daegling DJ. 2012. Primate feeding and foraging: integrating studies of behavior and morphology. Annual Review of Anthropology 41:203-219.

McGraw WS, Vick AE, Daegling DJ. 2014. Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): implications for fallback foods and dental adaptation. American Journal of Physical Anthropology 154:413-423.

McGraw WS, van Casteren A, Kane E, Geissler E, Burrows B, Daegling DJ. 2015. Feeding and oral processing behaviors of two colobine monkeys in Tai Forest, Ivory Coast. Journal of Human Evolution doi:10.1016/j.jhevol.2015.06.001.

McKey DB, Gartlan JS, Waterman PG, Choo GM. 1981. Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. Biological Journal of the Linnean Society 16:115-146.

Milton K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. American Naturalist 114:362–378.

Moreno-Black GS, Maples WR. 1977. Differential habitat utilization of four cercopithecidae in a Kenyan Forest. Folia Primatologica 27:85-107.

Mowry CB, Decker BS, Shure DJ. 1996. The role of phytochemistry in dietary choices of Tana River red colobus monkeys (*Piliocolobus badius rufomitratus*). International Journal of Primatology 17:63-84.

Nakagawa N. 2009. Feeding rate as valuable information in primate feeding ecology. Primates 50:131–141.

Norconk MA, Wright BW, Conklin-Brittain NL, Vinyard CJ. 2009. Mechanical and nutritional properties of food as factors in Platyrrhine dietary adaptations. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB, editors. South American primates: comparative perspectives in the study of behavior, ecology, and conservation. New York: Springer. pp. 279–319.

Nowak K, Lee PC. 2011. Demographic structure of Zanzibar red colobus populations in unprotected coral rag and mangrove forests. International Journal of Primatology 32:24-45.

Oates JF. 1988. The diet of the olive colobus monkey, *Procolobus verus*, in Sierra Leone. International Journal of Primatology 9:457-478.

Oates JF, Whitesids GH, Davies AG, Waterman PG, Green SM, Dasilva GL, Mole S. 1990. Determinants of variation in tropical forest primate biomass: new evidence from West Africa. Ecology 71:328-343.

Pampush JD, Duque AC, Burrows BR, Daegling DJ, Kenney WF, McGraw WS. 2013. Homoplasy and thick enamel in primates. Journal of Human Evolution 64:216–224.

Pérez-Barbería FJ, Gordon IJ. 1998. Factors affecting food comminution during chewing in ruminants: a review. Biological Journal of the Linnean Society 63:233–256.

Ravosa, MJ. 1996. Jaw morphology and function in living and fossil Old World monkeys. International Journal of Primatology 17:909-932.

Rogers M, Maisels F, Williamson E, Fernandez M, Tutin C. 1990. Gorilla diet in the Lope Reserve, Gabon: a nutritional analysis. Oecologia 84:326–339.

Ross CF, Eckhardt, Herrel A, Hylander WL, Metzger KA, Schaerlaeken, Washington RL, Williams SH. 2007. Modulation of intra-oral processing in mammals and lepidosaurs. Integ Computational Biology 47:118-136.

Ross CF, Reed DA, Washington RL, Eckhardt A, Anapol F, Shahnoor N. 2009a. Scaling of chew cycle duration in Primates. American Journal of Physical Anthropology 138:30-44.

Ross CF, Washington RL, Eckhardt A, Reed DA, Vogel ER, Dominy NJ, Machanda ZP. 2009b. Ecological consequences of scaling of chew cycle duration and daily feeding time in Primates. Journal of Human Evolution 56:570-585.

Ross CF, Iriarte-Diaz J, Nunn CL. 2012. Innovative approaches to the relationship between diet and mandibular morphology in primates. International Journal of Primatology 33:632-660.

Shipley LA, Gross JE, Spalinge, DE, Hobbs NT, Wunder BA. 1994. The scaling of intake rate in mammalian herbivores. American Naturalist 143:1055–1082.

Spencer MA. 1998. Force production in the primate masticatory system: electromyographic tests of biomechanical hypotheses. Journal of Human Evolution 34:25–54.

Strait, DS, Weber GW, Neubauer S, Chalk J, Richmond BG, Lucas PW, Spencer MA, Schrein C, Dechow P, Ross CF, Grosse I, Wright BW, Constantino P, Wood B, Lawn B, Hylander WL, Wang Q, Byron C, Slice DE, Smith AL. 2009. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. Proceedings of the National Academe of Sciences USA 106:2124–2129.

Strait DS, Constantino PJ, Lucas PW, Richmond BG, Spencer MA, Dechow PC, Ross

CF, Grosse IR, Wright BW, Wood BA, Weber GW, Wang Q, Byron C, Slice DE, Chalk J, Smith AL, Smith LC, Wood S, Berthaume M, Benazzi S, Dzialo C, Tamvada K, Ledogar JAD. 2013. Viewpoints: diet and dietary adaptations in early hominins: the hard food perspective. American Journal of Physical Anthropology 151:339-355.

Teaford MF, Lucas PW, Ungar PS, Glander KE. 2006. Mechanical defenses in leaves eaten by Costa Rican howling monkeys (*Alouatta palliata*). American Journal of Physical Anthropology 129:99–104.

Van Soest PJ. 1994. Nutritional ecology of the ruminant. Ithaca, NY: Cornell University Press.

Venkataraman VV, Glowacka H, Fritz J, Clauss M, Seyoum C, Nguyen N, Fashing PJ. 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). American Journal of Physical Anthropology 155:17-32.

Vogel ER, Zulfa A, Hardus M, Wich SA, Dominy NJ, Taylor AB. 2014. Food mechanical properties, feeding ecology, and the mandibular morphology of wild orangutans. Journal of Human Evolution 75: 110–124.

Waterman PG, Ross JAM, Bennet EL, Davies AG. 1988. A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. Biological Journal of the Linnean Society 34:1-32.

Wright BW. 2005. Craniodental biomechanics and dietary toughness in the genus *Cebus*. Journal of Human Evolution 48:473–492.

Wright BW, Ulibarri L, O'Brien J, Sadler B, Prodham R, Covert HH, Nadler T. 2008. It's tough out there: variation in the toughness of ingested leaves and feeding behavior among four Colobinae in Vietnam. International Journal of Primatology 29:1455-1466.

Wright BW, Wright KA, Chalk J, Verderane MP, Fragaszy D, Visalberghi E, Izar P, Ottoni EB, Constantino P, Vinyard C. 2009. Fallback foraging as a way of life: using dietary toughness to compare the fallback signal among capuchins and implications for interpreting morphological variation. American Journal of Physical Anthropology 140:687-699.

Yamashita N. 1998. Functional dental correlates of food perspectives in five Malagasy lemur species. American Journal of Physical Anthropology 106:169-188.

Yamashita N. 2003. Food procurement and tooth use in two sympatric lemur species. American Journal of Physical of Anthropology 121:125-133.

Yamashita N, Vinyard CJ, Tan CL. 2009. Food mechanical properties in three sympatric species of *Hapalemur* in Ranomafana National Park, Madagascar. American Journal of Physical Anthropology 139:68–381.

Yamashita N, Cuozzo FP, Sauther ML, Fitzgerald E, Riemenschneider A, Ungar PS. 2015. Mechanical food properties and dental topography differentiate three populations of *Lemur catta* in southwest Madagascar. Journal of Human Evolution doi:10.1016/j.jhevol.2015.09.006.

CHAPTER 4 REFERENCES

Anderson J, Cowlishaw G, Rowcliffe JM. 2007. Effects of forest fragmentation on the abundance of *Colobus angolensis palliatus* in Kenya's coastal forests. International Journal of Primatology 28:637-655.

BeMiller JN, Low NH. 2010. Carbohydrate analysis. In: Nielsen SS, editor. Food analysis. Aspen, Maryland. pp. 147–177.

Bligh EG, Dyer WJ. 1959. A rapid method of total fat extraction and purification. Canadian Journal of Biochemistry and Physiology 37:911–917.

Brereton RG. 2000. Introduction to multivariate calibration in analytical chemistry. Analyst 125:2125–2154.

Chapman CA, Chapman LJ, Rode KD, Hauck EM, McDowell LR. 2003. Variation in the nutritional value of primate foods: among trees, time periods and areas. International Journal of Primatology 24:317–333.

Conklin-Brittain NL, Dierenfeld ES, Wrangham RW, Norconk M, Silver SC. 1999. Chemical protein analysis: A comparison of Kjeldahl crude protein and total ninhydrin protein using wild, tropical vegetation. Journal of Chemical Ecology 25:2601–2622.

Cornejo J, Taylor R, Sliffe T, Bailey CA, Brightsmith DJ. 2012. Prediction of the nutritional composition of the crop contents of free-living scarlet macaw chicks by near-infrared reflectance spectroscopy. Wildlife Research 39:230–233.

Dubois M, Gilles KA, Hamilton JK, Rebers PA. 1956. Colorimetric method for determination of sugars and related substances. Analytical Chemistry 28:350–356.

Dunham NT, McGraw WS. 2014. Positional behavior and habitat use of Peters' Angola black and white colobus monkey (*Colobus angolensis palliatus*) in structurally distinct areas of the Diani Forest, Kenya. African Primates 9:1-14.

Dunham NT, Kane EE, Rodriguez-Saona LE. 2016. Quantifying soluble carbohydrates in tropical leaves using a portable mid-infrared sensor: implications for primate feeding ecology. American Journal of Primatology 78:701-706.

Felton AM, Felton A, Wood JT, Foley WJ. 2009a. Nutritional ecology of *Ateles chamek* in lowland Bolivia: how macronutrient balancing influences food choice. International Journal of Primatology 30:675–696.

Felton AM, Felton A, Raubenheimer D, Simpson SJ, Foley WJ, Wood JT, Wallis IR, Lindenmayer DB. 2009b. Protein content of diets dictates the daily energy intake of a free ranging primate. Behavioral Ecology 20:685–690.

Foley WJ, McIlwee A, Lawler I, Aragones L, Woolnough AP, Berding N. 1998. Ecological applications of near infrared reflectance spectroscopy: a tool for rapid, cost-effective prediction of the composition of plant and animal tissues and aspects of animal performance. Oecologia 116:293–305.

Johnson CA, Raubenheimer D, Chapman CA, Tombak KJ, Reid AJ, Rothman JM. 2015. Macronutrient balancing affects patch departure by guerezas (*Colobus guereza*). American Journal of Primatology DOI: 10.1002/ajp.22495.

Landau S, Glasser T, Dvash L. 2006. Monitoring nutrition in small ruminants with the aid of near infrared reflectance spectroscopy (NIRS) technology: a review. Small Ruminant Research 61:1–11.

Lawler IR, Aragones L, Berding N, Marsh H, Foley WJ. 2006. Near infrared spectroscopy is a rapid, cost-effective predictor of seagrass nutrients. Journal of Chemical Ecology 32:1353–1365.

Martens H. Naes T. 1989. Multivariate calibration. Wiley, Chichester, UK.

Maynard LA, Loosli JK. 1969. Animal nutrition, McGraw-Hill, New York.

Milton K, Dintzis FR. 1981. Nitrogen-to-protein conversion factors for tropical plant samples. Biotropica 12: 177–181.

Ortmann S, Bradley BJ, Stolter C, Ganzhorn JU. 2006. Estimating the quality and composition of wild animal diets: a critical survey of methods. In: Hohmann G, Robbins MM, Boesch C, editors. Feeding ecology of apes and other primates. Cambridge University Press, Cambridge, pp 397–420.

Osborne BG, Fearn T. 1986. Theory of near-infrared spectrophotometry. In Osborne BG, Fearn T, editors. Near infrared spectroscopy in food analysis. Longman Scientific and Technical, Essex, pp 13-35.

Rodriguez-Saona LE, Allendorf ME. 2011. Use of FTIR for rapid authentication and detection of adulteration of food. Annual Review of Food Science and Technology 2:467–483.

Rothman JM, Chapman CA, Hansen JL, Chemey DJ, Pell AN. 2009. Rapid assessment of the nutritional value of foods eaten by mountain gorillas: Applying near-infrared reflectance spectroscopy to primatology. International Journal of Primatology 30:729–742.

Rothman JM, Chapman CA, Struhsaker TT, Raubenheimer D, Twinomugisha D, Waterman PG. 2015. Long term declines in nutritional quality of tropical leaves. Ecology 96:873–878.

Rothman JM, Chapman CA, Van Soest PJ. 2012. Methods in primate nutritional ecology: a user's guide. International Journal of Primatology 33:542–566.

Rothman JM, Raubenheimer D, Chapman CA. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. Biology Letters 7:847–849.

Soxhlet F. 1879. Die gewichtsanalytische Bestimmung des Milchfettes. Dingler's Polytechnisches Journal 232:461–465.

Vance KC, Tolleson RD, Kinoshita K, Rodriguez J, Foley JW. 2016. Near infrared spectroscopy in wildlife and biodiversity. Journal of Near Infrared Spectroscopy 24:1-25.

Van Soest PJ, Robertson JB, Lewis BA. 1991. Methods for dietary fiber, neutral-detergent fiber and nonstarch polysaccharides in relation to animal nutrition. Journal of Dairy Science 74:3583-3597.

Williams PC, Norris KH. 1987. Qualitative applications of nearinfrared reflectance spectroscopy. In Williams P, Norris K, editors. Near-infrared technology in the agricultural and food industries. American Association of Cereal Chemists, St. Paul, MN, pp. 241-246.

Woolnough AP, du Toit. 2001. Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. Oecologia 129:585-590.

Woolnough AP, Foley WJ. 2002. Rapid evaluation of pasture quality for a critically endangered mammal, the northern hairy-nosed wombat (*Lasiorhinus krefftii*). Wildlife Research 29:91-100.

CHAPTER 5 REFERENCES

Anderson J, Rowcliffe JM, Cowlishaw G. 2007. The Angola black and white colobus (*Colobus angolensis palliatus*) in Kenya: historical range contraction and current conservation status. American Journal of Primatology 69:664-680.

Bocian CM. 1997. Niche separation of black-and-white colobus (*Colobus angolensis* and *C. guereza*) in the Ituri forest. Ph.D.thesis, City University of New York.

Behmer SY, Joern SA. 2008. Coexisting generalist herbivores occupy unique nutritional feeding niches. Proceedings of the National Academy of Sciences USA. 105: 1977–1982.

BeMiller JN, Low NH. 2010. Carbohydrate analysis. In: Nielsen SS, editor. Food analysis. Aspen: Maryland, pp 147–177.

Bligh EG, Dyer WJ. 1959. A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology 37:911–917.

Bridgett GR, Corriveau A, Teichroeb JA. 2016. The immediate impact of selective logging on Angolan colobus at Lake Nabugabo, Uganda. Podium Presentation. International Primatological Society Congress, Chicago, IL.

Burgess MA, Chapman CA. 2005. Tree leaf chemical characters: selective pressures by folivorous primates and invertebrates. African Journal of Ecology 43:242-250.

Chapman CA, Chapman LJ. 2002. Foraging challenges of red colobus monkeys: Influence of nutrients and secondary compounds. Computational Biochemistry and Physiology Part A 133:861–875.

Chapman CA, Chapman LJ, Bjorndal KA, Onderdonk DA. 2002. Application of protein to fiber ratios to predict colobine abundance on different spatial scales. International Journal of Primatology 23:283-310.

Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, McDowell LR. 2004. Predicting folivorous primate abundance: validation of a primate nutritional model. American Journal of Primatology 62:55-69.

Dasilva GL. 1994. Diet of *Colobus polykomos* on Tiwai Island: Selection of food in relation to its seasonal abundance and nutritional quality. International Journal of

Primatology 15:655-680.

Davies AG, Bennett EL, Waterman PG. 1988. Food selection by two south-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. Biological Journal of the Linnean Society 34:33-56.

Dubois M, Gilles KA, Hamilton JK, Rebers PA. 1956. Colorimetric method for determination of sugars and related substances. Analytical Chemistry 28:350–356

Dunham NT, McGraw WS. 2014. Positional behavior and habitat use of Peters' Angola black and white colobus monkey (*Colobus angolensis palliatus*) in structurally distinct areas of the Diani Forest, Kenya. African Primates 9:1-14.

Dunham NT. 2015. Ontogeny of positional behavior and support use among *Colobus angolensis palliatus* of the Diani Forest, Kenya. Primates 56:183-192.

Dunham NT, Kane EE, Rodriguez-Saona LE. 2016. Quantifying soluble carbohydrates in tropical leaves using a portable mid-infrared sensor: implications for primate feeding ecology. American Journal of Primatology 78:701-706

Fashing PJ, Dierenfeld ES, Mowry CB. 2007a. Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of *Colobus guereza* in Kakamega, Kenya. International Journal of Primatology 28:673-703.

Fashing PJ, Mulindahabi F. Gakima J, Masozera M, Mununura I, Plumptre AJ, Nguyen N. 2007b. Activity and ranging patterns of *Colobus angolensis ruwenzorii* in Nyungwe Forest, Rwanda: Possible costs of large group size. International Journal of Primatology 28:529-550.

Felton AM, Felton A, Lindenmayer DB, Foley WJ. 2009a. Nutritional goals of wild primates. Functional Ecology 23:70-78.

Felton AM, Felton A, Raubenheimer D, Simpson SJ, Foley WJ, Wood JT, Wallis IR, Lindenmayer DB. 2009b. Protein content of diets dictates the daily energy intake of a free-ranging primate. Behavioral Ecology 20:685-690.

Felton AM, Felton A, Wood JT, Foley WJ, et al. 2009c. Nutritional ecology of *Ateles chamek* in lowland Bolivia: how macronutrient balancing influences food choice. International Journal of Primatology 30:675-696.

Fimbel C, Vedder A, Dierenfeld E, Mulindahabi F. 2001. An ecological basis for large group size in *Colobus angolensis* in the Nyungwe Forest, Rwanda. African Journal of Ecology 39:83-92.

Freeland WJ, Janzen DH. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. American Naturalist 108:269-289.

Ganzhorn J, Arrigo-Nelson S, Carrai V, Chalise M, Donati G, et al. 2016. The importance of protein in leaf selection of folivorous primates. American Journal of Primatology: doi:10.1002/ajp.22550.

Glander KE. 1982. The impact of plant secondary compounds on primate feeding behavior. American Journal of Physical Anthropology 25:1-18

Gosby AK, Conigrave AD, Lau NS, Iglesias MA, Hall RM, et al. 2011. Testing protein leverage in lean humans: A randomised controlled experimental study. PLoS One 6:e25929.

Irwin MT, Raharison J-L, Raubenheimer DR, Chapman CA, Rothman JM. 2015. The nutritional geometry of resource scarcity: effects of lean seasons and habitat disturbance on nutrient intakes and balancing in wild sifakas. PLoS ONE 10:e0128046.

Johnson CA, Raubenheimer D, Rothman JM, Clarke D, Swedell L. 2013. 30 days in the life: daily nutrient balancing in a wild chacma baboon. PLoS ONE 8:e70383.

Johnson CA, Raubenheimer D, Chapman CA, Tombak KJ, Reid AJ, Rothman JM. 2015. Macronutrient balancing affects patch departure by guerezas (*Colobus guereza*). American Journal of Primatology: 10.1002/ajp.22495.

Koenig A, Beise J, Chalise MK, Ganzhorn JU. 1998. When females should contest for food-testing hypotheses about resource density, distribution, size and quality with Hanuman langurs (*Presbytis entellus*). Behavioral Ecology and Sociobiology 42:225–237.

Kool K. 1992. Food selection by the silver leaf monkey, *Trachypithecus auratus sondaicus*, in relation to plant chemistry. Oecologia 90:527-533.

Maisels F, Gautier-Hion A, Gautier JP. 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. International Journal of Primatology 15:681-701.

Martinez-Cordero C, Kuzawa CW, Sloboda DM, Stewart J, Simpson SJ, et al.2012. Testing the protein leverage hypothesis in a free-living human population. Appetite 59: 312–315.

Maynard LA, Loosli JK. 1969. Animal nutrition. New York: McGraw-Hill.

McKey DB, Gartlan JS, Waterman PG, Choo, GM. 1981. Food selection by black colobus monkeys (*Colobus satanas*) in relation to food chemistry. Biological Journal of the Linnean Society 16:115–146.

McKey DB, Gartlan JS, Waterman PG, Choo GM. 1981. Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. Biological Journal of the Linnean Society 16:115-146.

Milton K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. American Naturalist 114:362–378.

Mowry CB, Decker BS, Shure DJ. 1996. The role of phytochemistry in dietary choices of Tana River red colobus monkeys (*Piliocolobus badius rufomitratus*). International Journal of Primatology 17:63-84.

Mwamachi DM, Audho JO, Thorpe W, Baker RL. 1995. Evidence for multiple anthelmintic resistance in sheep and goats reared under the same management in coastal Kenya. Veterinary Parisitology 60:303–313.

Nakagawa N. 2009. Feeding rate as valuable information in primate feeding ecology. Primates 50:131–141.

National Research Council. 2003. Nutrient requirements of non-human primates. National Academy of Sciences, Washington D.C.

Oates JF, Waterman PG, Choo GM. 1980. Food selection by the South Indian leafmonkey, *Presbytis johnii*, in relation to leaf chemistry. Oecologia 45:45-56.

Oates JF, Whitesids GH, Davies AG, Waterman PG, Green SM, Dasilva GL, Mole S. 1990. Determinants of variation in tropical forest primate biomass: new evidence from West Africa. Ecology 71:328-343.

Oftedal OT, Whiten A, Southgate DAT, Van Soest P. 1991. The nutritional consequences of foraging in primates: the relationship of nutrient intakes to nutrient requirements. Philosophical Transactions of the Royal Society London B 334:1-10.

Raubenheimer D, Simpson SJ. 1993. The geometry of compensatory feeding in the locust. Animal Behavior 45:953–964.

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

Raubenheimer D, Machovsky-Capuska GE, Chapman CA, Rothman JM. 2015. Geometry of nutrition in field studies: an illustration using wild primates. Oecologia 177:223–234.

Righini N. 2014. Primate nutritional ecology: the role of food selection, energy intake, and nutrient balancing in Mexican black howler monkey (*Alouatta pigra*) foraging strategies. Ph.D. dissertation, Department of Anthropology, University of Illinois at Urbana-Champaign, Urbana.

Righini N, Garber PA, Rothman JM. 2015. The effects of plant nutritional chemistry on food selection of Mexican black howler monkeys (*Alouatta pigra*): The role of lipids. American Journal of Primatology DOI:10.1002/asp.22524.

Rothman JM, Raubenheimer D, Chapman CA. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. Biology Letters 7:847-849.

Rothman JM, Chapman CA, Van Soest PJ. 2012. Methods in primate nutritional ecology: a user's guide. International Journal of Primatology 33:542-566.

Simpson SJ, Batley R, Raubenheimer D. 2003. Geometric analysis of macronutrient intake in humans: The power of protein? Appetite 41: 123–140.

Simpson SJ, Raubenheimer D. 1993. A multi-level analysis of feeding behaviour: The geometry of nutritional decisions. Philosophical Transactions of the Royal Society London B 342:381-402.

Simpson SJ, Raubenheimer D. 2005. Obesity: The protein leverage hypothesis. Obesity Review 6:133–142.

Simpson SJ, Raubenheimer D. 2012. The Nature of nutrition: A unifying framework from animal adaptation to human obesity. Princeton: Princeton University Press.

Van Soest PJ, Robertson JB, Lewis BA. 1991. Methods for dietary fiber, neutral-detergent fiber and nonstarch polysaccharides in relation to animal nutrition. Journal of Dairy Science 74:3583-3597.

Waterman PG, Ross JAM, Bennet EL, Davies AG. 1988. A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. Biological Journal of the Linnean Society 34:1-32.

Yeager CP, Silver SC, Dierenfeld ES. 1997. Mineral and phytochemical influences on foliage selection by the proboscis monkey (*Nasalis larvatus*). American Journal of Primatology 41:117-128.

Van Soest PJ, Robertson JB, Lewis BA. 1991. Methods for dietary fiber, neutral-detergent fiber and nonstarch polysaccharides in relation to animal nutrition. Journal of Dairy Science 74:3583-3597.

Vogel ER, Rothman JM, Alavi SE, Bransford TD, Utami Atmoko SS, Erb WM, van Noorwwijk, Raubenheimer D. 2016. Different to be the same: individual variation in diet among wild Bornean orangutans (*Pongo pygmaeus wurmbii*) in a peatland habitat reflects regulation of macronutrient balance. Podium Presentation. International Primatological Society Congress, Chicago, IL.

Waterman PG, Ross JAM, Bennet EL, Davies AG. 1988. A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. Biological Journal of the Linnean Society 34:1-32.

White TCR. 1993. The inadequate environment: Nitrogen and the abundance of animals. Berlin: Springer-Verlag.

Yeager CP, Silver SC, Dierenfeld ES. 1997. Mineral and phytochemical influences on foliage selection by the proboscis monkey (*Nasalis larvatus*). American Journal of Primatology 41:117-128.

CHAPTER 6 REFERENCES

Altmann J. 1974. Observational study of behavior: Sampling methods. Behaviour 49: 227–267.

Anderson J, Rowcliffe JM, Cowlishaw G. 2007. The Angola black and white colobus (*Colobus angolensis palliatus*) in Kenya: historical range contraction and current conservation status. American Journal of Primatology 69:664-680.

Behmer SY, Joern SA. 2008. Coexisting generalist herbivores occupy unique nutritional feeding niches. Proceedings of the National Academy of Sciences USA. 105: 1977–1982.

BeMiller JN, Low NH. 2010. Carbohydrate analysis. In: Nielsen SS, editor. Food analysis. Aspen: Maryland, pp. 147–177.

Bligh EG, Dyer WJ. 1959. A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology 37:911–917.

Bocian CM. 1997. Niche separation of black-and-white colobus (*Colobus angolensis* and *C. guereza*) in the Ituri forest. Ph.D.thesis, City University of New York.

Chapman CA, Chapman LJ. 2002. Foraging challenges of red colobus monkeys: Influence of nutrients and secondary compounds. Computational Biochemistry and Physiology Part A 133:861–875.

Choong MF. 1996. What makes a leaf tough and how this affects the pattern of *Castanopsis fissa* leaf consumption by caterpillars. Functional Ecology 10:668-674.

Cords, M. 1987. Mixed species association of *Cercopithecus* monkeys in the Kakamega Forest, Kenya. Univ. Calif. Publ. Zool. Berkeley, University of California Press, 117: 1–109.

Darvell BW, Lee PKD, Yuen TD, Lucas PW. 1996. A portable fracture toughness tester for biological materials. Measurement Science and Technology 7:954–962.

Dasilva GL. 1994. Diet of *Colobus polykomos* on Tiwai Island: Selection of food in relation to its seasonal abundance and nutritional quality. International Journal of Primatology 15:655-680.

Dominy NJ, Lucas PW. 2001. Ecological importance of trichromatic vision to primates. Nature 410:363–366.

Dominy NJ, Lucas PW, Osorio D, Yamashita N. 2001. The sensory ecology of primate food perception. Evolutionary Anthropology 10:171-186.

Dominy NJ. 2002. Incidence of red leaves in the rainforest of Kibale National Park, Uganda: shade tolerators and light-demanders compared. African Journal of Ecology 40:94-96.

Dubois M, Gilles KA, Hamilton JK, Rebers PA. 1956. Colorimetric method for determination of sugars and related substances. Analytical Chemistry 28:350–356.

Dunbar RIM. 1987. Habitat quality, population dynamics, and group composition in colobus monkeys (*Colobus guereza*). International Journal of Primatology 8: 299–329.

Dunham NT, McGraw WS. 2014. Positional behavior and habitat use of Peters' Angola black and white colobus monkey (*Colobus angolensis palliatus*) in structurally distinct areas of the Diani Forest, Kenya. African Primates 9:1-14.

Dunham NT. 2015. Ontogeny of positional behavior and support use among *Colobus angolensis palliatus* of the Diani Forest, Kenya. Primates 56:183-192.

Elgart-Berry A. 2004. Fracture and toughness of mountain gorilla (*Gorilla gorilla beringei*) food plants. American Journal of Primatology 62:275-285.

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

Fashing PJ, Dierenfeld ES, Mowry CB. 2007. Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of *Colobus guereza* in Kakamega, Kenya. International Journal of Primatology 28:673-703.

Ganzhorn J, Arrigo-Nelson S, Carrai V, Chalise M, Donati G, et al. 2016. The importance of protein in leaf selection of folivorous primates. American Journal of Primatology: doi:10.1002/ajp.22550.

Hill DA, Lucas PW. 1996. Toughness and fiber content of major leaf foods of Japanese macaques (*Macaca fuscata yakui*) inYakushima. American Journal of Primatology 38:221–231.

Irwin MT, Raharison J-L, Raubenheimer DR, Chapman CA, Rothman JM. 2015. The nutritional geometry of resource scarcity: effects of lean seasons and habitat disturbance on nutrient intakes and balancing in wild sifakas. PLoS ONE 10:e0128046.

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

Lucas PW, Teaford MF. 1994. Functional morphology of colobine teeth. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour, and evolution. Cambridge: Cambridge University Press. p 173-204.

Lucas PW, Darvell BW, Lee PC, Yuen TDB, Choong MF. 1995. The toughness of plant cell walls. Philosophical Transactions of the Royal Society B 348:363–372.

Lucas PW, Darvell BW, Lee PKD, Yen TDB, Choong MF. 1998. Colour cues for leaf food selection by long-tailed macaques (*Macaca fascicularis*) with a new suggestion for the evolution of trichromatic colour vision. Folia Primatologica 69:139-152.

Maisels F, Gautier-Hion A, Gautier JP. 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. International Journal of Primatology 15:681-701.

Maynard LA, Loosli JK. 1969. Animal nutrition. New York: McGraw-Hill.

McKey DB, Gartlan JS, Waterman PG, Choo, GM. 1981. Food selection by black colobus monkeys (*Colobus satanas*) in relation to food chemistry. Biological Journal of the Linnean Society 16:115–146.

Milton K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. American Naturalist 114:362–378.

Mowry CB, Decker BS, Shure DJ. 1996. The role of phytochemistry in dietary choices of Tana River red colobus monkeys (*Piliocolobus badius rufomitratus*). International Journal of Primatology 17:63-84.

Mwamachi DM, Audho JO, Thorpe W, Baker RL. 1995. Evidence for multiple anthelmintic resistance in sheep and goats reared under the same management in coastal Kenya. Veterinary Parisitology 60:303–313.

Nagelkerke NJD. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691-692.

Nakagawa N. 2009. Feeding rate as valuable information in primate feeding ecology. Primates 50:131–141.

Nevo O, Heymann EW. 2015. Led by the nose: olfaction in primate feeding ecology. Evolutionary Anthropology 24:137-148.

Oates JF. 1978. Water, plant and soil consumption by guereza monkeys (*Colobus guereza*): relationship with minerals and toxins in the diet. Biotropica 10:241-253.

Oates JF, Waterman PG, Choo GM. 1980. Food selection by the South Indian leafmonkey, *Presbytis johnii*, in relation to leaf chemistry. Oecologia 45:45-56

Rode KD, Chapman CA, Chapman LJ, McDowell LR. 2003. Mineral resource availability and consumption by colobus in Kibale National Park. International Journal of Primatology 24:541-573.

Rothman JM, Chapman CA, Pell AN. 2008. Fiber-bound nitrogen in gorilla diets: implications for estimating dietary protein intake of primates. American Journal of Primatology 70:690-694.

Rushmore J, Leonhardt SD, Drea CM. 2012. Sight or scent: lemur sensory reliance in detecting food quality varies with feeding ecology. PLoS ONE 7(8):e41558. doi: 10.1371/ journal.pone.0041558.

Simpson SJ, Raubenheimer D. 2012. The Nature of nutrition: A unifying framework from animal adaptation to human obesity. Princeton: Princeton University Press

Teaford MF, Lucas PW, Ungar PS, Glander KE. 2006. Mechanical defenses in leaves eaten by Costa Rican howling monkeys (*Alouatta palliata*). American Journal of Physical Anthropology 129:99–104.

Vandercone RP, Dinadh C, Wijethunga G, Ranawana K, Rasmussen T. 2012. Dietary diversity and food selection in Hanuman langurs (*Semnopithecus entellus*) and purple-faced langurs (*Trachypithecus vetulus*) in the Kaludiyapokuna Forest Reserve in the Dry Zone of Sri Lanka. International Journal of Primatology 33:1382–1405.

Van Soest PJ, Robertson JB, Lewis BA. 1991. Methods for dietary fiber, neutral-detergent fiber and nonstarch polysaccharides in relation to animal nutrition. Journal of Dairy Science 74:3583-3597.

Venkataraman VV, Glowacka H, Fritz J, Clauss M, Seyoum C, Nguyen N, Fashing PJ. 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). American Journal of Physical Anthropology 155:17-32.

Wright BW, Ulibarri L, O'Brien J, Sadler B, Prodham R, Covert HH, Nadler T. 2008. It's tough out there: variation in the toughness of ingested leaves and feeding behavior among four Colobinae in Vietnam. International Journal of Primatology 29:1455-1466.

CHAPTER 7 REFERENCES

Altmann J. 1980. Baboon mothers and infants. Harvard University Press, Cambridge, MA.

AndersonvJ, Cowlishaw G, Rowcliffe JM. 2007a. Effects of forest fragmentation on the abundance of *Colobus angolensis palliatus* in Kenya's coastal forests. International Journal of Primatology 28:637-655.

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

Anderson J, Rowcliffe JM, Cowlishaw G. 2007c. The Angola black and white colobus (*Colobus angolensis palliatus*) in Kenya: historical range contraction and current conservation status. American Journal of Primatology 69:664-680.

Bocian CM. 1997. Niche separation of black-and-white colobus (Colobus angolensis and C. guereza) in the Ituri forest. Ph.D. thesis, City University of New York, New York.

Bridgett GR, Corriveau A, Teichroeb JA. 2016. The immediate impact of selective logging on Angolan colobus at Lake Nabugabo, Uganda. Podium Presentation. International Primatological Society Congress, Chicago, IL.

Chapman CA, Chapman LJ. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates 40:215-231.

Chapman CA, Chapman LJ, Gillespie TR. 2002. Scale issues in the study of primate foraging: red colobus of Kibale National Park. American Journal of Physical Anthropology 117:349-363.

Chapman CA, Chapman LJ, Rode KD, Hauck EM, McDowell LR. 2003. Variation in the nutritional value of primate foods: among trees, time periods and areas. International Journal of Primatology 24:317–333

DeWalt SJ, Schnitzer SA, Denslow JS. 2000. Density and diversity of lianas along a chronosequence in central Panamanian lowland forest. Journal of Tropical Ecology 16: 1–9.

Dominy NJ, Lucas PW, Osorio D, Yamashita N. 2001. The sensory ecology of primate food perception. Evolutionary Anthropology 10:171-186.

Fashing PJ, Dierenfeld ES, Mowry CB. 2007. Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of *Colobus guereza* in Kakamega, Kenya. International Journal of Primatology 28:673-703.
Fashing PJ. 2011. African colobine monkeys. In Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, editors. Primates in Perspective. Oxford University Press, Oxford. pp. 203-229.

Felton AM, Felton A, Raubenheimer D, Simpson SJ, Foley WJ, Wood JT, Wallis IR, Lindenmayer DB. 2009a. Protein content of diets dictates the daily energy intake of a free-ranging primate. Behavioral Ecology 20:685-690.

Felton AM, Felton A, Wood JT, Foley WJ, et al. 2009b. Nutritional ecology of *Ateles chamek* in lowland Bolivia: how macronutrient balancing influences food choice. International Journal of Primatology 30:675-696.

Fimbel C, Vedder A, Dierenfeld E, Mulindahabi F. 2001. An ecological basis for large group size in *Colobus angolensis* in the Nyungwe Forest, Rwanda. African Journal of Ecology 39:83-92.

Foley WJ, McIlwee A, Lawler I, Aragones L, Woolnough AP, Berding N. 1998. Ecological applications of near infrared reflectance spectroscopy: a tool for rapid, cost-effective prediction of the composition of plant and animal tissues and aspects of animal performance. Oecologia 116:293–305.

Irwin MT, Raharison J-L, Raubenheimer DR, Chapman CA, Rothman JM. 2015. The nutritional geometry of resource scarcity: effects of lean seasons and habitat disturbance on nutrient intakes and balancing in wild sifakas. PLoS ONE 10:e0128046.

Johnson CA, Raubenheimer D, Rothman JM, Clarke D, Swedell L. 2013. 30 days in the life: daily nutrient balancing in a wild chacma baboon. PLoS ONE 8:e70383.

Johnson CA, Raubenheimer D, Chapman CA, Tombak KJ, Reid AJ, Rothman JM. 2015. Macronutrient balancing affects patch departure by guerezas (*Colobus guereza*). American Journal of Primatology: 10.1002/ajp.22495.

Lovejoy TE, Bierregaard RO J, Rylands AB, Malcolm JR, Quintela CE, Harper LJ, Brown KS Jr., Powell AH, Powell GVN, Schubart HOR, Hays MB. 1986. Edge and other effects of isolation on Amazon forest fragments. In Soule ME, editor. Conservation biology: the science of scarcity and diversity. Sunderland, MA: Sinauer Associates. pp. 257–285.

Lucas PW, Darvell BW, Lee PC, Yuen TDB, Choong MF. 1995. The toughness of plant cell walls. Philosophical Transactions of the Royal Society B 348:363–372.

Maisels F, Gautier-Hion A, Gautier JP. 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. International Journal of Primatology 15:681-701.

Marshall AR, Topp-Jørgensen JE, Brink H, Fanning E. 2005. Monkey abundance and social structure in two high elevation forest reserves in the Udzungwa Mountains of Tanzania. International Journal of Primatology 26:127–145.

McGraw WS. 1994. Census, habitat preference, and polyspecific associations of six monkeys in the Lomako Forest, Zaire. American Journal of Primatology 34:395–407.

Moreno-Black G, Maples MR. 1977. Differential habitat utilization of four Cercopithecoidea in a Kenyan forest. Folia Primatologica 27:85-107.

Nakagawa N. 2009. Feeding rate as valuable information in primate feeding ecology. Primates 50:131–141.

Oftedal OT, Whiten A, Southgate DAT, Van Soest P. 1991. The nutritional consequences of foraging in primates: the relationship of nutrient intakes to nutrient requirements. Philosophical Transactions of the Royal Society London B 334:1-10.

Righini N. 2014. Primate nutritional ecology: the role of food selection, energy intake, and nutrient balancing in Mexican black howler monkey (*Alouatta pigra*) foraging strategies. Ph.D. dissertation, Department of Anthropology, University of Illinois at Urbana-Champaign, Urbana.

Rodgers WA. 1981. The distribution and conservation status of colobus monkeys in Tanzania. Primates 22:33-45.

Rothman JM, Dierenfeld ES, Hintz HF, Pell AN. 2008. Nutritional quality of gorilla diets: consequences of age, sex, and season. Oecologia 155:111-122.

Rothman JM, Raubenheimer D, Chapman CA. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. Biology Letters 7:847-849.

Rothman JM, Chapman CA, Van Soest PJ. 2012. Methods in primate nutritional ecology: a user's guide. International Journal of Primatology 33:542–566.

Rothman JM, Chapman CA, Struhsaker TT, Raubenheimer D, Twinomugisha D, Waterman PG. 2015. Long term declines in nutritional quality of tropical leaves. Ecology 96:873–878.

Rovero F, Marshall AR, Jones T, Perkin A. 2009. The primates of the Udzungwa Mountains: Diversity, ecology and conservation. Journal of Anthropological Sciences 87:93–126.

Silver S, Marsh LK. 2003. Dietary flexibility, behavioral plasticity, and survival in fragments: lessons from translocated howlers. In Marsh LK, editor. Primates in fragments: ecology and conservation. New York: Kluwer Academics. pp. 251-265.

Simpson SJ, Raubenheimer D. 2012. The Nature of nutrition: a unifying framework from animal adaptation to human obesity. Princeton: Princeton University Press.

Vance KC, Tolleson RD, Kinoshita K, Rodriguez J, Foley JW. 2016. Near infrared spectroscopy in wildlife and biodiversity. Journal of Near Infrared Spectroscopy 24:1-25.

van Noordwijk MA. 2012. From maternal investment to lifetime maternal care. In Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB, editors. The evolution of primate societies. Chicago: University of Chicago Press. p. 321-342.

Vedder A, Fashing PJ. 2002. Diet of a 300-member Angolan colobus monkey (*Colobus angolensis*) supergroup in the Nyungwe Forest. Rwanda. American Journal of Physical Anthropology Supplement 34:159.

Vogel ER, Rothman JM, Alavi SE, Bransford TD, Utami Atmoko SS, Erb WM, van Noorwwijk, Raubenheimer D. 2016. Different to be the same: individual variation in diet among wild Bornean orangutans (*Pongo pygmaeus wurmbii*) in a peatland habitat reflects regulation of macronutrient balance. Podium Presentation. International Primatological Society Congress, Chicago, IL.

Zhu H, Xu ZF, Wang,H, Li BG. 2004. Tropical rain forest fragmentation and its ecological and species diveristy changes in southern Yunnan. Biodiversity Conservation 13:1355–1372.

Appendix A. Wet chemistry reference method (Ref) values vs. NIRS predictions (Pred) values

Table A.1. Wet chemistry reference method (Ref) values vs. NIRS predictions (Pred) values for ash, CP, and fat content of leaves

		Ash		CP		Fat	
Sample	PP	Ref	Pred	Ref	Pred	Ref	Pred
Adansonia digitata	YL	12.1	12.1	13.8	14.4	3.8	3.9
Adansonia digitata	ML	16.0	14.9	13.6	15.9	-	-
Adenathera pavonina	ML	9.9	10.0	26.8	27.8	-	-
Adenathera pavonina	YL	6.3	8.1	26.8	26.0	-	-
Afzelia quanensis	YL	6.0	4.9	19.4	19.7	3.2	3.7
Afzelia quanensis	ML	9.6	9.7	14.2	17.7	3.2	3.0
Antiaris toxicaria	YL	5.9	5.4	22.2	20.9	2.7	2.8
Azadirachta indica	ML	9.1	9.0	14.3	14.9	-	-
Balanites maughamii	YL	8.2	6.3	17.4	16.2	3.1	3.2
Balanites maughamii	ML	12.0	11.7	19.2	17.6	5.9	5.9
Berchemia discolor	YL	5.3	5.8	20.0	18.7	2.8	3.1
Berchemia discolor	ML	9.5	7.8	18.3	16.2	3.4	3.8
Bougainvillea spectabilis	ML	16.2	16.3	23.5	25.6	-	-
Bougainvillea spectabilis	YL	13.6	11.7	26.8	23.4	-	-
Bourreria petiolaris	YL	9.8	9.5	18.7	19.5	4.3	4.7
Carpodiptera africana	ML	9.0	9.2	22.7	21.8	-	-
Cassia abbreviata	ML	6.9	8.2	16.9	17.9	2.6	2.8
Cassia abbreviata	YL	9.6	10.4	10.7	12.3	5.1	4.9
Cassia fistula	ML	10.0	10.2	15.1	14.1	-	-
Ceiba pentendra	ML	3.8	3.4	16.6	18.9	1.9	1.5
Cissus integrifolia	ML	12.0	11.9	15.3	16.5	4.5	4.3
Coccinia grandis	YL	11.6	10.0	25.2	23.4	3.5	3.8
Combretum schumannii	ML	5.7	6.5	28.6	28.2	-	-
Combretum schumannii	YL	4.9	4.7	16.6	15.9	-	-
Commiphora zanzibarica	YL	8.6	10.2	13.1	12.9	3.1	2.9
Commiphora zanzibarica	ML	13.0	12.4	15.6	15.0	5.0	4.5
Cordia goetzei	YL	8.3	7.6	16.0	14.5	4.0	3.9
Cussonia zimmermannii	YL	10.0	8.2	12.4	17.1	2.7	3.2
Cussonia zimmermannii	ML	9.4	8.9	14.0	11.9	3.4	3.4
Cyphostemma adenocaule	YL	9.6	9.1	24.3	22.3	-	-
Cyphostemma spp.	YL	11.5	11.0	17.4	15.4	4.0	4.2
Dalbergia vaccinifolia	ML	13.3	11.2	16.3	18.4	2.6	2.5

Continued

Table A.1 Continued

		Ash		CP		Fat	
Sample	PP	Ref	Pred	Ref	Pred	Ref	Pred
Dalbergia vaccinifolia	YL	9.6	11.7	19.0	21.6	3.5	3.3
Delonix regia	YL	7.3	7.9	20.2	16.1	-	-
Diospyros squarosa	ML	4.6	7.2	15.2	17.8	2.8	3.3
Diospyros squarosa	YL	5.2	5.4	17.4	16.0	4.0	3.9
Discorea hirtiflora	ML	6.3	5.7	25.8	29.5	6.0	6.3
Feretia apodanthera	ML	8.9	9.8	13.5	12.1	2.6	2.7
Feretia apodanthera	YL	10.0	9.0	11.6	14.5	2.7	2.7
Ficus exasperata	ML	10.3	9.8	19.4	22.2	3.4	3.2
Ficus exasperata	YL	8.2	9.2	25.0	16.7	3.9	3.8
Ficus pollita	ML	12.4	9.9	11.7	11.7	4.2	3.7
Ficus pollita	YL	8.0	8.1	11.6	17.5	4.3	4.0
Ficus zanzibarica	YL	10.3	9.7	22.1	20.6	2.1	1.9
Ficus zanzibarica	ML	11.2	10.9	13.8	10.3	3.2	3.2
Fluegea virosa	ML	7.3	7.4	23.2	21.4	3.9	4.0
Fluegea virosa	YL	7.3	6.4	23.4	17.3	4.1	4.4
Grewia holstii	YL	8.3	9.0	20.7	20.1	3.3	3.6
Grewia holstii	ML	8.8	9.6	16.3	11.8	4.7	4.7
Grewia plagiophylla	ML	10.0	9.2	18.3	17.7	-	-
Grewia vaughanii	YL	6.6	5.5	15.9	17.5	3.1	3.1
Grewia vaughanii	ML	11.8	10.5	23.2	23.6	-	-
Haplocoelum inopleum	YL	3.6	2.6	32.6	33.3	2.7	2.5
Haplocoelum inopleum	ML	6.9	5.7	14.0	13.0	3.2	3.5
Hibiscus rosa-senensis	YL	9.3	9.9	17.5	15.9	4.6	4.7
Hunteria zeylanica	ML	9.1	10.2	18.0	16.4	-	-
Hunteria zeylanica	YL	9.1	9.0	15.8	13.0	-	-
Lannea schweinfurthii	ML	9.1	10.2	14.4	15.8	-	-
Lannea schweinfurthii	YL	6.7	6.5	16.8	18.0	-	-
Lannea welwistchii	ML	9.6	9.4	14.0	16.0	-	-
Lecaniodiscus fraxinifolius	ML	6.3	6.2	13.0	13.4	-	-
Lecaniodiscus fraxinifolius	YL	3.6	3.9	9.0	10.0	-	-
Maerua triphylla	YL	5.7	3.9	24.2	23.3	6.0	5.5
Mangifera indica	YL	5.0	5.1	14.5	14.2	3.4	3.0
Markhamia zanzibarica	ML	8.3	9.3	20.0	21.3	-	-
Markhamia zanzibarica	YL	6.8	6.8	24.8	21.7	-	-
Millettia usaramensis	ML	8.7	10.8	23.6	23.7	-	-

Continued

Table A.1 Continued

		Ash		CP		Fat	
Sample	PP	Ref	Pred	Ref	Pred	Ref	Pred
Pithecellobium dulce	ML	11.0	11.9	27.3	26.9	-	-
Pithecellobium dulce	YL	10.2	10.9	22.5	22.3	-	-
Premna hildebrandtii	ML	11.1	9.9	21.3	22.7	-	-
Premna hildebrandtii	YL	9.7	9.5	21.6	19.8	-	-
Pycnocoma littoralis	ML	12.1	11.1	14.7	14.2	-	-
Rauvolfia mombasiana	YL	10.6	10.5	14.9	17.9	3.7	4.2
Sterculia africana	YL	7.5	7.7	12.1	11.3	3.9	3.7
Terminalia catappa	ML	10.0	10.5	14.5	16.1	-	-
Tinospora caffra	YL	6.8	6.9	14.9	15.6	2.8	2.9
Trema orientalis	YL	7.5	8.2	22.8	23.1	2.3	2.1
Trichilia emetica	YL	6.0	7.9	13.3	14.0	4.6	4.4
Trichilia emetica	ML	9.2	9.8	19.2	20.5	6.1	5.7
Uvaria acuminata	ML	10.4	11.2	18.9	18.2	-	-
Zanthoxylum chalybeum	YL	11.7	11.5	19.2	20.6	4.4	4.0
Zanthoxylum chalybeum	ML	12.5	11.6	18.3	20.0	-	-
Ziziphus mucronata	YL	9.8	11.0	18.6	19.1	4.4	4.4

pp = plant part; ML = msture leaf; YL = young leaf; CP = crude protein

Table A.2. Wet chemistry reference method (Ref) values vs. NIRS predictions (Pred) values for WSC, NDF, and ADF content of leaves

		WSC		NDF		ADF	
Sample	PP	Ref	Pred	Ref	Pred	Ref	Pred
Adansonia digitata	YL	4.4	4.3	31.2	41.1	21.7	22.2
Adansonia digitata	ML	2.4	2.2	42.7	37.0	20.9	22.8
Adenathera pavonina	ML	3.5	4.4	45.8	44.4	19.5	21.7
Adenathera pavonina	YL	3.2	3.3	34.6	40.8	19.3	21.0
Afzelia quanensis	YL	5.4	5.8	53.3	55.9	37.5	38.9
Afzelia quanensis	ML	5.2	5.3	61.5	56.5	39.1	38.1
Antiaris toxicaria	YL	5.0	5.2	53.0	45.7	31.9	26.5
Azadirachta indica	ML	3.4	2.6	45.5	41.6	32.4	31.8
Balanites maughamii	YL	4.7	5.2	33.0	39.7	16.5	19.6
Balanites maughamii	ML	5.8	5.8	45.5	43.8	31.2	31.7
Berchemia discolor	YL	6.7	6.6	45.8	39.4	21.6	20.9
Berchemia discolor	ML	4.6	5.5	52.9	47.8	30.3	26.5
Bougainvillea spectabilis	ML	2.8	2.6	45.4	47.3	19.5	18.6
Bougainvillea spectabilis	YL	3.8	2.7	37.7	42.1	17.0	15.8
Bourreria petiolaris	YL	6.0	5.6	47.2	41.5	25.0	22.1
Carpodiptera africana	ML	1.8	2.4	57.5	53.8	36.5	31.5
Cassia abbreviata	ML	5.6	5.8	55.7	62.4	35.1	35.7
Cassia abbreviata	YL	4.6	4.2	51.9	55.1	38.1	41.2
Cassia fistula	ML	2.9	3.5	55.0	52.8	38.3	41.6
Ceiba pentendra	ML	4.6	5.3	55.1	51.0	39.3	45.8
Cissus integrifolia	ML	5.7	4.8	78.9	80.4	19.2	21.0
Coccinia grandis	YL	2.7	3.1	50.5	44.6	12.1	9.9
Combretum schumannii	ML	2.1	2.5	35.6	37.6	25.1	22.5
Combretum schumannii	YL	2.6	2.7	28.6	29.9	24.8	22.5
Commiphora zanzibarica	YL	5.5	5.5	39.9	35.4	22.9	24.0
Commiphora zanzibarica	ML	5.3	4.9	35.7	41.1	29.4	24.2
Cordia goetzei	YL	2.2	1.7	45.9	35.6	38.6	36.0
Cussonia zimmermannii	YL	5.5	5.5	36.9	40.4	24.6	23.9
Cussonia zimmermannii	ML	5.6	5.4	41.6	45.7	25.9	30.1
Cyphostemma adenocaule	YL	4.6	5.3	50.2	43.9	23.4	18.4
Cyphostemma spp.	YL	3.9	3.9	45.4	40.8	21.3	20.0
Dalbergia vaccinifolia	ML	4.6	3.8	37.9	45.0	14.9	22.1
Dalbergia vaccinifolia	YL	4.4	4.3	41.5	46.8	18.5	21.8
Delonix regia	ML	4.1	3.7	31.6	32.9	22.6	27.4
Delonix regia	YL	4.3	3.7	29.2	33.6	29.2	37.7

Continued

Table A.2 Continued

		WSC		NDF		ADF	
Sample	PP	Ref	Pred	Ref	Pred	Ref	Pred
Diospyros squarosa	ML	5.1	5.5	60.8	61.5	42.8	39.8
Diospyros squarosa	YL	4.0	4.2	57.9	56.3	37.1	36.4
Discorea hirtiflora	ML	3.0	3.1	44.5	47.8	13.8	12.5
Feretia apodanthera	ML	5.9	5.8	33.3	37.0	25.9	26.2
Feretia apodanthera	YL	4.8	5.2	38.3	34.2	23.1	24.6
Ficus exasperata	ML	3.7	3.5	43.1	36.3	15.0	14.2
Ficus exasperata	YL	4.4	4.4	50.7	47.5	22.5	20.7
Ficus pollita	ML	5.5	5.4	45.1	43.4	34.8	30.1
Ficus pollita	YL	5.7	5.5	36.8	40.9	25.7	29.7
Ficus zanzibarica	YL	3.5	3.9	31.7	29.1	23.9	22.5
Ficus zanzibarica	ML	4.6	5.1	32.8	42.0	29.1	28.3
Fluegea virosa	ML	3.4	3.3	51.0	54.0	26.0	27.8
Fluegea virosa	YL	3.9	3.8	52.6	55.8	28.4	30.5
Grewia holstii	YL	5.0	4.7	61.8	55.7	28.6	26.3
Grewia holstii	ML	3.7	3.3	62.9	61.1	34.9	33.0
Grewia plagiophylla	ML	2.1	2.0	70.1	68.6	46.8	37.4
Grewia vaughanii	YL	5.0	5.4	48.9	50.0	27.4	28.8
Grewia vaughanii	ML	2.3	2.1	60.0	60.9	26.4	38.6
Haplocoelum inopleum	YL	6.5	6.2	42.2	52.1	12.9	15.7
Haplocoelum inopleum	ML	5.9	6.4	67.5	69.7	47.4	46.4
Hibiscus rosa-senensis	YL	5.3	4.7	39.3	42.1	17.6	20.2
Hunteria zeylanica	ML	1.5	2.4	64.6	64.2	47.6	50.1
Hunteria zeylanica	YL	2.0	1.6	58.0	56.1	35.3	38.0
Lannea schweinfurthii	ML	1.8	2.2	45.1	44.8	34.0	33.0
Lannea schweinfurthii	YL	1.5	2.3	40.7	47.9	32.7	36.5
Lannea welwistchii	ML	2.0	2.0	48.9	52.0	34.4	35.2
Lecaniodiscus fraxinifolius	ML	2.9	3.0	62.5	68.3	48.2	48.7
Lecaniodiscus fraxinifolius	YL	3.1	3.3	58.0	50.1	48.0	38.0
Maerua triphylla	YL	2.7	3.1	38.6	43.0	18.4	16.6
Mangifera indica	YL	6.1	6.0	43.2	37.7	24.7	24.8
Markhamia zanzibarica	ML	1.5	2.3	65.5	60.5	40.9	41.2
Markhamia zanzibarica	YL	2.4	2.3	45.5	41.4	26.6	24.1
Millettia usaramensis	ML	1.8	2.5	58.4	60.8	34.6	32.0
Pithecellobium dulce	ML	3.2	2.4	50.2	48.2	23.5	22.3
Pithecellobium dulce	YL	2.8	2.1	31.7	28.5	14.8	12.3
Premna hildebrandtii	ML	1.9	2.2	65.1	56.0	34.4	33.0

Continued

Table A.2 Continued

		WSC		NDF		ADF	
Sample	PP	Ref	Pred	Ref	Pred	Ref	Pred
Premna hildebrandtii	YL	1.9	1.7	50.4	49.9	33.8	32.0
Pycnocoma littoralis	ML	1.7	2.5	36.8	35.6	23.6	22.3
Rauvolfia mombasiana	YL	5.8	5.1	39.0	35.5	17.3	15.8
Sterculia africana	YL	3.9	2.9	61.2	55.4	41.1	37.0
Terminalia catappa	ML	5.8	6.2	54.8	57.3	39.4	41.2
Tinospora caffra	YL	1.1	0.9	40.8	37.7	18.4	16.2
Trema orientalis	YL	5.3	5.1	47.1	48.5	22.4	25.7
Trichilia emetica	YL	6.4	5.8	54.5	46.7	40.2	38.7
Trichilia emetica	ML	3.2	3.3	43.9	51.1	35.9	37.7
Uvaria acuminata	ML	2.6	2.8	45.3	43.7	33.7	31.1
Zanthoxylum chalybeum	YL	4.0	4.4	41.4	49.9	24.3	27.7
Zanthoxylum chalybeum	ML	2.3	2.1	39.3	46.8	27.2	30.7
Ziziphus mucronata	YL	4.4	4.2	49.1	54.7	25.1	29.9

pp = plant part; ML = mature leaf; YL = young leaf; WSC = water soluble carbohydrate; NDF = neutral detergent fiber; ADF = acid detergent fiber

Table A.3. Wet chemistry reference method (Ref) values vs. NIRS predictions (Pred) values for ash, CP, and fat content of fruits and flowers

		Ash		CP		Fat	
Sample	PP	Ref	Pred	Ref	Pred	Ref	Pred
Adansonia digitata	FLB	6.9	7.3	8.5	12.8	1.2	2.1
Adenia gummifera	FL	6.7	6.1	19.8	20.3	3.2	2.7
Adenia gummifera	UFR	3.6	3.6	-	-	3.2	3.9
Antiaris toxicaria	UFR	-	-	9.7	9.3	-	-
Bougainvillea spectabilis	FL	7.8	8.0	21.8	25.9	-	-
Bauhinia variegata	UFR	3.4	4.0	21.2	24.3	-	-
Cyphostemma adenocaule	UFR	7.4	6.3	13.9	16.7	6.1	5.5
Canavalia cathartica	UFR	2.9	3.4	-	-	1.4	0.7
Cassia fistula	FL	4.0	4.1	17.7	19.9	5.5	4.9
Coccinia grandis	UFR	-	-	23.0	21.8	5.6	5.3
Cissus integrifolia	UFR	10.7	10.6	-	-	3.8	4.9
Combretum schumannii	FL	6.6	5.6	-	-	2.9	2.7
Cussonia zimmermannii	FLB	8.7	8.6	10.6	12	1.6	2.3
Discorea hirtiflora	FL	-	-	-	-	-	-
Delonix regia	FL	4.4	4.8	13.4	11.9	1.5	2.3
Delonix regia	FLB	4.0	3.9	13.6	13.4	3.5	2.1
Delonix regia	RFR	3.7	3.7	16.8	15.5	2.1	2.4
Delonix regia	UFR	3.9	4.5	12.2	13.2	0.5	0.2
Dalbergia vaccinifolia	UFR	-	-	9.9	8.9	12.1	11.7
Ficus bubu	UFR	9.6	8.2	8.3	13.5	4.7	3.8
Ficus exasperata	UFR	9.6	9.9	15.1	16.9	4.6	3.8
Fernandoa magnifica	FL	6.2	6.1	19.8	12.2	1.4	1.6
Ficus sycomorus	UFR	6.4	6.6	7.1	8.8	2.6	2.4
Fluegea virosa	UFR	3.8	5.3	-	-	6.8	7.2
Ficus zanzibarica	UFR	5.6	5.5	7.4	8.1	3.2	2.2
Gliricida sepium	FL	4.0	3.4	11.7	10.7	2.2	3.3
Hunteria zeylanica	UFR	6.0	6.3	13.5	11.2	4.9	4.3
Lecaniodiscus fraxinifolius	FL	5.5	4.6	19.6	15.7	3.7	3.0
Lecaniodiscus fraxinifolius	RFR	2.6	2.6	-	-	4.2	4.7
Lecaniodiscus fraxinifolius	UFR	3.0	2.7	9.9	7.3	2.9	2.8
Ludia mauritiana	UFR	3.5	3.8	13.6	12.6	-	-
Lepisanthes senegalensis	RFR	3.4	4.5	7.9	8.9	1.3	1.9
Lannea welwistchii	UFR	-	-	7.4	7.3	11.3	10.4
Monodora grandidieri	FL	6.5	6.3	24.9	21.1	1.5	1.2

Continued

Table A.3 Continued

		Ash		CP		Fat	
Sample	PP	Ref	Pred	Ref	Pred	Ref	Pred
Moringa oleifera	FL	5.8	5.3	18.0	18.3	2.6	2.5
Moringa oleifera	UFR	7.0	7.7	-	-	0.9	0.4
Millettia usaramensis	FLB	6.0	6.0	26.0	22.9	2.2	3.2
Millettia usaramensis	UFR	4.2	4.5	9.8	5.3	3.3	3.6
Markhamia zanzibarica	FLB	6.4	5.3	16.6	17.7	2.9	2.0
Plumeria cultiver	FL	6.9	5.2	11.9	14.5	3.9	3.2
Pithecellobium dulce	FL	5.1	5.8	22.2	22.3	2.5	3.9
Pithecellobium dulce	FLB	5.1	5.9	27.5	28.4	3.6	3.9
Pithecellobium dulce	UFR	4.3	3.2	20.9	16.7	1.2	1.9
Premna hildebrandtii	FLB	6.7	6.7	17.1	11.9	2.3	3.1
Premna hildebrandtii	UFR	-	-	8.7	9.9	3.9	4.6
Plumeria obtusa	FL	6.8	6.5	7.5	8.6	3.9	4.2
Plumeria rubra	FL	-	-	6.7	7.5	-	-
Spathodea campanulata	FL	-	-	8.2	9.6	3.9	3.0
Sideroxylon inerme	RFR	-	-	-	-	11.9	11.1
Sideroxylon inerme	UFR	3.9	4.7	10.2	11.9	8.8	9.7
Tinospora caffra	UFR	6.1	5.8	10.5	8.8	2.0	1.6
Tamarindus indica	UFR	4.1	3.7	8.7	9.2	1.6	2.7
Trema orientalis	UFR	10.9	11.0	16.9	14.6	5.5	4.4

pp = plant part; FL = flower; FLB = flower bud; RFR = ripe fruit; UFR = unripe fruit; CP = crude protein

Table A.4. Wet chemistry reference method (Ref) values vs. NIRS predictions (Pred) values for WSC, NDF, and ADF content of fruits and flowers

		WSC		NDF		ADF	
Sample	PP	Ref	Pred	Ref	Pred	Ref	Pred
Adansonia digitata	FLB	-	-	51.7	58.8	31.6	32.7
Adenia gummifera	FL	9.9	4.9	60.1	50.2	44.6	52.1
Adenia gummifera	UFR	6.7	6.4	81.5	69.8	12.1	14.3
Antiaris toxicaria	UFR	-	-	60.8	51.1	15.2	11.9
Bougainvillea spectabilis	FL	-	-	53.4	61.0	22.5	27.4
Bauhinia variegata	UFR	5.4	5.0	70.7	75.7	26.7	31.4
Cyphostemma adenocaule	UFR	1.4	0.4	54.0	47.2	42.3	37.8
Canavalia cathartica	UFR	9.4	8.4	42.2	33.6	-	-
Cassia fistula	FL	8.4	8.8	-	-	-	-
Coccinia grandis	UFR	6.0	9.0	56.8	56.8	38.4	35.5
Cissus integrifolia	UFR	4.2	7.5	58.3	54.1	34.6	26.9
Combretum schumannii	FL	4.1	4.0	30.1	32.8	17.2	17.6
Cussonia zimmermannii	FLB	7.3	7.3	46.3	52.7	35.4	38.6
Discorea hirtiflora	FL	8.1	6.7	55.5	51.6	37.8	33.0
Delonix regia	FL	11.7	12	46.3	45.5	31.6	28.9
Delonix regia	FLB	8.3	7.4	54.2	51.2	40.2	35.8
Delonix regia	RFR	12.9	10.0	46.4	43.1	-	-
Delonix regia	UFR	7.4	6.4	59.0	51.2	-	-
Dalbergia vaccinifolia	UFR	9.7	11.5	-	-	-	-
Ficus bubu	UFR	5.8	4.4	57.7	61.1	-	-
Ficus exasperata	UFR	5.0	6.8	50.4	47.4	30.9	31.6
Fernandoa magnifica	FL	-	-	37.5	39.8	20.4	24.3
Ficus sycomorus	UFR	6.1	9.9	51.3	53.8	48.4	41.3
Fluegea virosa	UFR	6.0	5.2	73.7	72.2	57.4	53.3
Ficus zanzibarica	UFR	9.9	9.0	47.9	55.1	39.6	42.1
Gliricida sepium	FL	34	31.7	36.6	30.5	24.7	26.7
Hunteria zeylanica	UFR	8.6	14.1	48.6	46.0	26.3	33.8
Lecaniodiscus fraxinifolius	FL	8.6	8.3	45.8	56.3	29.4	32.2
Lecaniodiscus fraxinifolius	RFR	15.4	16.3	42.8	47.0	17.2	15.2
Lecaniodiscus fraxinifolius	UFR	9.3	8.1	56.7	49.0	26.0	25.1
Ludia mauritiana	UFR	10.0	9.0	25.0	24.2	15.1	17.1
Lepisanthes senegalensis	RFR	-	-	30.8	39.7	13.4	20.5
Lannea welwistchii	UFR	2.3	4.9	74.9	76.2	-	-
Monodora grandidieri	FL	3.7	4.9	49.0	48.2	30.2	28.7

Continued

Table A.4 Continued

		WSC		NDF		ADF	
Sample	PP	Ref	Pred	Ref	Pred	Ref	Pred
Moringa oleifera	FL	13.8	11.7	52.2	46.1	30.7	22.6
Moringa oleifera	UFR	21.0	21.8	32.6	36.4	10.1	10.2
Millettia usaramensis	FLB	-	-	51.7	53.0	37.2	36.6
Millettia usaramensis	UFR	8.2	6.6	-	-	53.0	47.0
Markhamia zanzibarica	FLB	6.7	7.1	62.8	63.7	46.8	45.1
Plumeria cultiver	FL	13.6	17.3	33.1	39.6	25.0	24.2
Pithecellobium dulce	FL	6.5	7.5	54.2	52.2	31.2	30.3
Pithecellobium dulce	FLB	7.0	6.9	52.4	60.0	28.7	32.6
Pithecellobium dulce	UFR	6.3	9.8	56.8	48.5	35.9	27.0
Premna hildebrandtii	FLB	9.4	4.9	63.9	64.9	44.2	46.6
Premna hildebrandtii	UFR	5.6	4.6	81.9	79.9	-	-
Plumeria obtusa	FL	19.8	16.8	33.0	34.5	18.2	26.6
Plumeria rubra	FL	-	-	29.1	37.7	22.4	23.7
Spathodea campanulata	FL	-	-	29.0	26.0	22.5	24.0
Sideroxylon inerme	RFR	17.8	16.1	53.1	44.2	32.2	30.3
Sideroxylon inerme	UFR	8.9	8.7	33.6	32.6	41.7	48.9
Tinospora caffra	UFR	16.7	17.6	64.4	58.1	35.6	28.3
Tamarindus indica	UFR	2.3	3.2	63.6	60.8	45.8	50.1
Trema orientalis	UFR	3.0	1.6	50.2	59.1	30.9	30.1

pp = plant part; FL = flower; FLB = flower bud; RFR = ripe fruit; UFR = unripe fruit; WSC = water soluble carbohydrate; NDF = neutral detergent fiber; ADF = acid detergent fiber

Appendix B. Mean nutritional content of all plant samples using wet chemistry assays and NIRS prediction equations

Table B.1. Mean nutritional content of all leaf samples

Sample	PP	Ash	CP	Fat	ADF	NDF	AP	WSC	TNC
Acalypha fruticosa	ML	4.6	14.7	2.7	11.1	29.0	12.0	2.7	51.6
Acalypha fruticosa	YL	10.0	21.4	4.9	11.0	32.5	20.0	3.7	32.7
Adansonia digitata	ML	10.1	23.9	3.6	23.7	42.3	21.2	3.2	22.8
Adansonia digitata	YL	10.3	23.6	4.6	25.3	57.5	19.8	3.0	7.8
Adenathera pavonina	ML	7.8	20.1	3.5	33.2	54.2	15.5	2.3	18.9
Adenathera pavonina	YL	8.4	20.6	3.1	23.6	48.9	17.4	2.2	22.2
Adenia gummifera	ML	8.5	17.4	3.8	14.7	50.9	13.3	2.9	23.3
Adenia gummifera	YL	10.4	20.5	5.9	17.0	62.6	15.7	2.2	5.4
Afzelia quanensis	ML	10.6	23.1	3.0	38.3	47.5	21.0	2.2	17.9
Afzelia quanensis	YL	10.6	16.6	2.9	28.9	50.1	12.5	1.5	23.8
Alchornea laxiflora	ML	3.6	10.0	3.0	32.4	51.0	3.0	3.3	39.5
Alchornea laxiflora	YL	10.1	15.9	3.4	25.3	44.9	12.0	2.1	29.7
Almandra cathatica	ML	14.9	16.5	3.9	23.0	37.3	12.7	2.2	31.2
Almandra cathatica	YL	9.1	14.5	3.7	26.6	41.8	11.7	2.6	33.7
Antiaris toxicaria	YL	10.2	19.5	3.8	26.9	47.1	16.3	3.0	22.6
Azadirachta indica	ML	7.5	14.1	3.0	27.8	62.3	7.7	2.3	19.4
Balanites maughamii	ML	8.9	17.6	3.2	31.6	57.6	15.2	4.9	15.0
Balanites maughamii	YL	7.9	16.2	3.1	19.5	50.1	14.5	2.9	24.5
Berchemia discolor	ML	8.7	15.3	3.3	26.6	41.8	12.4	6.2	33.8
Berchemia discolor	YL	8.0	19.6	3.8	20.8	39.6	17.4	5.4	31.1
Bougainvillea spectabilis	ML	9.0	18.5	4.7	17.3	44.9	15.0	4.2	26.4
Bougainvillea spectabilis	YL	10.1	19.1	4.2	15.8	42.2	16.4	5.3	27.2
Bourreria petiolaris	ML	10.2	23.3	3.6	22.5	36.8	21.5	3.1	27.9
Bourreria petiolaris	YL	16.7	16.9	3.9	22.2	63.9	13.7	5.0	1.8
Brassia actinophylla	ML	11.6	20.0	3.7	29.7	46.1	16.9	2.1	21.6
Brassia actinophylla	YL	12.1	14.6	4.1	31.8	40.1	11.9	4.3	31.8
Bridelia cathatica	ML	8.0	18.3	3.4	37.4	52.0	16.1	5.3	20.5
Bridelia cathatica	YL	4.9	19.2	4.3	44.8	55.9	18.4	5.8	16.4
Capparis viminea	ML	4.8	21.3	3.8	36.8	48.7	18.7	5.6	24.0
Capparis viminea	YL	9.5	12.7	6.2	50.1	55.2	9.9	3.1	19.3
Carpodiptera africana	ML	7.4	21.2	5.4	32.0	53.9	19.3	3.3	14.1
Cassia abbreviata	ML	8.0	17.9	4.1	36.6	54.6	14.4	5.2	18.9
Cassia abbreviata	YL	10.7	16.5	4.2	38.9	39.9	15.4	4.8	29.8
Cassia fistula	ML	8.1	14.0	4.4	37.5	42.4	10.9	3.8	34.1
Cassia fistula	YL	11.0	13.3	4.0	36.7	43.6	10.1	5.1	31.2
Cassia spp.	ML	6.2	27.3	3.3	37.0	47.8	26.4	4.7	16.3
Cassia spp.	YL	8.5	11.9	4.2	37.8	67.3	8.6	4.4	11.4
Ceiba pentandra	ML	7.5	16.7	4.4	43.9	44.5	14.0	5.8	29.6
Ceiba pentandra	YL	7.2	13.6	6.1	26.2	48.4	8.6	5.7	29.7
Cissus integrifolia	ML	11.4	19.9	5.0	20.8	51.9	17.4	4.3	14.3
Cissus integrifolia	YL	8.8	24.0	4.2	12.8	36.0	23.8	4.5	27.2
Cissus quadrangularis	ML	6.5	21.8	4.8	20.8	49.5	19.8	4.5	19.5

Continued

Table B.1
Continued

Sample	PP	Ash	CP	Fat	ADF	NDF	AP	WSC	TNC
Cissus quadrangularis	YL	9.9	19.8	6.1	13.5	44.2	18.2	4.4	21.6
Clerodendrum glabrum	ML	9.5	11.8	2.9	23.1	61.3	7.9	3.4	18.4
Clerodendrum glabrum	YL	7.2	18.6	5.3	22.9	53.0	15.3	5.1	19.2
Coccina spp.	YL	0.8	14.5	3.9	21.4	40.6	13.3	6.0	41.5
Coccinia grandis	ML	9.1	14.7	4.5	12.6	45.8	11.7	4.0	29.0
Coccinia grandis	YL	8.5	18.7	3.6	10.2	45.5	15.4	4.8	27.0
Combretum schumannii	ML	7.3	15.8	3.9	23.9	44.5	11.9	5.4	32.4
Combretum schumannii	YL	9.1	18.1	4.0	20.8	38.4	14.2	5.2	34.3
Commiphora zanzibarica	ML	8.8	18.2	3.5	24.4	41.0	15.5	5.8	31.2
Commiphora zanzibarica	YL	7.2	16.6	3.4	21.6	51.2	14.6	5.0	23.7
Cordia goetzei	ML	2.3	33.3	4.1	28.6	50.7	29.2	6.2	13.6
Cordia goetzei	YL	6.7	16.2	4.4	32.2	47.8	12.4	5.4	28.7
Cussonia zimmermannii	ML	8.0	20.3	3.3	29.7	50.6	17.3	4.8	20.7
Cussonia zimmermannii	YL	11.9	16.2	3.4	23.8	34.6	13.9	4.5	36.2
Cyphostemma adenocaule	ML	9.5	14.7	4.3	17.7	35.4	13.5	4.8	37.2
Cyphostemma adenocaule	YL	9.0	18.8	4.4	17.9	44.5	14.9	5.3	27.1
Cyphostemma spp.	ML	9.0	19.0	3.1	15.7	42.4	15.7	4.8	29.9
Cyphostemma spp.	YL	5.5	21.1	3.4	20.1	50.2	18.5	3.9	22.4
Dalbergia vaccinifolia	ML	10.9	14.8	5.7	20.8	47.7	11.4	4.4	24.3
Dalbergia vaccinifolia	YL	8.3	14.7	4.4	21.2	54.5	11.9	3.5	20.9
Delonix regia	ML	10.9	13.5	4.9	23.4	43.9	11.8	4.9	28.4
Delonix regia	YL	10.0	14.9	3.3	29.5	58.9	10.9	5.2	16.9
Diospyros squarosa	ML	8.4	19.1	3.9	40.2	59.3	16.2	5.7	12.1
Diospyros squarosa	YL	8.9	11.7	4.6	36.6	40.9	10.1	4.2	35.5
Discorea hirtiflora	ML	5.7	18.7	6.2	12.6	49.2	15.3	3.1	23.6
Drypetes reticulata	ML	10.1	15.4	3.4	45.5	56.1	12.0	3.7	18.5
Drypetes reticulata	YL	9.7	20.4	3.4	31.9	42.4	16.8	5.4	27.7
Feretia apodanthera	ML	9.7	24.5	4.4	24.4	49.1	23.7	4.0	13.2
Feretia apodanthera	YL	7.9	14.3	4.5	26.6	58.5	10.7	5.2	18.3
Fernandoa magnifica	ML	14.7	13.3	3.3	30.5	49.7	9.2	5.5	23.1
Fernandoa magnifica	YL	11.0	13.3	4.3	29.2	43.6	10.1	5.1	31.0
Ficus bubu	YL	3.1	12.5	4.1	28.4	59.8	9.2	5.6	23.9
Ficus exasperata	ML	11.2	14.8	3.8	14.3	38.8	12.9	4.7	33.4
Ficus exasperata	YL	8.4	22.1	4.0	20.9	42.1	19.5	5.5	26.0
Ficus pollita	ML	12.7	25.7	4.6	30.4	51.8	24.4	4.5	6.5
Ficus pollita	YL	11.2	21.2	3.5	29.7	50.3	17.8	5.5	17.2
Ficus sur	ML	18.5	24.7	2.8	22.0	43.7	21.3	9.8	13.7
Ficus sur	YL	8.0	23.4	3.4	22.0	41.8	21.8	5.8	25.0

Continued

Table B.1
Continued

Sample	PP	Ash	CP	Fat	ADF	NDF	AP	WSC	TNC
Ficus sycomorus	YL	8.6	29.2	3.6	26.4	45.5	27.1	3.2	15.2
Ficus zanzibarica	ML	8.4	8.3	3.0	28.3	44.1	5.4	4.3	39.1
Ficus zanzibarica	YL	7.0	20.6	2.8	22.5	48.9	19.9	5.8	21.4
Flacourtia indica	ML	9.0	26.5	4.3	36.0	43.0	26.8	3.8	16.8
Flacourtia indica	YL	11.0	20.7	3.6	16.0	44.1	19.4	5.4	21.8
Flueggea virosa	ML	7.9	17.0	3.1	27.7	52.5	13.8	5.3	22.8
Flueggea virosa	YL	9.8	14.4	3.0	27.0	49.7	9.6	4.8	28.0
Gliricida sepium	ML	13.6	10.1	5.2	23.1	48.3	7.9	4.0	25.0
Gliricida sepium	YL	6.9	13.7	4.9	21.4	63.3	12.7	7.2	12.1
Grewia holstii	ML	15.0	15.6	3.3	33.3	44.7	13.6	4.3	23.4
Grewia holstii	YL	12.5	13.7	3.6	24.5	44.9	10.9	5.5	28.1
Grewia plagiophylla	ML	7.6	19.9	4.4	44.7	62.2	15.5	3.9	10.4
Grewia vaughanii	ML	11.9	21.9	4.8	29.1	52.2	17.7	6.9	13.4
Grewia vaughanii	YL	14.2	20.1	5.5	28.4	55.9	17.4	6.0	6.9
Haplocoelum inopleum	ML	8.1	21.8	3.1	44.4	48.9	18.9	4.4	21.0
Haplocoelum inopleum	YL	7.9	17.9	3.3	23.7	47.6	13.4	5.3	27.8
Hibiscus rosa-senensis	ML	10.7	19.7	2.8	21.2	58.6	18.0	4.1	9.9
Hibiscus rosa-senensis	YL	10.9	9.5	3.4	19.4	52.1	5.9	5.2	27.7
Hoslundia opposita	ML	10.6	10.1	4.2	34.4	48.5	8.0	1.6	28.7
Hoslundia opposita	YL	8.2	15.8	3.4	35.6	41.2	14.2	5.2	32.9
Hunteria zeylanica	ML	8.6	20.1	4.8	40.3	57.1	16.9	4.8	12.5
Hunteria zeylanica	YL	7.9	14.8	4.6	38.0	58.0	10.6	4.6	19.0
Jasminium merijohonnes	ML	8.2	19.9	5.2	14.1	48.8	18.4	5.4	19.4
Jasminium merijohonnes	YL	9.2	16.0	4.6	17.3	49.1	12.2	4.2	24.9
Jasminium spp.	ML	11.1	12.3	3.9	28.6	54.4	7.1	5.5	23.5
Jasminium spp.	YL	10.1	10.2	3.5	28.0	43.4	6.0	5.4	37.1
Lannea schweinfurthii	ML	10.3	23.8	3.8	32.7	65.4	20.3	5.2	0.3
Lannea schweinfurthii	YL	9.2	14.2	4.3	34.5	56.3	12.7	3.1	17.5
Lannea welwistchii	ML	10.4	16.9	3.8	36.9	45.1	13.6	5.1	27.0
Lannea welwistchii	YL	10.0	29.9	4.0	34.5	48.5	27.8	3.0	9.7
Lecaniodiscus fraxinifolius	ML	10.6	21.1	3.7	47.4	53.6	19.9	4.9	12.2
Lecaniodiscus fraxinifolius	YL	13.4	20.1	3.4	36.1	68.4	17.9	6.9	3.1
Lepisanthes senegalensis	ML	15.7	21.8	3.9	39.7	46.1	20.7	3.8	13.6
Lepisanthes senegalensis	YL	8.8	11.5	3.9	31.3	45.0	9.7	2.8	32.6
Maerua triphylla	ML	4.8	38.3	5.4	17.2	52.3	35.8	3.9	1.8
Maerua triphylla	YL	8.9	19.0	4.7	21.1	43.4	17.0	4.6	26.0
Mangifera indica	ML	11.2	18.4	4.0	37.7	40.7	16.3	4.6	27.7
Mangifera indica	YL	9.4	12.9	5.0	27.9	47.9	9.8	4.9	27.9

Continued

Table B.1
Continued

Sample	PP	Ash	CP	Fat	ADF	NDF	AP	WSC	TNC
Markhamia zanzibarica	ML	7.7	11.6	4.6	41.4	55.9	7.8	2.9	24.1
Markhamia zanzibarica	YL	7.0	12.4	3.2	23.8	49.1	10.8	5.4	30.0
Mayena tetraphylla	ML	11.6	22.6	4.1	25.3	47.6	21.5	5.4	15.3
Mildbraedii carpinifolia	ML	15.9	12.6	4.3	32.2	40.1	10.1	5.6	29.6
Mildbraedii carpinifolia	YL	11.8	12.2	4.4	31.6	43.8	10.0	5.8	30.1
Millettia usaramensis	ML	9.0	14.7	4.2	32.0	43.1	12.1	4.5	31.6
Millettia usaramensis	YL	9.2	14.5	4.0	18.8	38.0	13.5	4.6	35.3
Monodora grandidieri	ML	13.6	24.2	4.9	27.6	45.1	22.9	3.6	13.5
Monodora grandidieri	YL	12.3	26.6	4.8	21.1	54.3	23.4	5.4	5.2
Moringa oleifera	ML	11.8	14.3	5.0	10.0	40.5	12.2	5.1	30.6
Moringa oleifera	YL	9.4	17.4	4.6	13.5	49.9	15.7	5.8	20.4
Oncoba spinosa	ML	9.2	15.8	4.4	27.6	48.7	11.7	5.1	26.0
Oncoba spinosa	YL	6.1	19.0	3.9	33.9	55.6	15.6	3.9	18.7
Pithecellobium dulce	ML	9.0	22.9	4.2	22.2	40.1	21.2	4.6	25.5
Pithecellobium dulce	YL	8.4	17.4	3.6	10.4	42.5	13.9	5.4	31.6
Plumeria cultiver	ML	8.4	17.5	2.9	21.2	52.3	14.1	4.3	22.2
Plumeria cultiver	YL	9.3	23.4	2.5	20.5	49.4	21.5	4.1	17.2
Plumeria obtusa	YL	8.3	21.9	4.3	25.0	38.0	19.2	6.5	30.1
Plumeria rubra	ML	5.2	20.2	3.8	30.0	39.5	18.4	1.1	33.1
Plumeria rubra	YL	5.8	10.6	3.0	22.8	41.5	8.6	5.5	41.1
Premna discolour	ML	5.8	27.0	3.4	25.0	47.4	23.3	5.0	20.2
Premna discolour	YL	7.8	20.8	3.9	26.5	43.5	17.5	5.2	27.3
Premna hildebrandtii	ML	7.9	20.8	3.7	34.8	49.3	19.1	4.3	19.9
Premna hildebrandtii	YL	9.1	22.1	3.3	28.4	40.8	20.1	4.1	26.7
Pycnocoma littoralis	ML	8.9	9.8	3.6	22.4	47.7	7.1	5.5	32.7
Rauvolfia mombasiana	ML	6.9	7.8	2.9	17.1	34.6	4.5	6.7	51.1
Rauvolfia mombasiana	YL	6.0	12.4	3.8	15.8	44.3	8.2	5.0	37.6
Salacia erecta	ML	7.8	6.9	1.7	31.8	37.5	1.7	6.7	51.4
Salacia steuhlmania	YL	7.6	24.6	2.9	23.7	60.3	22.3	2.8	6.9
Senna seamea	ML	8.9	14.6	4.0	38.4	38.1	12.2	5.7	36.8
Senna seamea	YL	12.8	22.5	2.4	18.7	42.6	22.0	3.8	20.1
Sideroxylon inerme	ML	10.9	12.9	3.7	44.2	38.4	10.2	5.9	36.8
Sideroxylon inerme	YL	7.2	13.7	1.9	41.1	40.4	12.5	5.9	38.0
Spathodea campanulata	ML	2.3	33.3	4.2	27.9	50.7	29.2	6.2	13.5
Spathodea campanulata	YL	7.4	12.6	4.0	20.8	47.7	7.1	5.4	33.7
Sterculia africana	ML	13.0	10.2	2.5	35.2	40.1	7.1	3.7	37.3
Sterculia africana	YL	7.7	16.4	4.5	35.9	49.9	11.8	5.9	26.2
Suregada zanzibariensis	ML	7.4	13.9	3.8	33.4	42.1	11.9	5.8	34.9

Continued

Table B.1
Continued

Sample	PP	Ash	CP	Fat	ADF	NDF	AP	WSC	TNC
Tamarindus indica	ML	7.7	21.4	5.0	30.0	40.4	18.9	5.5	28.0
Tamarindus indica	YL	10.0	13.5	3.3	31.2	39.1	10.7	4.3	36.9
Terminalia catappa	ML	6.4	10.0	6.3	41.1	59.3	4.8	6.2	23.1
Thevetia peruviana	ML	4.4	12.2	2.8	21.9	38.7	11.7	3.4	42.4
Tinospora caffra	ML	5.0	20.6	2.2	14.7	53.1	18.8	4.1	20.9
Tinospora caffra	YL	6.9	14.7	2.9	16.7	40.9	11.6	5.3	37.7
Trema orientalis	ML	8.0	16.6	3.6	31.8	45.4	15.6	5.8	27.4
Trema orientalis	YL	8.9	18.5	3.5	25.4	39.3	16.2	4.9	32.1
Trianolepis africana	ML	8.1	14.4	4.4	26.5	40.1	9.4	6.9	38.0
Trianolepis africana	YL	9.1	25.3	4.1	21.1	47.9	22.3	4.4	16.6
Trichilia emetica	ML	9.3	16.1	4.5	31.6	37.9	14.4	5.4	34.0
Trichilia emetica	YL	8.1	25.8	4.4	36.7	48.7	23.6	3.7	15.1
Uvaria acuminata	ML	11.1	15.4	3.1	31.5	41.0	11.8	3.9	33.1
Uvaria welwistchii	ML	4.1	12.9	4.1	34.0	36.9	10.2	5.4	44.7
Vepris eugenifolia	ML	3.3	27.0	3.6	27.9	52.9	22.6	3.7	17.6
Vernonia hildebrandtii	ML	8.0	21.7	3.2	28.3	44.5	21.2	4.2	23.1
Vernonia hildebrandtii	YL	10.2	23.3	2.8	24.5	36.8	21.5	3.1	28.7
Ximenia americana	ML	7.2	11.9	2.6	24.0	49.4	10.1	2.1	30.8
Ximenia americana	YL	5.8	21.1	4.6	28.7	39.2	18.9	5.2	31.5
Zanthoxylum chalybeum	ML	10.7	24.3	3.7	29.5	46.6	22.7	5.2	16.3
Zanthoxylum chalybeum	YL	8.3	20.6	3.4	16.9	46.0	17.7	5.1	24.6
Zanthoxylum spp.	ML	9.6	19.0	3.6	18.5	49.5	16.5	6.2	20.7
Ziziphus mucronata	ML	4.9	19.2	3.3	33.6	55.9	18.4	5.8	17.5
Ziziphus mucronata	YL	6.7	22.4	3.3	25.2	42.8	20.7	5.9	26.4

pp = plant part; ML = mature leaf; YL = young leaf; CP = crude protein; ADF = acid detergent fiber; NDF = neutral detergent fiber; AP = available protein; WSC = water soluble carbohydrate; TNC = total nonstructural carbohydrate

Table B.2. Mean nutritional content of all fruit samples

Sample	PP	Ash	CP	Fat	ADF	NDF	AP	WSC	TNC
Adenathera pavonina	UFR	4.3	18.8	0.9	44.8	19.5	14.2	8.7	35.8
Adenia gummifera	UFR	3.5	6.8	3.7	79.5	55.0	7.1	6.6	6.2
Antiaris toxicaria	UFR	6.4	9.4	2.3	53.0	12.4	10.7	13.6	27.6
Bauhinia variegata	UFR	3.8	24.7	4.7	66.0	29.9	22.8	4.9	2.7
Canvalia cathartica	RFR	3.0	19.6	0.7	37.7	13.4	19.6	6.2	39.0
Cissus integrifolia	UFR	10.8	17.1	4.8	54.7	28.4	15.2	6.5	14.5
Coccinia grandis	UFR	4.8	21.9	5.3	56.8	36.2	16.4	8.6	16.6
Cyphostemma adenocaule	UFR	6.8	16.4	5.6	49.2	40.2	9.0	1.0	29.5
Dalbergia vaccinifolia	UFR	14.0	12.8	12.6	65.1	59.9	7.4	10.9	0.9
Delonix regia	RFR	3.0	22.7	2.7	57.9	32.0	19.3	4.5	17.1
Delonix regia	UFR	4.5	13.0	0.2	52.8	37.7	9.0	6.6	33.5
Ficus bubu	UFR	8.2	9.7	3.6	65.8	57.3	6.0	3.9	16.4
Ficus exasperata	UFR	9.1	18.7	3.6	49.6	37.3	14.8	5.1	22.8
Ficus sycomorus	UFR	6.6	8.5	2.4	53.4	42.5	3.6	9.4	34.0
Ficus zanzibarica	UFR	5.3	9.3	3.7	58.6	48.1	4.6	7.6	27.8
Flueggea virosa	UFR	4.8	7.3	7.2	72.0	51.9	6.0	5.5	9.9
Hunteria zeylanica	UFR	6.3	11.5	3.8	46.2	32.6	7.9	14.7	35.8
Lannea welwistchii	UFR	4.6	7.2	10.6	76.1	62.7	6.2	4.5	2.5
Lecaniodiscus fraxinifolius	RFR	2.7	2.6	4.6	45.6	14.9	2.7	15.7	44.5
Lecaniodiscus fraxinifolius	UFR	3.3	10.5	2.2	56.1	28.2	7.0	7.9	31.4
Lepisanthes senegalensis	RFR	4.4	8.8	1.8	38.6	19.5	6.8	20.2	48.4
Ludia mauritiana	UFR	3.6	13.5	15.2	23.8	15.9	11.6	10.6	45.8
Millettia usaramensis	UFR	4.5	4.9	3.6	55.0	48.6	4.5	9.5	32.4
Moringa oleifera	UFR	7.9	16.4	0.4	33.6	11.2	13.8	21.5	44.3
Pithecellobium dulce	UFR	3.2	15.5	1.9	49.7	25.6	13.6	9.4	31.5
Premna hildebrandtii	UFR	7.8	10.3	3.5	73.1	54.7	7.9	6.7	7.6
Sideroxylon inerme	RFR	5.3	12.8	11.3	45.6	32.8	8.2	16.6	29.8
Sideroxylon inerme	UFR	4.5	7.5	9.5	63.5	51.7	4.3	9.1	18.2
Tamarindus indica	UFR	4.0	9.6	2.5	65.2	49.4	4.7	2.9	23.6
Tinospora caffra	UFR	5.9	8.9	1.7	32.5	29.9	6.7	17.5	53.2
Trema orientalis	UFR	9.9	17.2	5.8	64.3	48.0	11.8	0.8	8.3

pp = plant part; RFR = ripe fruit; UFR = unripe fruit; CP = crude protein; ADF = acid detergent fiber; NDF = neutral detergent fiber; AP = available protein; WSC = water soluble carbohydrate; TNC = total nonstructural carbohydrate

Table B.3. Mean nutritional content of all flower samples

Sample	PP	Ash	CP	Fat	ADF	NDF	AP	FBP	WSC	TNC
Adansonia digitata	FLB	6.7	13.3	2.1	68.5	42.5	9.1	4.2	4.4	13.6
Adenia gummifera	FL	6.1	20.3	2.8	51.1	20.4	16.8	3.6	5.7	23.3
Bougainvillea spectabilis	FL	6.8	17.4	4.0	40.7	20.8	13.6	3.7	14.8	35.0
Cassia fistula	FL	4.1	19.6	4.9	69.0	47.0	12.6	7.0	8.7	9.5
Coccinia grandis	FL	5.9	27.5	2.2	40.2	17.3	21.8	5.8	10.6	30.0
Combretum schumannii	FL	6.0	22.4	2.7	30.3	16.7	11.1	11.3	4.0	50.0
Cussonia zimmermannii	FLB	8.7	11.9	2.3	51.8	38.4	8.5	3.3	7.4	28.6
Delonix regia	FL	5.4	16.8	3.4	61.3	38.7	9.5	7.3	17.0	20.5
Delonix regia	FLB	3.8	14.4	2.2	52.6	34.0	8.5	5.9	10.3	32.9
Discorea hirtiflora	FL	8.5	20.8	4.9	52.1	33.4	15.7	5.1	6.9	18.9
Fernandoa magnifica	FL	6.1	16.8	1.6	39.4	24.0	12.5	4.3	22.3	40.4
Fernandoa magnifica	FLB	7.6	25.5	0.9	51.1	30.4	20.4	5.1	11.2	20.1
Gliricida sepium	FL	3.5	11.8	2.6	34.5	29.4	8.8	2.9	28.1	50.6
Grewia plagiophylla	FL	5.9	13.5	3.6	33.2	19.0	8.0	5.5	2.6	49.3
Lecaniodiscus fraxinifolius	FL	4.7	16.0	3.0	55.5	31.7	12.7	3.3	8.4	24.1
Mangifera indica	FL	1.3	11.1	5.8	31.9	11.0	12.1	1.0	18.4	49.0
Markhamia zanzibarica	FLB	6.2	18.2	2.1	66.9	47.6	12.2	6.0	7.2	12.7
Millettia usaramensis	FLB	7.1	24.9	2.9	45.7	30.8	16.5	8.4	5.9	27.7
Monodora grandidieri	FL	6.4	21.6	1.2	48.4	28.9	14.3	7.3	4.8	29.7
Moringa oleifera	FL	5.6	17.9	2.8	42.1	20.7	14.7	3.1	11.4	34.7
Pithecellobium dulce	FL	6.1	24.9	4.0	55.7	30.7	20.2	4.6	8.0	14.0
Plumeria cultiver	FL	6.5	13.3	3.4	39.0	23.1	9.5	3.8	17.7	41.7
Plumeria obtusa	FL	6.6	8.5	4.0	35.0	26.3	5.1	3.5	19.3	49.3
Plumeria rubra	FL	6.5	8.4	3.5	35.2	22.8	5.2	3.2	20.4	49.7
Premna hildebrandtii	FLB	6.7	15.9	3.1	65.3	46.5	9.9	6.0	5.2	15.0
Spathodea campanulata	FL	3.4	7.1	3.1	26.4	24.2	3.2	3.9	26.8	63.9
Suregada zanzibariensis	FL	16.2	19.5	2.9	38.6	38.9	16.1	3.4	8.8	26.3
Tinospora caffra	FL	7.5	25.8	2.5	44.5	22.4	22.7	3.1	8.9	22.8
Zanthoxylum spp.	FL	6.5	29.5	4.4	58.3	30.1	24.0	5.5	6.7	6.8

pp = plant part; FL = flower; FLB = flower bud; CP = crude protein; ADF = acid detergent fiber; NDF = neutral detergent fiber; AP = available protein; WSC = water soluble carbohydrate; TNC = total nonstructural carbohydrate