EFFECTS OF FOOD NUTRITIONAL AND MECHANICAL PROPERTIES ON FORAGING OF JUVENILE IN WILD TANA RIVER MANGABEYS, *CERCOCEBUS GALERITUS,* KENYA

by

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ABSTRACT OF THE DISSERTATION

"Effects of food mechanical and nutrition properties on foraging of juvenile in wild

Tana River mangabeys, *Cercocebus galeritus,* Kenya"

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Food is an essential for individual survival and reproduction, but intrinsically presents a variety of mechanical obstacles that must be met and nutritional requirements that must be overcome by the consumer. Mechanically, foods may be hard, tough, or stiff enough to inflict dental, damage on teeth, cranium, or facial form while chemically, it may be packed with toxins, nutrient deficiencies or in excess, which may harm the consumers' fitness. Therefore, feeding efficiency and challenges associated with foods provide a strong selective mechanism potentially influencing the evolution of foraging behavior and diet. The problems of accessing food and ensuring sufficient intake of energy and protein are likely to have a greater impact on juveniles than adults, as juveniles are smaller, less experienced and generally more inefficient foragers. Detailed studies testing the effects of these formative factors on juvenile feeding have yet to be conducted, however, and there is a poor understanding of how adult-juvenile foraging differs in nonhuman primates. The main debate on this issue centers on the development of juvenile

foraging efficiency, particularly on the effects of body size, nutritional needs, and experience in driving the suggested adult-juvenile differences in feeding. In order to clarify understanding of adult-juvenile foraging differences, I collected data and compared the diet choice, metabolizable energy intake, the mechanical and nutritional properties of foods, and the interactive effects of these properties on food selectivity in the Tana River mangabeys, *Cercocebus galeritus.* This research addressed the following questions about the implications of mechanical and nutritional properties of foods on foraging. Compared to adult lactating females, how do juveniles differ in: (1) diet, particularly in food choice and energy intake?; (2) the influence of mechanical and nutritional properties on foraging decisions?; and, (3) food electivity as a result of interactive effects of the mechanical and nutritional properties of foods? I collected data on feeding behavior using focal animal sampling from two wild groups (Kitere & Mchelelo groups) in lower Tana River forest fragments, Kenya. I measured the fracture toughness and elastic modulus of the primary and fallbacks foods of the mangabeys using a portable FLS-1 food tester machine. Finally, I performed laboratory analyses to determine the nutritional properties of the foods. Overall, I found that dietary breath (B_A) was wider in lactating females (B_A = 0.13) than in juveniles (B_A = 0.11) and was higher in Mchelelo group (0.22 & 0.17) than in the more anthropogenically impacted Kitere group (0.15 & 0.11) for both age classes, respectively. Juveniles' mean metabolizable energy intake per metabolic body mass per minute was higher than in lactating females. Juveniles also ingested more available protein per metabolic body mass per minute than the lactating females. Lactating females ingested foods with

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significantly higher fracture toughness than juveniles, but elastic modulus values of the food did not differ between the two age classes. Moreover, fruit availability and the mechanical and nutritional properties of foods interacted to influence the diet selection across seasons of different fruit availability, but there were no age class differences. These findings supported my predictions that juveniles will ingest more protein and metabolizable energy per unit of metabolic body mass compared to lactating females potentially due to increased nutritional needs for growth. Additionally, differences in the mechanical properties of the foods ingested by juveniles and lactating females support the Need-To-Learn hypothesis that juveniles that require time to learn and acquire competence in feeding skills.

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This dissertation is dedicated to my beloved parents Mrs. Elizabeth Munyiva Kivai

aka Katundu and Mr. Kivai Mbindyo, my loving wife Jeniffer and three sons Samuel,

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CHAPTER ONE: GENERAL INTRODUCTION

1.1 Introduction

Feeding is a matter of unconstrained choice for primates; it is, however, a risky venture yet it dictates individual's lifetime fitness. Thus, the cost-benefit ratios of food choices are paramount for all species of primates. Empirical evidence shows that energy and nutrient intake is a fundamental correlate of individual fitness in primates (Stephens et al., 2007; Senior et al., 2015). Individuals efficient in obtaining food will have higher survivorship and reproductive success and will contribute more offspring to the following generation (Sinclair et al., 2011). Therefore, the problems of foraging constitute key selective pressures on behavioral and dietary adaptations.

One early analytical approach, optimal foraging theory, posited that foraging decisions maximize benefit: cost ratio associated with net rate of energy returns (Schoener, 1971; Stephens et al., 2007; Gunst et al., 2010). The nutritional properties of food were viewed as challenges in achieving foraging efficiency (Lambert & Rothman, 2015), and have been suggested to explain morphological and physiological adaptations both in extant primates and early hominins (Norconk et al., 2009; Lambert, 2010; Strait et al., 2012; Daegling et al., 2013; Hartstone-Rose et al., 2015). It is important to emphasize that nutritional properties of food are expected to operate synergistically with physical characteristics to shape primate behavioral adaptations. These interactive effects are poorly understood, however, both in early hominins and extant primates. The implications of these two properties of foods are especially highlighted through a comparative study of adults

and juveniles. This is because, compared to adults, juveniles are more potentially constrained by mechanical and nutritional properties of foods due to the developmental challenges of growth and maturation, as well as small body size (Pereira & Fairbanks, 2002; Gunst et al., 2010).

Although studies focusing on the interactive effects of physical and chemical properties of foods are still limited, over the last decade research on the role of each of these two food properties on primate evolution and adaptation has advanced (Dominy et al., 2003; Lambert, 2004; Laden & Wrangham, 2005; Norconk & Veres, 2009; Felton et al., 2009; Marshall et al., 2009; Constantino et al., 2012; Lucas et al., 2012; Johnson et al., 2013; McGraw et al., 2014; Lambert & Rothman, 2015; Herzog et al., 2016). The role of food mechanics has attracted considerable attention, particularly of hard fallback foods in shaping the evolution of early hominin cranial-dental morphology and nonhuman primate foraging behavior (Kinzey & Norconk, 1990; Lambert, 2004; Ungar, 2004; Wright et al., 2008; Strait et al., 2009; Constantino et al., 2012; Vogel et al., 2014). Similarly, the field of primate nutritional ecology has made significant progress in the understanding of how food chemical properties influence foraging goals and reproduction of primates (Felton et al., 2009; Rothman et al., 2015; Senior et al., 2015; Herzog et al., 2016). While there is no doubt that studies of nutritional and mechanical properties of food continue to generate insightful information, in this dissertation one of my main focus is to investigate how these two properties interactively influence juvenile primate feeding behavior and evolution of dietary adaptations, which remains poorly understood.

The ongoing debate surrounding primate juvenile foraging competency partly concerns both the nature of juvenile-adult differences in feeding and the sources of these differences in terms of experience, body size, or both (Gunst et al., 2010; Lonsford & Ross, 2012). In addition contradictory results on the timing of juvenile competence whereby in some species it appears to be delayed close to maturity but in others it occurs long before maturity (Janson & van Schaik, 1993; Gunst et al., 2008; Pereira & Fairbanks, 2002). An analysis that incorporates field data on both the mechanical *and* nutritional characteristics of food items, and how juveniles and adults achieve foraging efficiency has yet to be attempted but holds great potential to resolve these theoretical debates.

Juveniles are generally considered to be less efficient foragers than adults (Pereira & Fairbanks, 2002; Gunst et al., 2010) and therefore, foraging constraints are potentially amplified in juveniles. For these reasons, a study of their foraging provides an important opportunity for clarifying the ecological and evolutionary implications of the interactive effects of mechanical and nutritional properties of their diet.

In this dissertation, I present data on juvenile Tana River mangabeys (*Cercocebus galeritus*) to answer the following questions. Compared to adult lactating females, how do juveniles differ in: (1) diet, particularly in food choice? (2) the influence of mechanical and nutritional properties on foraging decisions? (3) behavioral strategies employed to overcome the nutritional and mechanical constraints? and, (4) how can the results obtained in questions 1, 2 and 3 inform the conservation of the endangered Tana River mangabey? Answering these questions

will enhance our understanding of juvenile foraging ecology and competence as well as the evolution of primate dietary adaptations.

1.1.1 Theoretical Background

The two primary theoretical areas addressed by this dissertation study concern juvenile feeding ecology and juvenile development in the nutrition ecology in the context of foraging.

1.1.1.1 Primate foods and their ecological significance

It is known that food type significantly impacts ecology and evolution of both fossil and living primates (Lambert, 2007; Harrison & Marshall, 2011). The constraints encountered by foraging primates exploiting different foods constitute the underlying mechanisms driving such adaptations. Of particular importance are the nutritional profile, accessibility and seasonal availability of foods (Norconk et al., 2009). The nutritional content of food is affected partly by the habitat quality and edaphic factors (White, 2012), while availability is determined by seasonal variations in forest productivity, phenological cycles, and crop size (Chapman et al., 2003; Milton et al., 2005). The degree of accessibility is a function of the challenges posed by food or food parts, such as mechanical or chemical plant secondary metabolites (Norconk et al., 2009). Food availability, accessibility, and the need to balance nutrient intake for survival and reproduction presents a strong selection pressure on primate feeding behavior, masticatory morphology, and digestive anatomy as well as speciation and extinction processes (Marshall et al., 2009; Lucas et al., 2012; Lambert & Rothman, 2015).

Research on weanling yellow baboons (*Papio cynocephalus*) in Amboseli, Kenya, provides compelling evidence that success in obtaining adequate energy and protein as a youngster is likely to predict survival to adulthood, the subsequent length of reproductive career, fecundity, and lifetime reproductive success (Altmann, 1998). This is due to the risks and difficulties associated with feeding and this is particularly true for juveniles in unpredictable environments. Food resource availability, energy requirements, life history, habitat quality, predation, and competition are some of the factors that influence primate food intake (Chapman et al., 2004; Rothman et al., 2008; Vogel et al., 2008; McGraw et al., 2014; Senior et al., 2015). Therefore, based on these factors it is expected that food intake should show high variability on spatial-temporal scales.

Primate foods fall into two general, but ecologically important categories: preferred foods and less-preferred or "fallback" foods (Lambert et al., 2004; Marshall & Wrangham, 2007; Lambert, 2010). Preferred foods are defined as those selected disproportionately more than would be suggested by their abundance within the habitat. Fallback foods are those whose use is significantly negatively correlated with the abundance of preferred foods (Marshall et al., 2009). Preferred foods are generally more abundant, calorically rich, easily accessed processed than fallback foods. The less-preferred status of fallback foods may arise in two ways: The foods may be high in nutritional value but much harder to find and process or are may be abundant and easy to access, but low in nutritive value. Thus, these foods are utilized as "fallbacks" in periods of relatively low abundance of the preferred foods (Constantino & Wright, 2009; Lambert, 2010).

Lambert (2010) argues that less-preferred foods exert stronger selection than preferred foods on the evolution of feeding adaptations for two reasons. First, they are abundant and require less processing time although they may be poor in energy or nutritional content. Such foods include vegetative plant parts like leaves, petioles, and bark. Second, some less-preferred foods are actually rich in energy, but their "less preferred" status derives from the mechanical barriers they present to processing. Such foods include the reproductive and energy parts of plants, such as fruits, seeds, nuts, tubers, and corms. This class of less-preferred/fallback foods is ecologically and evolutionarily more important than preferred food class because it can facilitate maintenance of high-energy-yield diets during lean periods (Lambert, 2010; McGraw et al., 2014). Overall, abundant low quality and difficult-to-process foods are potentially important in driving specialized food processing adaptations while relatively rare, high quality and easy-to-process foods promote behavioral adaptations (Lambert, 2007; Harrison & Marshall, 2011).

Although preferred foods may typically be more easily found and processed, they are not usually continuously available over time and space (Marshall et al., 2009; McGraw et al., 2014). Thus, temporal dietary switching to less-preferred food is a common strategy to maintain adequate energy intake (Constantino & Wright, 2009; Rosenberger, 2013; Lambert & Rothman, 2015). An individual's ability to exploit less-preferred foods during lean periods is likely to affect strongly survival and reproductive success, especially where reliance on such foods is inevitable (Lambert, 2004; Marshall et al., 2009; Senior et al., 2015). Consequently, behaviors and morphologies that enhance the locating, procuring, ingesting, and processing of

less-preferred or fallback foods will be favored, even though such features may be less relevant during those major parts of the year when preferred foods are relatively abundant (Lucas et al., 2012; McGraw et al., 2014).

1.1.1.2 Juveniles and foraging competence

Compared to other mammals, primate juveniles show more prolonged periods of immaturity and delayed age at first reproduction (Pereira & Fairbank, 2002). Life-history models have revealed that such differences are potentially explained by trade-offs among a number of variables, such as sexual maturity, adult body size, age-specific mortality and fecundity (Charnov, 1993; Rubinstein, 2002). These studies assert that delayed maturity tends to favor the growth of relatively large body size which leads to longer lives and protracted reproductive careers. On the contrary, quick maturation is associated with lower adult body size, elevated chances of living to reproduce age and shortened longevity. The sources and rates of juvenile and adult mortality have a significant influence on a species' life-history strategy. Data on primate mortality across sites indicate that 15% of the juveniles die annually compared to 8% of the adults, and on average, less than half of all the newborns survive to the age of maturity (Ross & Jones, 1999). Risk and difficulties in obtaining food have been demonstrated as a key factor underlying this mortality (Altman, 1998; Janson & van Schaik, 2002; van Noordwijk et al., 2002; Kivai, 2013). Therefore, achieving foraging competence in juvenility is extremely important: it simply means increased chance of survival and reaching the reproductive stage.

Two alternatives, but not entirely mutually exclusive, hypotheses have been proposed to explain the adaptive design features of juvenility in the context of foraging (Pereira & Fairbank, 2002; Gunst et al., 2010; Lonsford & Ross, 2012). The Need-To-Learn (NTL) hypothesis suggests that attaining adult foraging efficiency requires long periods of juvenile social learning, enhanced cognitive ability, independent practice, and physical maturation (Pereira & Fairbank, 2002; Gurven et al., 2006; Gunst et al., 2008; Eadie, 2015). Given the complex feeding strategies that are argued to characterize many primates, this hypothesis predicts that, compared to adults, juveniles will necessarily be less efficient foragers due to limitations in foraging experience, feeding skill proficiency, cognitive abilities, physical strength (to break food mechanical defenses), and nutritional demands to sustain growth (Altmann, 1998; Altmann & Alberts, 2005; Gunst et al., 2010; Chalk et al., 2016). The need for a long period for the development of foraging capabilities may be particularly crucial for species that feed on hard foods, such as nuts and seeds, or those that engage in extractive foraging (Wieczkowisk, 2009; Gunst et al., 2010; Yamashita et al., 2012).

The alternative Ecological Risk Aversion (ERA) hypothesis argues that slow growth is an adaptive response to the fitness problems of starvation and predation risk, which then secondarily explains adult-juvenile foraging differences (Janson & van Schaik, 1993; O`mara, 2015). This hypothesis assumes that juveniles are more vulnerable to starvation, predation, and adult aggressive interference as they are smaller, weaker, and have poorer antipredator strategies when compared to adults. This vulnerability reduces their foraging efficiency (Janson & van Schaik, 1993;

Lonsford & Ross, 2012). Consequently, juveniles are more likely than adults to forage selectively in areas of low predation risk, which may have poor food resources that, in turn, necessitates more time spent in feeding. Adult-juvenile foraging differences are argued to emerge from this profile (Pereira & Fairbank, 2002).

Adult traits are of course the outcome of developmental processes that are themselves the product of complex selective pressures (Daegling et al., 2013). Therefore, knowledge of how juveniles attain foraging competence provides an opportunity to fully understand primate dietary adaptations. Pereira & Fairbank (2002) use the term "juvenile" to refer to a weaned individual old enough to likely survive the death of its primary caretaker, but not yet sexually mature. For the purpose of this study, the term juvenile will be used to refer to "sexually immature and independently foraging individuals (weaned or unweaned) that are unable to obtain adequate nutrients to support their body metabolic needs from suckling and are capable of surviving the death of their primate caretakers". Despite their relative independence, juveniles face numerous challenges in the acquisition of adequate energy and nutrients to support growth and maintenance.

We know very little, if anything at all, on how juveniles overcome the foraging constraints in the course of maturation Such information is valuable in understanding the adaptive and ecological role of both preferred and less-preferred foods in influencing survival, behavioral, and morphological traits (such as food and patch selection, food processing, ingestion rate, enamel thickness, cranial and facial form). This is because foraging competence is particularly important where food

items are difficult to locate, process, masticate, and ingest (Gunst et al., 2010). As a result, consumption of such challenging foods has great relevance to understanding juvenile foraging competence (Janson & van Schaik, 1993; Lonsford & Ross, 2012).

While the NTL hypothesis has been supported by developmental studies of yellow baboons (Altmann, 1998), brown capuchin monkeys (*Cebus paella*) (Gunst et al., 2010; Resende et al., 2014; Chalk et al., 2015), and chimpanzees (*Pan troglodytes*) (Lonsdorf et al., 2004) it appears irrelevant for other species, such as mountain gorillas (*Gorilla gorilla berengei*), Japanese macaques (*Macaca fuscata*), and common squirrel monkeys (*Saimiri sciureus*) (Gunst et al., 2010). On the basis of these findings it has been hypothesized that crucial variable reconciling these ostensibly contradictory findings is the ecological profile of food as shown by Lamberts' (2010) scheme: juvenile-adult foraging efficiency differences are likely to be particularly pronounced for foods that are difficult-to-find and process that is for less preferred foods (Gunst et al., 2010).

Although there are some data showing age differences in foraging on such challenging foods, the timing of food acquisition proficiency remains unclear (Gunst et al., 2008). For instance, while in some species, such as squirrel monkeys, proficiency occurs well before maturity (Hauser, 1987; Boinski & Fragaszy, 1989), in others, such as brown capuchin monkeys, it is delayed until shortly before sexual maturity (Gunst et al., 2008). The question of how juveniles achieve proficiency for different key preferred and less-preferred foods utilized by different primates is yet to be answered. However, based on the characteristics of these two classes of foods, it can be predicted that feeding proficiency will be attained earlier for the preferred

foods. This is because relatively high abundance and frequency of utilizing such foods are likely to improve opportunities to learn and practice the skill required to exploit such resources compared to less-preferred foods, which are consumed occasionally (Lambert, 2010). Exploitation of fallback foods may require cognitive mechanisms because such foods are hard to locate and process (Pereira & Fairbank, 2002). Such cognitive abilities may, however, take a long period to develop due to slow brain development, thus, delaying feeding proficiency.

Alternatively, data from tufted capuchin monkeys, (*Cebus apella*) and common squirrel monkeys (*Saimiri sciureus*) appear to partly support ERA hypothesis by suggesting that body size effects influence foraging efficiency in species that feed on food items that are difficult-to-access and extract, compared to species that consume small or easily manipulated foods (Boinski & Fragaszy, 1989; Visalberghi & Neel, 2003), but this principle does not hold across the primate taxon broadly. Again, the ERA hypothesis assumption that juveniles are inefficient foragers compared to adults is not always supported with species such as squirrel monkeys (Pereira & Fairbanks, 2002) and tufted capuchin monkey (Chalk et al., 2016), which show no adult-juvenile foraging differences.

This study compares mangabey diets and the food processing efficiency by juveniles at different stages of development with adult females to clarify whether juvenile foraging efficiency is dependent on body size, experience or synergetic effects of both.

1.1.1.3 **The influence of mechanical and nutritional food properties on foraging behavior**

The decision to consume a particular food item largely depends on the balance between the costs and benefits involved in finding, ingesting and also digesting it. The benefits should outweigh the costs for diet preference to prevail. In the context of foraging, the benefits are the nutritional returns gained from the food resource, while the costs include the risks and energy expended in finding and processing the food (Visalberghi et al., 2016). The mechanical and chemical defenses of foods increase the costs of foraging. Because of the need to maintain a positive benefit-cost balance in feeding, primates have evolved behavioral, anatomical and physiological adaptations to overcome or minimize the foraging costs (Lambert, 2007). For juveniles, behavioral feeding adaptations are fundamental in balancing the foraging cost-benefits because the anatomical and physiological mechanisms may take longer to achieve full functionality.

Over the past four decades, anthropologists and biologists have increasingly attempted to measure the mechanical properties of foods in order to understand the relationship between diet foraging behavior, and functional morphology (Kay, 1975; Lucas & Luke, 1984; Kinzey & Norconk, 1990; Lucas & Teaford, 1994; Strait, 1997; Dumont, 1999; Elgart-Berry, 2004; Lambert et al., 2004; Lucas, 2004; Dominy et al., 2008; Lucas et al., 2012; Vogel et al., 2014; Laird et al., 2016). Mechanical or physical properties refer most fundamentally to the characteristics of food material that influence its fragmentation (Chalk, 2011). The majority of previous studies have employed three material properties to describe food physical properties: toughness,

Young's modulus (or elastic modulus), and yield stress (or hardness). Fracture toughness describes either the intrinsic resistance of a solid material to fracture (R) or the effect of a crack on the stress field in an object that has linear elastic behavior (T) (Lucas, 2004; Lucas et al. 2008). Therefore, based on these two material characteristics toughness can be defined as, "the amount of work required to propagate a unit area of crack on food material surface (measured in Joules per meter squared, $J\ m^{-2}$)" or "the value of a quantity combining the average stress and the square root of crack length (MPa $m^{1/2}$) at the critical point when the stress is sufficient for the crack to extend" (Lucas et al., 2008). Young's modulus, or elastic modulus, refers to food's material ability to resist elastic deformation and can be defined as the ratio of force to deformation at small, essentially linear, displacements (Strait, 1997; Lucas, 2004; Chalk, 2011). Hardness *(*although in a strict sense is not considered a material characteristic) describes the resistance of food material to plastic deformation and is measured through indentation (Lucas, 2004; Chalk, 2011). Hardness is measured as the amount of force applied to the indenter divided by the projected area measured in the same plane as the surface (Lucas, 2004).

There is growing evidence linking the influence of mechanical properties of foods with the evolution of masticatory apparatus structure (in both early hominin and extant primates), specialized foraging behaviors, and success in colonization of new environments (Daegling, 1992; Kinzey & Norconk, 1990; Spencer, 1997; Strait, 1997; Yamashita, 1998; Lambert et al., 2004; Daegling & McGraw, 2007; Ungar, 2007; Wright, 2007; Vogel et al., 2008; Gunst et al., 2010; Ravosa et al., 2010, 2014;

Scott et al., 2014). Food ingestion among primates involves complex, time-consuming and energy demanding strategies related to finding food, dextral manipulation, oral, and post ingestion processes (Gunst et al., 2010). Where mechanical barriers such as tough casing or fibrous materials protect food, foraging primates may employ repetitive chewing combined with enough force loading on the masticatory apparatus (Hylander & Johnson, 1994; Agrawal et al., 1998; Ross et al., 2007). Oral processing of such foods exerts stress and strain on the masticatory apparatus, which has a threshold above which deformation occurs (Vogel et al., 2014). Consequently, mechanical properties are expected to play a key role in shaping morphological, behavioral and dietary adaptation especially in primates that live in unpredictable environments where reliance on fallback foods is inevitable.

Feeding strategies should reflect solutions to these ecological, chemical, and mechanical problems posed by foods (Lambert, 2010). Behavioral strategies are one class of possible solutions among juveniles. Consumption of tough, hard, and stiff foods often may require extractive and/or cognitive skills to procure, process, and ingest, compared to other foods that are easy to obtain and do not need such skills to exploit (Gunst et al., 2010). Special processing skills based on certain specialized dental adaptations are critical in the exploitation of such mechanically challenging foods but may be absent or less developed in juveniles (Dominy et al., 2008; Constantino et al., 2012; Chalk et al., 2011; Daegling et al., 2013). Of the handful studies on juvenile foraging, very few have addressed competency in the context of mechanical challenges foods (Noordwijk & van Schaik, 2005; Gunst et al., 2008; Biro

et al., 2009; Gunst et al., 2010; Chalk et al., 2016), and nearly all of these focus on capuchin monkeys or apes, and all fail to integrate *both* the mechanical and nutritional properties of foods.

Tool use, which has been intensively documented in the majority of wild populations of chimpanzees, orangutans, and capuchin monkeys, is one of the behavioral-cognitive adaptations that characterize complex extractive foraging (van Schaik & Knott, 2001; Hayashi et al., 2006; Bentley-Condit & Smith, 2010). The ability to manufacture and/or use tools facilitates feeding on high-quality foods that are protected by hard husks or found in hidden substrates (Gunst et al., 2010). Palm nut cracking using stones and palm pounding using a pestle by Bossou chimpanzees in West Africa (Humle & Matzusawa, 2004), nut cracking stone hammer and anvil by wild capuchins in Brazil (Fragaszy et al., 2004), and use of sticks to remove lipid-dense seeds from stinging *Neesia* fruit by Sumatran orangutans (*Pongo abelii*), (van Schaik & Knott, 2001) are good examples of how tool use to overcome the mechanical challenges of foraging. For the first time I report in this dissertation extractive foraging that resembles tool use behavior in wild Tana River mangabeys, and I argue it is a strategy to overcome mechanically challenging foods.

Food cheek pouching among the cercopithecines presents another potential behavioral-anatomical strategy to overcome both mechanical and chemical barriers of foods (Murray et al., 2006). Buccal pouches refer to bilateral, oblong sacculations that are formed in the interior portion of the buccinator pocket in the oral cavity, and, among primates, they are restricted to the cercopithecinae (Murray et al., 2006). They are equipped with a slit-like orifice that allows lateral distention

depending on food size stored. The interior parts of the check pouches are lined with a mucous membrane, whereby the mucous glands are concentrated at the anterior and posterior creases of the pouch and around the orifice. The glandular tracts are aligned with the passage of food in and out of the cheek pouches and play a lubricant role in food processing.

Cheek pouches represent an interface between behavior and morphological adaptations to feeding (Murray, 1975; Lambert, 2005). Different hypotheses supported by data from cercopithecine monkeys have been suggested to specify dietary functional of cheek pouches. These include; separation of intake and digestion of food (Hediger, 1964), food storage and facilitation of terrestrial forays (Hill, 1966; Lambert, 2005), buffering conspecific food competition (Hill, 1966; Napier, 1970), and predation counter strategy (Smith et al. 2008), and salivary pre-digestion of food (Gautier-Hion, 1971). Examination of cheek pouch contents of wild-shot and captive specimens provide compelling evidence that members of the genus *Cercocebus* and *Cercopithecus* hold hard food materials (seeds, kernels, small nuts, wood chips, lizard bones) in their cheek pouches over prolonged periods of time (Haddow, 1952; Fooden, 1971; Murray, 1975). Further experiments on yellow baboons and rhesus macaques (*Macaca mulatta*) have confirmed that pouches fill up to one-third of their relaxed dimension with parotid and mucous secretions (Murray, 1975). Data from macaques (*Macaca* sp.), vervet monkeys (*Chlorocebus pygerythrus*), and recently the hamadryas baboons (*Papio hamadryas*) showed high levels of alpha-amalyse in the parotid glands (Jacobens, 1970; Lambert, 2007; Mau et al. 2010). In addition, food samples retrieved from the cheek pouches of living

Cercopithecines are well inundated in the saliva and mucous secretions (Murray, 1975). These lines of evidence clearly indicate the potential behavioral responses and pre-digestion strategies to handle mechanically and chemically challenging foods.

Other potentially counter strategies for minimizing the chemical and mechanicals deterrents include seed spitting or swallowing (Vogel et al., 2016). Captive and field studies of long-tailed macaques (*Macaca fascicularis*), have demonstrated the utilization of this strategy in handling tough seeds (Corlett & Lucas, 1990). For examples, long-tailed macaques spat intact seeds from 69% of the ripe fruits eaten. This strategy of handling seeds has also been reported in wild guenons, such as Putty-nosed monkeys (*Cercopithecus nictitans*), blue monkeys (*C. mitis*), and red-tailed monkeys (*C. ascanius*) (Gautier-Hion, 1980; Rowell & Mitchell, 1991; Lambert, 2002). This strategy is believed to be a counter strategy for *both* mechanical and chemical challenges of food because seeds not only contain toxins but also possess hard mesocarps that deter consumption (Janzen, 1974).

Food intake regulation and partial or complete avoidance constitute another set of behavioral strategies primates employ in countering the chemical and mechanical costs (Milton, 1980). For instance, using geometric framework analysis, primate nutrition ecologists have empirically demonstrated nutrient balancing in primate foraging (Raubenheimer & Simpson, 2004; Hemingway & Bynum, 2005; Felton et al., 2009; Raubenheimer et al., 2009). Although it is clear that primates have specific nutritional goals and need to balance their nutrient intake, the available evidence suggests that this is attained through food selection that involves

food switching, avoidance or regulation of plant secondary metabolites, controlled fiber intake, maximization of protein and energy and inclusion of rare minerals or other micro-nutrients that may be required in small quantities (Freeland & Janzen, 1974; Milton, 1980; Altmann, 1998; Rothman et al., 2008; Felton et al., 2009; Gunst et al., 2010; Vogel et al., 2014).

Food sharing, scrounging (where individual cedes portion of food monopolized by another, where costs of defending it exceeds the benefits) or foraging on left-overs (here used to refer to partially processed food fragments that are either dropped or abandoned by a competent forager becoming available to another individual, who is incompetent or low ranking forager) are other behavioral means juvenile primates utilize to achieve the nutritional goals while navigating the mechanical constraints of food (Gunst et al., 2010). These set of behaviors are potentially effective where individuals are tolerant of each other or assist immatures to learn food items eaten and the manipulative procedures. These behaviors stimulate food exploration and independent food processing facilitating learning of foraging skills (Rapaport & Brown, 2008). Data from wild brown capuchin monkey demonstrate the use of these behavioral strategies by juveniles to overcome mechanical constraints and meet daily energy intake goals during periods of high consumption of the difficult-to-process maripa palm fruit, *Maximiliana maripa*, (Gunst et al., 2010). This study observed that youngsters unable to harvest and open the maripa palm fruit compensated their foraging incompetence by gnawing unplucked fruit and opportunistically feeding on partially processed fruits abandoned by competent conspecifics. The same has been illustrated in the tufted

capuchins, which share food and tolerate young individuals unable to open nutritionally rewarding nuts, (Fragaszy et al., 1997). This study established that 35% of juveniles' attempts to get food from the adults were suggesting that juveniles have behavioral tactics to exploit difficult-to-process foods before they can achieve adult processing competence. This nutritional benefit to the immatures may be especially crucial in environments where hard-to-process foods constitute the main energy source.

Pre-ingestion visual, olfactory and dental food inspection also serves as a potential behavioral means of discerning the chemical and mechanical properties of food items (Dominy, 2004; Yamashita et al., 2012). Dominy (2004) found that primates use color and deliberate smelling, combined with tactile and dental evaluation, to select the appropriate fruit to ingest. Interestingly he found a positive correlation of ethanol (a potential olfactory cue) with the concentration of soluble sugars in fruits eaten by primates. Thus, a combination of visual, olfactory, tactile and dental cues are likely to offer a potentially an important strategy to discriminate food on basis of chemical and mechanical characteristics.

1.1.2 Study species

1.1.2.1 **Ecology of the study species, Tana River Mangabey,** *Cercocebus galeritus*

The Tana River mangabey was selected as an appropriate species model to test my research questions for several reasons. Foremost, the species dietary adaptations to feed on hard objects (McGraw et al., 2012) and seasonality in food

abundance in its habitat (Wieczkowski & Kinnaird, 2008) were considered critical factors in understanding the implications of mechanical and nutritional properties of food on feeding behavior. In addition, *Cercocebus galeritus* is considered to be among the most threatened primates globally (Mittermeier & Konstant, 2002). The species is endemic to the lower Tana River forest galleries and faces an eminent threat of habitat loss, degradation and fragmentation due to both anthropogenic and natural processes (Butynski & Mwangi, 1994; Butynski et al., 2008; Kivai, 2013). Thus, the data on the species nutritional ecology and foraging behavior generated by this study would also be fundamental in the conservation of the species.

The Tana River mangabey is restricted to the lower Tana River forest galleries in southeast Kenya, specifically within the last the 60km stretch of the river before entering the Indian Ocean (Medley, 1993). This section of the river constitutes 62 forest fragments of which only 40 are inhabited by the mangabey (Wieczkowski, 2003). According to Wieczkowski (2004), mangabey abundance is correlated with fragment size and tree density. The species is largely terrestrial spending 56 - 72% of the active time on the ground (Homewood, 1978; Wieczkowski, 2010). The mating and social organization of this population resembles that observed in olive baboons and yellow baboons, with clear social hierarchy among both males and females. The Tana River mangabeys display a polygynous mating system in which high-ranking males dominate mating with estrus females (Kinnaird, 1990). However, on several occasions, I observed the formation of male alliances precipitating successful takeovers of receptive females from the dominant males. Although mangabeys live in multi-female-multi-male

groups the females are philopatric (Rowe, 2016). Group territories overlap and aggressive encounters are common especially during the period of low food availability (Kivai pers. obs., 2015; Kinnaird, 1990).

The Tana River Mangabey is considered a frugivore-granivore where its diet consists of 46.5% seeds and 25.6% fruits (Homewood, 1978; Wieczkowski & Kinnaird, 2008). The diet consists of hard and tough food items, which reflect the apparent species dental and craniofacial adaptations ideal for handling and ingestion of tough-skinned fruits, seeds, and nuts (Kivai pers. obs., 2015; Wieczkowski, 2009; Daegling et al., 2011). Although the general feeding ecology of the Tana River mangabey has been described (Homewood, 1978; Wieczkowski & Kinnaird, 2008; Wieczkowski, 2009), nutritional ecology and food mechanics have received very little attention. Early attempts by Homewood (1978) to perform nutritional analysis generated little information due to field methodological problems. Use of the agricultural food tester to measure more food mechanics provide useful preliminary data that are, however, less precise than the FLS-1 tester machine that I used.

1.1.2.2 **Mangabey dietary adaptations**

The mangabeys (*Cercocebus* & *Lophocebus*) are members of the Old World monkeys of the tribe *Papionini* (Harris, 1999). According to Harris, they do not conform to population genetics theory prediction of monophyly, but instead, they are polyphyletic. Consequently, *Cercocebus* is considered the sister taxon of

Mandrillus, whereas *Lophocebus* constitute an unresolved trichotomy with *Papio* and *Theropithecus* (Disotell, 1994). Despite the unresolved relationship, the *Cercocebus-Mandrillus* clade displays skeletal and dental adaptations for consumption of hard-object foods that resist decomposition on the forest floor over long times (Daegling et al., 2013). There is a morphological convergence of *Cercocebus* and *Lophocebus* and both share many ecological and behavioral traits, which include: commonalities of vocalization, group size, social organization, and diet (Homewood, 1978; Olupot, 1998; Shah, 2003; Bouchet et al., 2010). Nevertheless, there is growing evidence that the two mangabey genera *Cercocebus* and *Lophocebus* differ in their dietary adaptations (Daegling & McGraw, 2007). The members *Cercocebus* are more terrestrial while *Lophocebus* are arboreal, and both are considered as generally frugivorous seed predators. Evidence also suggests that these two mangabey groups show marked variations in the hardness of the seeds they consume, processing behavior, and dental morphology (Fleagle & McGraw, 2002).

As a group, mangabeys possess a set of dietary adaptations comprising: very thick enamel, large incisors, powerful jaws, and a facial configuration capable of generating the large occlusal forces necessary for hard food fragmentation (Hylander, 1975; Kay, 1981; Singleton, 2005; Daegling & McGraw, 2007). These morphological traits play a major role in durophagy (defined as a diet of hard food objects), which characterize the mangabey taxa. With the raging debate on the role of food mechanics in early human evolution, especially with the utilization of fallback foods, and few available data on the influence of food mechanics on Old

World monkeys' dietary adaptations, the comparison of the mangabey groups is fundamental to improving our understanding of these aspects. While data on durophagy exist for majority previous studies of the mangabeys, such as sooty mangabeys, *Cercocebus atys*, (Daegling & McGraw, 2007; McGraw et al., 2012), grey cheeked mangabeys (*Lophocebus albigena*) (Lambert et al., 2004), and red capped mangabeys (*Cercocebus torquatus*)*,* (Dumont, 1995), there are any hardly any detailed data on the same for Tana River mangabeys except preliminary work by Wieczkowski (2009).

1.1.3 Goals and Dissertation Research Layout

The primary goal of this dissertation is to compare the foraging behavior with the mechanical and nutritional properties of foods eaten by juveniles and lactating females to investigate how juveniles overcome both chemical and mechanical challenges of food to achieve foraging competence. Results from the study will deepen our understanding of the role of food properties in shaping behavioral and dietary adaptations of primates as well as informing the conservation of the endangered Tana River mangabeys. In order to achieve this goal, I will answer my research questions, on the implications of mechanical and nutritional properties of food on juvenile foraging behavior by testing different hypotheses and predictions in different chapters of this dissertation.

Chapter 1: This chapter provides an overall general introduction of different thematic areas covered in this dissertation including the research questions. It offers the broad theoretical background of the primate foods and their ecological significance, the suggested hypotheses explaining juvenile foraging competence and

the debate about them, introduces the study species and associated dietary adaptations, and presents the research questions investigated.

Chapter 2: In this chapter, I investigate the food choice and metabolizable energy intake by juveniles and lactating females relative to metabolic body mass. To achieve this I present data on dietary composition and preference of the two age classes by calculating their dietary breadth and selectivity index of all the food species they ingested. To compare energy intake, I present data on metabolizable energy intake between the two age classes.

Chapter 3: This chapter focuses on the nutritional properties of foods and macro- and micro-nutrients intake by juveniles and the lactating females. First, to understand the nutrition properties of the mangabey foods and influence on foraging, I present data on available protein, crude fat, fiber (nitrogen detergent fiber - NDF, acid detergent fiber - ADF, & acid detergent lignin-ADL), and minerals content of the different foods eaten by the two age classes and estimate their daily energy intake. I compare nutrient intake between juveniles and lactating females and also relate it to fruit availability measured through phenological assessment. Second, I compare the plant secondary metabolites in the foods ingested by the Tana River mangabeys to examine whether mangabeys forage selectively to avoid foods with high concentration of such compounds.

Chapter 4: In this chapter, I examine the mechanical properties of foods eaten by the Tana River mangabeys and investigate the interactive effects of nutritional and mechanical properties on diet electivity. I present data on toughness and elastic modulus of the food materials eaten by both juveniles and lactating

females and proceed to compare the differences between the two age classes concerning the mechanical properties of the foods they ingest. Finally, I explore how nutritional properties (available protein and metabolizable energy) interact with mechanical properties (fracture toughness and elastic modulus) to influence diet selectivity.

Chapter 5: This constitutes the conclusion section whereby I review all my findings highlighting whether my data analysis supported the proposed hypotheses and predictions that were tested in chapters 2, 3 and 4. I summarize the implications of my results towards on the ongoing debate on the Need-to-Learn hypothesis and ecological risk aversion hypothesis in explaining juvenile-adult foraging differences as well as the potential role of food mechanical and nutritional food properties in shaping the dietary adaptations in primates with extension to hominin dietary adaptations. I will also provide the implications of my results in the field of primatology, long-term conservation of the endangered Tana River mangabeys, and recommend the new research gaps I have identified.

1.2 References

Agrawal, K. R., Lucas, P. W., Bruce, I. C., & Prinz, J. F. (1998). Food properties that influence neuromuscular activity during human mastication. *Journal of Dental Research*, *77*(11), 1931-1938.

Altmann, J., & Alberts, S. C. (2005). Growth rates in a wild primate population: ecological influences and maternal effects. *Behavioral Ecology and Sociobiology*, *57*(5), 490-501.

Altmann, S.A. (1998). *Foraging for survival: yearling baboons in Africa*. Chicago: University of Chicago Press.

Bentley-Condit, V. K. (2009). Food choices and habitat use by the Tana River yellow baboons (*Papio cynocephalus*): a preliminary report on five years of data. *American journal of primatology*, *71*(5), 432-436.

Biro, D., Sousa, C., & Matsuzawa, T., (2006). Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: case studies in nut cracking and leaf folding. In*: Matsuzawa, T., Tomonaga, M. & Tanaka, M. (Eds.), *Cognitive development in chimpanzees* (pp. 476-508). Tokyo: Springer.

Boinski, S., & Fragaszy, D. M. (1989). The ontogeny of foraging in squirrel monkeys, *Saimiri oerstedi*i. *Animal Behaviour*, *37*, 415-428.

Bouchet, H., Pellier, A. S., Blois-Heulin, C., & Lemasson, A. (2010). Sex differences in the vocal repertoire of adult red-capped mangabeys (*Cercocebus torquatus*): a multi-level acoustic analysis. *American Journal of Primatology*, *72*(4), 360-375.

Butynski, T. M., & Mwangi, G. (1994). Conservation status and distribution of the Tana River red colobus and crested mangabey for Zoo Atlanta. *Kenya Wildlife Service, National Museums of Kenya, Institute of Primate Research, and East African Wildlife Society*, *68*.

Butynski, T.M., Struhsaker, T., Kingdon, J. & De Jong, Y. (2008). *Cercocebus galeritus*. *In*: IUCN 2013. IUCN *Red List of Threatened Species.* Version 2013.2. <www.iucnredlist.org>. Downloaded on 28 January 2014.

Buzzard, P. J. (2006). Cheek pouch use in relation to interspecific competition and predator risk for three guenon monkeys (*Cercopithecus spp.*). *Primates*, *47*(4), 336-341.

Chalk, J. (2011). *The effects of feeding strategies and food mechanics on the ontogeny of masticatory function in the Cebus libidinosus cranium* (Doctoral dissertation, The George Washington University).

Chalk, J., Wright, B. W., Lucas, P. W., Schuhmacher, K. D., Vogel, E. R., Fragaszy, D., Visalberghi, E., Izar, P. & Richmond, B. G. (2016). Age-related variation in the mechanical properties of foods processed by *Sapajus libidinosus*. *American journal of physical anthropology*, *159*(2), 199-209.

Chalk, J., Wright, B. W., Vogel, E. R., & Lucas, P. W. (2013) Developmental perspectives on feeding in wild tufted capuchins (*Cebus libidinosus*). *American journal of physical anthropology, 150* (S56):97.

Chapman, C. A., Chapman, L. J., Naughton-Treves, L., Lawes, M. J., & Mcdowell, L. R. (2004). Predicting folivorous primate abundance: validation of a nutritional model. *American Journal of Primatology*, *62*(2), 55-69.

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

Charnov, E. L. (1993). *Life history invariants: some explorations of symmetry in evolutionary ecology* (Vol. 6). Oxford University Press, USA.

Constantino, P. J., & Wright, B. W. (2009). The importance of fallback foods in primate ecology and evolution. *American journal of physical anthropology*,*140*(4), 599-602.

Constantino, P. J., Lee, J. J. W., Gerbig, Y., Hartstone-Rose, A., Talebi, M., Lawn, B. R., & Lucas, P. W. (2012). The role of tooth enamel mechanical properties in primate dietary adaptation. *American journal of physical anthropology*, *148*(2), 171-177.

Corlett, R. T., & Lucas, P. W. (1990). Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia*, *82*(2), 166-171.

Daegling, D. J. (1992). Mandibular morphology and diet in the genus *Cebus*. *International Journal of Primatology*, *13*(5), 545-570.

Daegling, D. J., & McGraw, W. S. (2007). Functional morphology of the mangabey mandibular corpus: relationship to dental specializations and feeding behavior. *American journal of physical anthropology*, *134*(1), 50-62.

Daegling, D. J., Judex, S., Ozcivici, E., Ravosa, M. J., Taylor, A. B., Grine, F. E., Teaford, M. F., & Ungar, P. S. (2013). Viewpoints: Feeding mechanics, diet, and dietary adaptations in early hominins. *American journal of physical anthropology*, *151*(3), 356-371.

Daegling, D. J., McGraw, W. S., Ungar, P. S., Pampush, J. D., Vick, A. E., & Bitty, E. A. (2011). Hard-object feeding in sooty mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. *PloS one*, *6*(8), e23095.

De Resende, B. D., Ottoni, E. B., & Fragaszy, D. M. (2008). Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): a Perception–action perspective. *Developmental science*, *11*(6), 828-840.

Disotell, T. R. (1994). Generic level relationships of the Papionini (*Cercopithecoidea*). *American Journal of Physical Anthropology*, *94*(1), 47-57.

Dominy, N. J. (2004). Fruits, fingers, and fermentation: the sensory cues available to foraging primates. *Integrative and comparative biology*, *44*(4), 295-303.

Dominy, N. J., Vogel, E. R., Yeakel, J. D., Constantino, P., & Lucas, P. W. (2008). Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evolutionary Biology*, *35*(3), 159-175.

Dumont, E. R. (1995). Enamel thickness and dietary adaptation among extant primates and chiropterans. *Journal of Mammalogy*, *76*(4), 1127-1136.

Dumont, E. R. (1999). The effect of food hardness on feeding behaviour in frugivorous bats (*Phyllostomidae*): an experimental study. *Journal of Zoology*, *248*(2), 219-229.

Eadie, E. C. (2015). Ontogeny of foraging competence in capuchin monkeys (*Cebus capucinus*) for easy versus difficult to acquire fruits: a test of the needing to learn hypothesis. *PloS one*, *10*(9), e0138001.

Elgart-Berry, A. (2004). Fracture toughness of mountain gorilla (*Gorilla gorilla beringei*) food plants. *American Journal of Primatology*, *62*(4), 275-285.

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

Felton, A. M., Felton, A., Wood, J. T., & Lindenmayer, D. B. (2008). Diet and feeding ecology of *Ateles chamek* in a Bolivian semi humid forest: the importance of Ficus as a staple food resource. *International Journal of Primatology*, *29*(2), 379-403.

Fleagle, J. G., & McGraw, W. S. (2002). Skeletal and dental morphology of African papionins: unmasking a cryptic clade. *Journal of human evolution*, *42*(3), 267-292.

Fooden, J. (1971). Female genitalia and taxonomic relationships of *Macaca assamensis*. *Primates*, *12*(1), 63-73.

Fragaszy, D. M., Feuerstein, J. M., & Mitra, D. (1997). Transfers of food from adults to infants in tufted capuchins (*Cebus apella*). *Journal of Comparative Psychology*, *111*(2), 194.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B., & de Oliveira, M. G. (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, *64*(4), 359-366.

Freeland, W. J., & Janzen, D. H. (1974). Strategies in herbivory by mammals: the role of plant secondary compounds. *The American Naturalist*, *108*(961), 269-289.

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

Glowacka, H., McFarlin, S. C., Vogel, E. R., Stoinski, T. S., Ndagijimana, F., Tuyisingize, D., Mudakikwa A & Schwartz, G. T. (2017). Toughness of the Virunga mountain gorilla (*Gorilla beringei beringei*) diet across an altitudinal gradient. *American Journal of Primatology*. ;79:e22661. https://doi.org/10.1002/ajp.22661.

Gunst, N., Boinski, S., & Fragaszy, D. M., (2008). Acquisition of foraging competence in wild brown capuchins (*Cebus apella*) with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour*, *145*(2),195-229.

Gunst, N., Leca, J.B., Boinski, S., & Fragaszy, D., (2010). The ontogeny of handling hard-to-process food in wild brown capuchins (*Cebus apella apella*): evidence from foraging on the fruit of *Maximiliana maripa*. *American journal of primatology*, *72*(11), 960-973.

Gurven, M., Kaplan, H., & Gutierrez, M. (2006). How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span. *Journal of human evolution*, *51*(5), 454-470.

Haddow, A. J. (1952, August). Field and laboratory studies on an African monkey, *Cercopithecus ascanius* schmidti Matschie. In *Proceedings of the Zoological Society of London* (Vol. 122, No. 2, pp. 297-394). Blackwell Publishing Ltd.

Harris, E. E. (2000). Molecular systematics of the Old World monkey tribe *Papionini*: analysis of the total available genetic sequences. *Journal of Human Evolution*, *38*(2), 235-256.

Harrison, M. E., & Marshall, A. J. (2011). Strategies for the use of fallback foods in apes. *International journal of primatology*, *32*(3), 531-565.

Hartstone-Rose, A., Parkinson, J. A., Criste, T., & Perry, J. M. (2015). Comparing apples and oranges—the influence of food mechanical properties on ingestive bite sizes in lemurs. *American journal of physical anthropology*, *157*(3), 513-518.

Hauser, M. D, (1987). The behavioral ecology offree ranging vervet monkeys: Proximate and ultimate levels of explanation. Phd dissertation, University of California, Los angelos.

Hayashi, M., Takeshita, H., & Matsuzawa, T. (2006). Cognitive development in apes and humans assessed by object manipulation. In *Cognitive development in chimpanzees* (pp. 395-410). Springer Tokyo.

Hemingway, C. A., & Bynum, N. O. R. A. (2005). The influence of seasonality on primate diet and ranging. In: Brockman, D.K. & van Schaik, C.P (Eds), *Seasonality in primates: Studies of living and extinct human and non-human primates* (pp. 44 - 57). Cambridge: Cambridge University Press.

Hill, W. C. O. (1966). *Primates, Comparative Anatomy and Taxonomy: Catarrhini, Cercopithecoidea, Cercopithecinae* (No. 3). University Press.

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

Humle, T., & Matsuzawa, T. (2002). Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *American Journal of Primatology*, *58*(3), 133-148.

Hylander, W. L. (1975). Incisor size and diet in anthropoids with special. *Science*, *808855*(1095), 189.

Hylander, W. L., & Johnson, K. R. (1994). Jaw muscle function and wishboning of the mandible during mastication in macaques and baboons. *American Journal of Physical Anthropology*, *94*(4), 523-547.

Jacobsen, N. (1970). Salivary amylase. II. Alpha-amylase in salivary glands of the Macaca irus monkey, the Cercopithecus aethiops monkey, and man. *Caries research*, *4*(3), 200-205.

Janson C. & van Schaik C. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira M.E. & Fairbanks L.A., (Eds.), *Juvenile primates: life history, development, and behavior* (pp. 57 – 76). New York: Oxford University Press.

Johnson, C. A., Raubenheimer, D., Rothman, J. M., Clarke, D., & Swedell, L. (2013). 30 Days in the life: daily nutrient balancing in a wild chacma baboon. *PloS one*, *8*(7), e70383.

Kay, R. F. (1975). The functional adaptations of primate molar teeth. *American Journal of Physical Anthropology*, *43*(2), 195-215.

Kay, R. F. (1981). The nut-crackers–a new theory of the adaptations of the Ramapithecinae. *American Journal of Physical Anthropology*, *55*(2), 141-151.

Kinnaird, M. F. (1990). Behavioraland demographic responses to habitat change by the Tana Rive crested mangabey (*Cercocebus galeritus galeritus*). Unpublished Ph.D. Dissertation University of Florida, Gainesville, Florida.

Kinnaird, M. F. (1992). Phenology of flowering and fruiting of an East African riverine forest ecosystem. *Biotropica*, 187-194.

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

Kivai, S. (2013). Predation on an Endemic and Endangered Tana River Mangabey (*Cercocebus galeritus*) by a Sympatric Yellow Baboon (*Papio cynocephalus*) in Tana River National Primate Reserve, Kenya. *African Primates* 8, 59-62.

Lambert J. E. (2007). Seasonality, fallback strategies, and natural selection: a chimpanzee and cercopithecoid model for interpreting the evolution of hominin diet. In: Evolution of the human diet. Ungar PS, (ed). Oxford: Oxford University Press. p 324–343.

Lambert J.E. (2005). The ecomorphology of anterior dentition: an analysis of food handling and processing in a community of African cercopithecoids. *Am J Primatol* 66, 136.

Lambert, J. E. (2002). Resource switching and species coexistence in guenons: a community analysis of dietary flexibility. *In: The Guenons: Diversity and Adaptation in African Monkeys.* Glenn, M. E., and Cords, M. (Eds.), pp. 309-323. Kluwer Academic/Plenum Press, New York.

Lambert, J. E. (2010). Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In: Campell, C., Fuentes, A., Mackinnon, K. C., Panger, M., and Beadner, S. (Eds), *Primates in perspective* (pp. 482-495). Oxford: Oxford University Press.

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

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

Lonsdorf, E.V., & Ross, S.R., (2012). Socialization and Development of Behavior. In*:* Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.), *The evolution of primate societies* (pp. 245-268). Chicago: University of Chicago Press.

Lonsdorf, E.V., Eberly, L.E., & Pusey, A. E., (2004). Sex differences in learning in chimpanzees. *Nature*, *428*(6984), 715-716.

Lucas, P. W., & Luke, D. A. (1984). Optimum mouthful for food comminution in human mastication. *Archives of Oral Biology*, *29*(3), 205-210.

Lucas, P. W., & Teaford, M. F. (1994). Functional morphology of colobine teeth. *Colobine monkeys: Their ecology, behaviour and evolution*, 173-203.

Lucas, P. W., Copes, L., Constantino, P. J., Vogel, E. R., Chalk, J., Talebi, M., Landis, M. & Wagner, M. (2012). Measuring the toughness of primate foods and its ecological value. *International Journal of Primatology*, *33*(3), 598-610.

Lucas, P. W., Darvell, B. W., Lee, P. K. D., Yuen, T. D. B., & Choong, M. F. (1995). The toughness of plant cell walls. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *348*(1325), 363-372.

Lucas, P., Constantino, P., Wood, B., & Lawn, B. (2008). Dental enamel as a dietary indicator in mammals. *BioEssays*, *30*(4), 374-385.

Lucas, P.W., 2004. Dental Functional Morphology: How Teeth Work. Cambridge University Press, Cambridge.

Marshall, A. J., & Wrangham, R. W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*, *28*(6), 1219.

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

Mau, M., Südekum, K. H., Johann, A., Sliwa, A., & Kaiser, T. M. (2010). Indication of higher salivary α-amylase expression in hamadryas baboons and geladas compared to chimpanzees and humans. *Journal of medical primatology*, *39*(3), 187-190.

McGraw, W. S., & Daegling, D. J., (2012). Primate feeding and foraging: integrating studies of behavior and morphology. *Annual Review of Anthropology*, *41*, 203-219.

McGraw, W. S., Vick, A. E., & Daegling, D. J. (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*(1), 140-153.

McGraw, W. S., Vick, A. E., & Daegling, D. J. (2014). Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): Implications for fallback foods and dental adaptation. *American journal of physical anthropology*, *154*(3), 413-423.

Medley, K. E. (1993). Extractive forest resources of the Tana River National Primate Reserve, Kenya. *Economic Botany*, *47*(2), 171-183.

Milton, K., Giacalone, J., Wright, S. J., and Stockmayer, G. 2005. Do frugivore population fluctuations reflect fruit production? Evidence from Panama. In J. L. Dew and J. P. Boubli (eds.), Tropical Fruits and Frugivores: The Search for Strong Interactions (pp. 5–35). Dordrecht, The Netherlands: Springer.

Milton, K. (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *The American Naturalist*, *114*(3), 362-378.

Milton, K. (1980). *The Foraging Strategy of Howler Monkeys*. New York: Columbia University Press.

Milton, K. (1984). The role of food-processing factors in primate food choice. *Adaptations for foraging in nonhuman primates*, 249-279.

Milton, K. (1999). Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us? *Nutrition*, *15*(6), 488-498.

Murray, C. M., Eberly, L. E., & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (Pan troglodytes). *Behavioral Ecology*, *17*(6), 1020-1028.

Murray, P. (1975). The role of cheek pouches in cercopithecine monkey adaptive strategy. *Primate Functional Morphology and Evolution*, 151-194.

Napier, J. R. (1970). Paleoecology and catarrhine evolution. *Old World monkeys: evolution, systematics, and behavior. New York: Academic Press. p*, 53-95.

Norconk, M. A., & Veres, M. (2011). Physical properties of fruit and seeds ingested by primate seed predators with emphasis on sakis and bearded sakis. *The Anatomical Record*, *294*(12), 2092-2111.

Norconk, M. A., Wright, B. W., Conklin-Brittain, N. L., & Vinyard, C. J. (2009). Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In: Garber, P. A., Estrada, A., Bicca-Marques, J. C., Heymann, E. & Strier, K. B (Eds), *South American Primates* (pp. 279-319). New York: Springer.

O'mara, M. T. (2015). Ecological risk aversion and juvenile ring-tailed lemur feeding and foraging. *Folia Primatologica*, *86*(1-2), 96-105.

Olupot, W., Waser, P. M., & Chapman, C. A. (1998). Fruit finding by mangabeys (Lophocebus albigena): are monitoring of fig trees and use of sympatric frugivore calls possible strategies?. *International Journal of Primatology*, *19*(2), 339-353.

Pereira, M.E., Fairbanks, L.A., (2002). *Juvenile Primates: Life history, Development and Behavior*. New York: Oxford University Press.

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews*, *17*(4), 189-201.

Raubenheimer, D., & Simpson, S. J. (2004). Organismal stoichiometry: quantifying non-independence among food components. *Ecology*, *85*(5), 1203-1216.

Raubenheimer, D., Simpson, S. J., & Mayntz, D. (2009). Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology*, *23*(1), 4-16.

Ravosa, M. J., Ross, C. F., Williams, S. H., & Costley, D. B. (2010). Allometry of masticatory loading parameters in mammals. *The Anatomical Record*, *293*(4), 557-571.

Ravosa, M. J., Scott, J. E., McAbee, K. R., Veit, A. J., & Fling, A. L. (2015). Chewed out: an experimental link between food material properties and repetitive loading of the masticatory apparatus in mammals. *PeerJ*, *3*, e1345.

Rosenberger, A. L. (2013). Fallback foods, preferred foods, adaptive zones, and primate origins. *American journal of primatology*, *75*(9), 883-890.

Ross, C. E., & Jones, K. E. (1999). Socioecology and the evolution of primate reproductive rates. *Comparative primate socioecology*, 73-110.

Ross, C. F., Dharia, R., Herring, S. W., Hylander, W. L., Liu, Z. J., Rafferty, K. L., Ravosa, M.J. & Williams, S. H. (2007). Modulation of mandibular loading and bite force in mammals during mastication. *Journal of Experimental Biology*, *210*(6), 1046-1063.

Rothman, J. M., Dierenfeld, E. S., Hintz, H. F., & Pell, A. N. (2008). Nutritional quality of gorilla diets: consequences of age, sex, and season. *Oecologia*, *155*(1), 111-122.

Rothman, J. M., Chapman, C. A., Struhsaker, T. T., Raubenheimer, D., Twinomugisha, D., & Waterman, P. G. (2015). Long-term declines in nutritional quality of tropical leaves. *Ecology*, *96*(3), 873-878.

Rothman, J. M., Dierenfeld, E. S., Molina, D. O., Shaw, A. V., Hintz, H. F., & Pell, A. N. (2006). Nutritional chemistry of foods eaten by gorillas in Bwindi Impenetrable National Park, Uganda. *American Journal of Primatology*, *68*(7), 675-691.

Rowe, N. and Myers, M. (2016). *All the World's Primates*. Pongonias press.

Rowell, T. E., & Mitchell, B. J. (1991). Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. *Journal of Tropical Ecology*, *7*(2), 269-274.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual review of ecology and systematics*, *2*(1), 369-404.

Scott, J. E., McAbee, K. R., Eastman, M. M., & Ravosa, M. J. (2014). Experimental perspective on fallback foods and dietary adaptations in early hominins. *Biology letters*, *10*(1), 20130789.

Shah, N.F. (2003). Foraging strategies in two sympatric mangabey species (*Cercocebus agilis* and *Lophocebus albigena*). (*Ph.D. dissertation thesis, Stony Brook University, Stony Brook, NY)*

Sinclair, A. R., Fryxell, J., & Caughley, G. (2011). *Wildlife ecology, conservation and management*. Wiley. com.

Simpson, S. J., Le Couteur, D. G., & Raubenheimer, D. (2015). Putting the balance back in diet. *Cell*, *161*(1), 18-23.

Singleton, M. (2005). Functional shape variation in the cercopithecine masticatory complex. In *Modern morphometrics in physical anthropology* (pp. 319-348). Springer US.

Senior, A. M., Charleston, M. A., Lihoreau, M., Buhl, J., Raubenheimer, D., & Simpson, S. J. (2015). Evolving nutritional strategies in the presence of competition: a geometric agent-based model. *PLoS Comput Biol*, *11*(3), e1004111.

Smith, L. W., Link, A., & Cords, M. (2008). Cheek pouch use, predation risk, and feeding competition in blue monkeys (Cercopithecus mitis stuhlmanni). *American Journal of Physical Anthropology*, *137*(3), 334-341.

Spencer, M. A. (1997). Force production in the primate masticatory system: electromyographic tests of biomechanical hypotheses. *Journal of human evolution*, *34*(1), 25-54.

Stephens, D., Brown, J. & Ydenberg, R. C. (2007). *Foraging: behavior and ecology*. University of Chicago Press.

Strait, D. S., Constantino, P., Lucas, P. W., Richmond, B. G., Spencer, M. A., Dechow, P. C., Callum F. R., Ian R. G., Barth W. W., Bernard A. W., Gerhard W. W., Qian W, Craig B., Dennis E. S., Janine C., Amanda L. S., Leslie C. S., Sarah W., Michael B., Stefano B., Christine D & Ledogar, J. A. (2013). Viewpoints: Diet and dietary adaptations in early hominins: The hard food perspective. *American journal of physical anthropology*, *151*(3), 339-355.

Strait, D. S., Weber, G. W., Constantino, P., Lucas, P. W., Richmond, B. G., Spencer, M. A., Dechow, P. C., Ross, C. F., Grosse, I. R., Wright, B. W., Wood, B. A., Wang, Q., Byron, C. & Slice, D. E. (2012). Microwear, mechanics and feeding adaptations of *Australopithecus africanus*. *Journal of human evolution*, *62*(1), 165-168.

Strait, D. S., Weber, G. W., Neubauer, S., Chalk, J., Richmond, B. G., Lucas, P. W., Spencer, M.A., Schrein, C., Dechow, P.C., Ross, C.F & Grosse, I. R. (2009). The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proceedings of the National Academy of Sciences*, *106*(7), 2124-2129.

Strait, S. G. (1997). Tooth use and the physical properties of food. *Evolutionary Anthropology: Issues, News, and Reviews*, *5*(6), 199-211.

Ungar, P. S. (Ed.). (2007). Evolution of the human diet: The known, the unknown, and the unknowable. Oxford: Oxford University Press.

Ungar, P. (2004). Dental topography and diets of *Australopithecus afarensis* and early Homo. *Journal of Human Evolution*, *46*(5), 605-622.

van Noordwijk, M. A., & van Schaik, C. P. (2005). Development of ecological competence in Sumatran orangutans. *American Journal of Physical Anthropology*, *127*(1), 79-94.

van Noordwijk, M. A., Hemelrijk, C. K., Herremans, L. A., & Sterck, E. H. (2002). Spatial position and behavioral sex differences in juvenile long-tailed macaques. *Juvenile primates: life history, development and behavior. Chicago: University of Chicago Press. p*, 77-85.

Van Schaik, C. P., & Knott, C. D. (2001). Geographic variation in tool use on Neesia fruits in orangutans. *American Journal of Physical Anthropology*, *114*(4), 331-342.

Visalberghi, E., & Néel, C. (2003). Tufted capuchins (*Cebus apella*) use weight and sound to choose between full and empty nuts. *Ecological Psychology*,*15*(3), 215-228.

Visalberghi, E., Albani, A., Ventricelli, M., Izar, P., Schino, G., & Fragazsy, D. (2016). Factors affecting cashew processing by wild bearded capuchin monkeys (*Sapajus libidinosus*, Kerr 1792). *American journal of primatology*, *78*(8), 799-815.

Vogel E.R, Kivai S. M. & Alavi S. (2016). Foraging strategies. *International Encyclopedia of Primatology*. In Press

Vogel, E. R., van Woerden, J. T., Lucas, P. W., Utami Atmoko, S. S., van Schaik, C. P., & Dominy, N. J. (2008). Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *Journal of Human Evolution*, *55*(1), 60-74.

Vogel, E.R, Zulfa, A., Hardus, M., Wich, S.A. & Dominy, N.J (2014). Food mechanical properties, feeding ecology, and the mandibular morphology of the wild Orangutans. *Journal of Human Evolution*, http://dx.doi.org/10.1016/j.jhevol.2014.05.007

White, T. C. (2011). The significance of unripe seeds and animal tissues in the protein nutrition of herbivores. *Biological Reviews*, *86*(1), 217-224.

Wieczkowski J. (2003). *Aspects of the ecological flexibility of the Tana mangabey (Cercocebus galeritus) in its fragmented habitat, Tana River, Keny*a. Ph.D. dissertation thesis. Athens, GA: University of Georgia.

Wieczkowski, J. (2004). Ecological correlates of abundance in the Tana mangabey (*Cercocebus galeritus*). *American Journal of Primatology*, *63*(3), 125-138.

Wieczkowski, J. (2009). Brief communication: Puncture and crushing resistance scores of Tana River Mangabey (*Cercocebus galeritus*) diet items. *American journal of physical anthropology*, *140*(3), 572-57.

Wieczkowski, J. (2009). Brief communication: Puncture and crushing resistance scores of Tana river mangabey (*Cercocebus galeritus*) diet items. *American journal of physical anthropology*, *140*(3), 572-577.

Wieczkowski, J., & Kinnaird, M. (2008). Shifting forest composition and primate diets: a 13-year comparison of the Tana River mangabey and its habitat. *American Journal of Primatology*, *70*(4), 339-348.

Wieczkowski, J., & Kinnaird, M. (2008). Shifting forest composition and primate diets: a 13-year comparison of the Tana River mangabey and its habitat. *American Journal of Primatology*, *70*(4), 339-348.

Wright, K. A. (2007). The relationship between locomotor behavior and limb morphology in brown (*Cebus apella*) and weeper (*Cebus olivaceus*) capuchins. *American Journal of Primatology*, *69*(7), 736-756.

Yamashita, N. (1998). Functional dental correlates of food properties in five Malagasy lemur species. *American Journal of Physical Anthropology*, *106*(2), 169-188.

Yamashita, N., Cuozzo, F. P., & Sauther, M. L. (2012). Interpreting food processing through dietary mechanical properties: a *Lemur catta* case study. *American journal of physical anthropology*, *148*(2), 205-214.

CHAPTER TWO: DIETARY CHOICE AND ENERGY INTAKE IN JUVENILE TANA RIVER MANGABEYS, *CERCOCEBUS GALERITUS*

Abstract

Acquisition of adequate energy to meet the requirements of basal metabolism, physical activities, growth, and reproduction is important, particularly in juveniles and lactating mothers among primates. Compared to adults, juveniles are faced with increased energetic demands than adults due to need for fast growth and high physical activity. Lactating females as well have to meet the energetic requirements for milk production, infant transport, and general body maintenance. However, adults are more competent foragers than juveniles, which are disadvantaged as inexperienced foragers. Consequently, little is known about how juveniles achieve their energy requirements and whether their dietary breadth and intake rates differ from those of adults. To address this problem I tested the Need-to-Learn hypothesis in juvenile Tana River mangabeys, which posits that juveniles: a) are less efficient foragers because they are still learning appropriate food choices and processing skills and are developing the relevant physical and motor capabilities; and b) require more energy per unit of body mass for growth. First, I predicted that juveniles will have a narrower dietary breadth and their diet selectivity will be skewed towards preferred foods in the diet; and second, they will ingest more relative metabolizable energy (ME) (per metabolic body mass) to maintain the higher metabolic needs resulting from smaller body size.

I collected feeding data using the focal animal sampling method to determine food selectivity (preference), dietary breadth, and energy intake. I calculated dietary breadth from feeding data using standardized Levin's index (BA), while for diet selectivity I used Vanderploeg and Scavia (1979) electivity index (E*). To examine energy intake, I collected samples of the mangabey foods in the field and performed laboratory nutritional analyses using the standard field and laboratory procedures. Compared to lactating females, juveniles differed significantly in food electivity in both Mchelelo (W = -1004, p < 0.0001, N = 66) and in Kitere (W = - 1637, p < 0.0001, N =71) study groups as I expected. Juveniles' food electivity was skewed towards both preferred and avoided foods. True to my prediction, juveniles had a narrower dietary breath (BA = 0.11) compared to the females (BA = 0.13). The relative ME intake varied significantly in response to age class, and juveniles exhibited higher intake of energy than lactating female for both the per minute analysis (F = 38.02, df = 60, p < 0.0001; t = 6.17, p < 0.0001, N = 63) and the per feeding bout analysis (F = 38.09, df = 61, p < 0.0001; t = -6.17, df = 61, p < 0.0001, N = 63) supporting my prediction. These findings supported my hypothesis that juveniles are less efficient in foraging and ingest more energy per unit of body mass for growth compared to the adults.

2.1 Introduction

2.1.1 Background

Despite several decades of rigorous primate research on feeding and behavioral ecology, data on juvenile foraging strategies continue to be limited for the majority of primate species. However, over the last two decades the situation has improved with studies of juveniles in yellow baboons (*Papio cynocephalus*) (Altmann, 1998), capuchin monkeys (*Cebus* sp.) (Janson & van Schaik, 1993; Fragaszy & Boinski 1995; Gunst et al., 2010; Chalk et al., 2016), long-tailed macaques (*Macaca fascicularis*) (Janson & van Schaik, 1993), Sumatran orangutan (*Pongo abelii*) (van Noordwijk & van Schaik, 2005; Jaeggi et al., 2008; Schuppli et al., 2016), and ring-tailed lemurs (*Lemur catta*) (O'Mara, 2015). These studies indicate that juveniles are incompetent foragers and experience feeding challenges in meeting their nutritional requirements, thus, informing understanding of the factors that influence juvenile foraging ontogeny and associated lifetime fitness consequences in the wild. Primate juveniles are characterized by protracted periods of immaturity, relative to expectations from trends in mammalian body size (Pereira & Fairbanks, 2002). This life-history trait, coupled with complex foraging strategies, implies that ontogenetic factors strongly influence juvenile food choice and energy acquisition (Janson & van Schaik, 1993; MacKinnon, 2006; Gunst et al., 2010; Chalk et al., 2016).

Evidence from the few studies on foraging in juvenile primates suggests they differ from adults in food choices, energy intake, and food processing (Pereira & Fairbanks, 2002; MacKinnon, 2006; Gunst et al., 2010). Four hypotheses have been

proposed to explain these differences. First, the ecological risk aversion hypothesis (Janson & van Schaik, 1993) argues that slow growth rates evolved as a counter-strategy to feeding competition, reduced access to resources, or reduced intake rates in juveniles. The reason is that juveniles are relatively poor competitors and may be pushed to the periphery of the group, where predation risk is higher and resources are more reduced than at the core of the group (Janson & van Schaik, 1993). Second, the need-to-learn hypothesis posits that juvenile-adult differences in feeding behavior emerged due to variation in learning opportunities (Visalberghi & Fragaszy, 2002). This may be more applicable in species that feed disproportionately on challenging foods, which require juveniles to master complex foraging processes. Under these conditions, juveniles may spend a greater proportion of their time observing competent individuals, as opposed to active foraging. Thirdly, the physical immaturity hypothesis proposes that juveniles are limited in solving feeding tasks requiring strength and manual dexterity (Gunst et al., 2010). That is, juveniles experience lower ingestion rates of foods where individual motor skills are necessary to extract them or break mechanical barriers before ingestion (Fragaszy & Boinski, 1995; Eadie, 2015). Finally, the nutritional requirements hypothesis states that the energetic demands of growth are high for juveniles, and they may target nutrient dense plant parts or prey more than adults while feeding (Altmann, 1998; Albert & Altmann, 2005; Felton et al., 2009).

2.1.2 Juveniles-adult feeding differences

Although little is known about juvenile foraging strategies among the majority of primates, some inferences can be drawn from the few existing studies.

For instance, in wedge-capped capuchin monkeys (*Cebus olivaceous*) juveniles included lower amounts of fruits in their diets and engaged more in less strenuous foraging activities than adults (Fragaszy, 1986; Fragaszy & Boinski, 1995). Juveniles were less efficient than adults in foraging on plant materials. Because capuchin monkeys are hard object feeders, these results also suggest possible parallels with the Tana River mangabeys (see below). Further compelling evidence on juvenile-adult differences comes from a detailed study of yearling yellow baboons in Amboseli National Park, Kenya (Altmann, 1998). Dietary intake at an early age of these baboons was highly variable, and during periods of food scarcity, juveniles experienced a 55.7% shortfall in energy intake.

Juveniles differ from adults in ingestion of different nutrients. In mountain gorillas (*Gorilla beringei*) juveniles consumed more minerals per kilogram of body weight compared to silverback males and adult females (Rothman et al., 2008a). The daily mean intake of protein relative to body mass was higher in both juveniles and adult females than silverbacks. These patterns likely result from the nutritional requirements imposed by lactation in females and by growth in juveniles.

The nutritional returns and mechanical (processing) challenges of foods are likely to influence the foraging efficiency (e.g., energy intake/time) of juveniles and adults. This has been demonstrated in wild juvenile brown capuchin monkeys (*Cebus apella*), which do not attain adult efficiency in plucking the Maripa palm (*Attalea maripa*) fruit until the age of 3 years, at which time the required behavioral skills and physical strength have been attained. For ingestion of beetle (*Myelobia* sp.) larvae, however, efficiency is not achieved until 6 years of age (Gunst et al.,

2010). These larvae are an excellent source of protein, but exploitation requires extractive foraging, which involves successfully learning to identify the appropriate bamboo substrate, detecting the concealed larvae via auditory, olfactory, tactile and visual cues, and finally possessing the manual strength to rip off the bamboo stalk. These observations support both the need-to-learn and physical maturation hypotheses in explaining adult-juvenile foraging differences.

The prediction of the ecological risk aversion hypothesis that predation risk impacts energy intake (Pereira & Fairbanks, 2002) is well supported by data from the ring-tailed lemur (*Lemur catta*). When foraging together in areas of high predation risk, juveniles had significantly lower ingestion rates than adults for the majority of foods (O'Mara, 2015). This study also found that juveniles did not attain adult intake rates of young leaves as the primary diet until the age of 2 years.

2.1.3 Primate dietary strategies and challenges

Primate diets exhibit high complexity regarding the structure, content, and spatio-temporal distribution of foods (Robbins & Hohmann, 2006). Understanding the factors that govern the dietary selection and energy intake is fundamental to providing insights about feeding ecology, especially in juveniles. Primates utilize a wide array of foods, including: leaves, fruits, flowers, seeds, insects, fungi, bark, roots, underground storage organs, pith, gum, and meat. Three broad dietary strategies exist among primates, based on the major food component included in their diet: frugivory (eat more fruits), folivory (eat more leaves), and insectivory/faunivory (eat more insects) (Janson & Chapman, 1999). Primates supplement these core diets with other food items such as nectar, flowers, gum, sap,

corms, grasses and small vertebrates, which at times may be good sources of limited macronutrients or even energy (Garber, 1987; Felton et al., 2009). Individual choices of food are directly or indirectly influenced by some factors such as plant food chemical and mechanical properties, body size, metabolic or physiological needs, and energy intake demands (Havey & Clutton-Brock, 1981). Other factors scaled to body size, such as gut size, the rate of food passage, home range size, and locomotive energetics, critically influence dietary choice as well (Chivers & Hladik, 1984; Estrada & Coates-Estrada, 1984; Havey & Clutton-Brock, 1981).

Primates are confronted by multiple challenges that are likely to limit energy intake. Some of these derive from the foods, such as the abundance and patchiness of distribution (which influences competition and predation risk) and plant chemical and mechanical defenses, while others are intrinsic to the consumers themselves, such as the need for nutrient balancing (Milton, 1984; Garber, 1987; Felton et al., 2009; Lambert & Rothman, 2015). Dietary choices are expected to reflect a delicate trade-off between the need to maximize energy intake to meet the optimal body metabolic needs and the effort to navigate food-related foraging constraints.

Distinct sets of adaptations may help primates to overcome the foraging problems that limit nutrient acquisition and achievement of energetic goals. For instance, insectivores need specialized dental and enzymatic adaptations to process and break down the chitinous exoskeleton of insects (Garber, 1987), namely high crowned molars and production of enzyme chitinase (Janson & Boinski, 1992; Strier, 2016). The availability, distribution, and size of insects affect search time and

acquisition rate, such that their consumption is mostly limited to small-bodied primates ranging from 300 to 3000g (Janson & Chapman, 1999).

Fruits also pose nutritional and ecological problems to frugivorous primates. Although ripe, fruits are relatively easy to ingest and high in simple sugars (Milton, 1999), they are poor in protein and fat, and their availability is typically limited by spatial and temporal patchiness (Janzen, 1983; Gautier-Hion et al., 1985; Janson & Chapman, 1999; Milton, 1999; Boyer et al., 2006; Vogel et al., 2016). Overcoming the latter problem often necessitates that frugivores range and search widely for fruit patches, which is energetically costly. Unripe fruits are armed with chemical and/or physical defense mechanisms against herbivory, which consumers must overcome to exploit this food resource (Milton, 1999; Vogel et al., 2016). In addition, plants have evolved adaptive mechanisms to limit dispersal to a small fraction of mammalian consumers, such as morphological features, toxicity, taste, and delayed ripening (Mack, 2000; Stevenson et al., 2005). Thus, not all of the available fruits are nutritionally beneficial because the combination of these adaptive strategies offers a substantial barrier to efficient fruit utilization. Selective foraging and good spatial memory remain some of the major strategies primates employ in resolving these problems. For example, in primates, spatial memory has been found to improve foraging efficiency by 300% in relation to random food searching (Janson, 1998; Boyer et al., 2006; Reynolds, 2012).

Folivory requires avoidance of complex structural and chemical defenses to herbivory, particularly when focused on mature leaves (Garber, 1987; Janson & Chapman, 1999). Cellulose limits exploitation due to indigestibility properties

(Lambert, 1998; Felton et al., 2009). The presence of gut protozoans or bacterial symbionts, combined with behavioral, and anatomical adaptive mechanisms, help to overcome this problem (Lambert, 1998). Selection of young leaves, which are typically lower in cellulose and plant secondary metabolites, represents a good example of behavioral strategies to avoid these chemical constraints (Milton, 1984).

Flexibility, rather than pronounced specialization, characterizes the diets of most primates (Harding, 1981; Janson & Chapman, 1998). Faunivorous and anatomical folivorous primates can afford to be relative specialists given their dietary adaptations, body size, and the abundance and distribution of their foods, but most primates show considerable dietary flexibility despite the possible bias towards certain food categories (Robbins & Hohmann, 2006). Indeed, dietary and foraging strategies differ even within closely related taxa (Sussman, 1987). Flexibility in dietary patterns can be complex and dynamic. This may include broadening or narrowing of diets, seasonal shifts, sex differences in foraging and ranging behavior, and response to food scarcity by group disintegration (Boyer et al., 2006; Rothman et al., 2008a; Sato et al., 2015; Vogel et al., 2017).

2.1.4 Nutritional and energetic influences on food choice

In recent years, studies of primate nutritional ecology have made significant advances in developing systematic approaches (especially Geometric Framework - GF that include Right-angled Mixture Triangle - RMT) in understanding how individual or species-specific nutritional requirements influence foraging strategies, dietary choices, and energy intake (Simpson et al., 2003; Felton et al., 2008, 2009; Raubenheimer et al., 2009; Rothman et al., 2007; Rothman et al., 2011;

Raubenheimer et al., 2015). Although GF is not used in this study, its application in these studies has provided compelling evidence that, certain nutritional requirements dictates the type and quantity of foods selected by primates (Felton et al., 2009; Raubenheimer et al., 2015). The majority of these studies concur that primate nutritional goals drive food choice and foraging strategies (Felton et al., 2009). Evidence obtained through the application of GF and RMT indicates that primate dietary choices and feeding strategies are shaped by macronutrient priorities. These include energy or protein maximization (Schoener, 1971; Mattson, 1980), minimizing the dietary fiber or intake of secondary metabolites (Milton, 1979; Freeland & Janzen, 1974) and balancing of nutrient intake (Raubenheimer & Simpson, 2004; Raubenheimer et al., 2015).

Although studies focusing on primate nutritional priorities are still scanty, there is substantial evidence of energy maximization in northern muriquis (*Brachyteles hypoxanthus*) (Strier, 1992). Primate's feeding behavioral strategies, which suggest energy maximization, include: minimizing energy expenditure (often corresponds to folivory), and maximizing energy intake (common with frugivory) (Felton et al., 2009). Muriquis' annual diet included 51%, 32 %, and 11%, leaves, fruits, and flowers, respectively. According to this study, the high proportion of leaves in their diet and the high consumption of fruits whenever they are available, conform to predictions based on body size energetics and indicate combination of the two behavioral strategies of energy maximization (i.e., folivory-frugivory). The species exhibit physical adaptations that allow mobility for efficient exploitation of fruits and digestive and dental adaptations that allow breakdown of fibrous leaf diet

enhancing energy intake (Strier, 1992). Other feeding strategies that suggest energy-maximization in primates are short food retention times and preference for sugar and lipid rich fruits (Milton, 1981; Di Fiore et al., 2008; Strier, 2016). These feeding strategies are represented in some cercopithecines, such as blue monkeys, (*Cercopithecus mitis*), Tana River mangabeys, chacma baboons (*Papio ursinus*) and vervet monkeys (*Chlorocebus pygerythrus*) (Kinnaird, 1992; Barton & Whiten, 1994; Isbell et al., 1998; Van Doorn et al., 2010) suggesting possible energy maximization among these species.

Protein plays a central role in metabolic processes, cellular structure, and genetic coding, and is thus a limiting factor in growth and reproduction (Felton et al., 2009). Consequently, Rothman et al. (2008b) argue that primate dietary intake is influenced by the need to acquire sufficient nutrients and juvenile and lactating females ingest more dry matter of food than males to meet their protein needs. Nutritional studies of blue monkeys (*Cercopithecus mitis stuhlmanni*) and golden monkeys (*Cercopithecus mitis kandti*) in Kibale and Mgahinga Gorilla National Parks, Uganda (Twinomugisha et al., 2006) as well as of olive baboons (*Papio anubis*) in Laikipia plateau in Kenya (Barton & Whiten, 1994) illustrate how these species carefully select food items to meet protein demands. Altmann (1998) emphasizes protein intake as a particularly crucial factor influencing juvenile survival and future reproductive fitness in yellow baboons.

Evidence of the prioritization of protein has also been found in Peruvian or black-faced black spider monkeys, *(Ateles chamek)* (Felton et al., 2009). Geometric analysis has demonstrated that dietary composition of this species is governed by

the regulation of protein intake as opposed to carbohydrate and fat intake. Similarly, using right-angled mixture triangles and data from different field data, Raubenheimer et al. (2015) showed that the dietary composition of plant parts eaten by blue monkeys, chimpanzees (*Pan troglodytes*), red-tailed monkeys (*Cercopithecus ascanius*), and grey-cheeked mangabeys (*Lophocebus albigena*) in Kibale National Park, Uganda as well as mountain gorillas in Virunga and Bwindi National Parks in Uganda and Rwanda, respectively, reflect balancing of protein, non-structural carbohydrates and fiber. This was revealed by balancing of protein: non-structural carbohydrates intake increasing from chimpanzees to gorillas, with the value for monkeys falling at intermediate values. However, red-tailed monkeys showed a high target of protein by including a significant proportion of insects while gorillas consumed more fiber compared to the rest.

Dietary fiber, which consists of cellulose, hemicelluloses, and lignin, requires specialized adaptations to digest, except for lignin, which is indigestible (Felton et al., 2009). The digestion of fiber is achieved through enzymes produced by symbiotic gut micro-organisms, which break it down into fatty acids and microbial protein (Clement et al., 2009). Consequently, dietary fiber affects food selection and net energy gain. The colobines are the most adapted in handling dietary fiber among the cercopithecoids (Chapman & Chapman, 2002), particularly through their compartmentalized stomach and foregut fermentation. Other less anatomically specialized species avoid consumption of plants with high dietary fiber through highly selective foraging (Waterman et al., 1988; Whiten et al., 1991; Chapman & Chapman, 2002).

2.1.5 Ecology of the Tana River mangabeys

The Tana River mangabeys live in multimale-multi-female societies with mean group sizes ranging from 17 - 50 individuals (Homewood, 1978; Kinnaird, 1990; Wieczkowski, 2003). Females are philopatric and reach sexual maturity earlier (2.5 - 3 years) than males (5 - 6.5 years), which typically disperse (Homewood, 1978; Wieczkowski & Butynski, 2007; Rowe & Myers, 2015). Groups are territorial in the sense that aggression is site-specific and home range overlap is minimal (Kinnaird, 1990). The expression of territoriality, however, is reduced when resources are limited. Home range size is on average 1.75 ha, and day range is about 1395 m (Wieczkowski, 2003). Breeding occurs throughout the year, but peaks between October and February. Inter-birth intervals range between 18 - 24 months (Kinnaird, 1990).

The Tana River mangabeys are semi-terrestrial and spend about 56% of daily time budgets foraging on the ground (Wieczkowski & Butynski, 2007). They are hard object feeders whose diet largely comprises fruit (44%) and seeds (32%) (Homewood, 1978; Wieczkowski, 2003) but also fungi and insects (24%) (Kinnaird, 1990; Kivai per. obsv. 2015). Their craniofacial morphology is characterized by adaptations for the consumption of hard foods (McGraw et al., 2014), but how this influences adult-juvenile feeding differences remains unclear. Previous studies have shown that dietary composition varies across groups in different areas of the Tana River and ranges from 68 – 96 plant species (Homewood, 1978, Wieczkowski, 2003). However, there are no previous studies that have focused on dietary breadth or energy intake between juveniles and adults, which are fundamental in

understanding foraging strategies, juvenile feeding ontogeny, and dietary adaptations.

This species is restricted to the gallery forests of the lower Tana River, a habitat characterized by high aridity and unpredictable climatic conditions (Njue, 1992). Thus, food resources are quite seasonal. Such environmental factors may adversely affect the juveniles' ability to ingest enough energy, especially if they lack the skills and strength to exploit critical fallback foods, which are critical in alleviating nutritional stress during paucity of food resources. "Fallback foods" are defined as less preferred foods that are consumed during periods of low abundance of preferred foods (Wrangham et al., 2009). The lower Tana River area is endowed with important fallback foods (e.g., *Hyphaene compressa, Borassus aethiopum, Oncoba spinosa, Acacia robusta* and *Saba comorensis*) that are hard to process, but are potentially significant sources of energy during periods of food scarcity and nutritional stress (Njue, 1992; Kinnaird, 1992). However, there is no data on mangabeys' selectivity and feeding competence of these fallback foods and the nutritional incentives of their utilization across the age classes. Attaining feeding efficiency on fallback foods is important, particularly in juveniles, which are potentially more constrained during lean periods as poor foragers.

Data on nutritional ecology as well as juvenile foraging strategies in the Tana River mangabeys (*Cercocebus galeritus*) are entirely missing. More important, it is unclear how juveniles meet their high energetic demands in the face of food chemical and mechanical constraints. Previous research mainly focused on the general behavior, feeding ecology, population ecology, and parasitology of this

population (Homewood, 1978; Kinnaird, 1990, 1992; Butynski & Mwangi, 1994; Mbora et al., 2009; Wieczkowski, 2003). Because Tana River mangabeys are hard object feeders (Wieczkowski, 2009), juvenile-adult feeding differences, and subsequently energy intake, are likely to be pronounced (Gunst et al., 2010). Investigating how juvenile Tana River mangabeys forage differently from adult females, and whether they vary in energy intake, contributes to broadening the understanding of why these differences exist as well as why they do no exit in other species.

2.1.6 Tests of hypotheses

In this study, I test the Need-to-Learn hypothesis in juveniles Tana River mangabeys. This hypothesis posits that juveniles: (a) are less efficient foragers than? because they are still learning appropriate food choices and processing skills and developing the relevant physical and motor capabilities; and (b) require more energy per unit of body mass for growth. I test two predictions of this hypothesis. Using lactating females as a control comparison, I predict that juveniles: **(P1)** will have a narrower dietary breadth, but will try feeding on a higher number of different foods unevenly, and will show a stronger higher preferences (diet selectivity) skewed towards preferred foods in the diet; and (**P2**) ingest more metabolizable energy (ME) per a unit of metabolic body mass (MBM), which I refer to below as relative metabolizable energy, to maintain the higher metabolic needs resulting from smaller body size.

The rationale of my (P1) is guided by the fact that, primates engage in complex foraging strategies and ingest wide array of diets in a balanced manner in

order to meet their daily energetic needs (Chapman et al., 2012). Thus, foraging efficiency is necessary to consume required energy, which requires learning coordinated manipulative behaviors, preforming cognitively challenging feeding tasks, and mastering the proper diet (Gunst et al., 2010; Jaeggi et al., 2010). These skills take time to be achieved because they may require physical strength, anatomical and morphological maturation, and extended period of practicing (Pereira & Fairbanks, 2002; Chalk et al., 2016). These aspects limit juveniles' ability to acquire, process, and ingest enough energy rendering them inefficient foragers (Fragaszy & Boinski, 1995; Chalk et al., 2016). This is further complicated by seasonality of primates' food availability and the high energetic requirements of juveniles for growth and maintenance (Altmann, 1998). Diet selection and switching between foods on basis of their nutritional quality, especially when food resources are limited, present one of the feeding strategies to maximize energy intake while at the same time minimizing costs of foraging (Lambert & Rothman, 2015; Vogel et al., 2016). However, because of lack of foraging experience and higher energetic demands compared to adults, juveniles are likely to engage in trial and error approach in effort to learn the complete diet (Schuppli et al., 2012), but elect to consume high-energy foods that are easily acquired to meet the energetic needs. Therefore, juveniles may sample more food species than adults, but may consume them in unevenly and/or concentrate on foods with high energy gains resulting to a narrower dietary breadth. To understand dietary breadth and food preference between the two age classes to test this prediction (P1), I will analyze the dietary selectivity relative to the abundance of those foods in the environment.

The second prediction (P2) is anchored on the understanding that primate energy budgets are determined by energetic requirements for maintenance of basal metabolic rate (BMR), daily physical activities, and life stage physiological functions, such as reproduction (especially lactation) in females and growth in juveniles (Sorensen et al., 2005; Chapman et al., 2012). The energy to meet these processes derives from various macronutrients in foods, which primarily include lipids, carbohydrates, protein, and to a lesser extent, fiber (Neutral Detergent Fiber –NDF) for animals capable of digesting it (NRC, 2003; Conklin-Brittain et al., 2006). However, Kleiber's law posits that BMR in mammals is a negative allometric function of body weight (BW), $BW^{0.75}$ (Kleiber, 1947; Chapman et al., 2012), suggesting that smaller bodies require more energy per unit body mass than large bodies to maintain. Unlike the adults, juveniles at a life stage of fast growth and also engage more in energetically demanding activities such as play and practice of locomotor activities to learn navigation skills through arboreal environments (Pereira & Fairbank, 2002). Consequently, because of the smaller body size, need for growth, and activity levels, juveniles' energetic needs are likely to overshoot those of lactating females. Thus, juveniles will require more energy per unit body weight than adults. Because total metabolizable energy (ME) is an abstraction from protein, fat, total non-structural carbohydrates, and NDF component of fiber, to test this prediction (P2) I will estimate the intake of these macronutrients from foods and use the conventional physiological fuel (i.e., the ME concentrations of 4 Kcal/g of dry matter of food for proteins and carbohydrates, 9 Kcal/g for fats) values to estimate

ME (NRC, 2003; Conklin-Brittain et al., 2006). Increased ME intake will be reflected

through high intake of these macronutrients per minute or feeding bout.

2.2.0 Materials and Methods

2.2.1 Study site

Data were collected in the Tana River Primate National Reserve (TRPNR), which is located in the lower Tana River floodplains, Tana River County, in the coastal region of Kenya (Fig 2.1). The reserve lies between 1°40' - 2°15' S and 40°07' - 40°10' E, and 20 - 40 m above sea level (Wieczkowski, 2003). Mean annual precipitation is 470 mm ranging from 122 mm to 1020 mm (Decker, 1994). Temperatures range from 17.5°C to 36.5°C, with annual mean minimum and the maximum temperature of 21.4°C and 33°C, respectively (Wieczkowski, 2003).

A high level of faunal and floral endemism characterizes the lower Tana River gallery forests. The forests are home to five species of diurnal primates, including the yellow baboons, vervet monkeys, lowland sykes monkeys (*Cercopithecus mitis albotorquatus*), Tana River red colobus, (*Procolobus rufomitratus*), and the Tana River mangabeys. There are also three nocturnal strepsirrhine species in the forest: the Kenyan coast galago, (*Galagoides cocos*), Northern lesser galago, (*G. senegalensis*), and Northern greater galago (*Otolemur garnettii*) (Butynski & Mwangi, 1994). The species diverge in habitat preferences whereby vervet and yellow baboons mostly utilize the open savanna woodland and riverine forests, while the mangabeys, red colobus, and sykes monkeys exclusively depend on the riverine forests (Wahungu, 1998; Wieczkowski, 2003; Bentley-Condit, 2009; Kivai, 2013). The main predators of the Tana River mangabeys include, crown eagles (*Stephanoaetus coronatus*), pythons (*Python sebae*), leopards (*Panthera pardus*), and yellow baboons (Weiczkowski et al., 2012; Kivai, 2013).

My study focused on two field sites within the TRPNR, the Mchelelo and Kitere forest areas, which are located in the north and south of the reserve, respectively. These two areas represent ecologically distinct microhabitats. The Mchelelo forest patches have experienced minimal anthropogenic disturbance compared to those at Kitere, due to the former's proximity to the Kenya Wildlife Service Reserve headquarters (Moinde-Fockler et al., 2007). The two sites were characterized by the presence of essential mangabey plant foods. The most common ones included *Phoenix reclinata, Vachellia robusta, Synsepalum msolo, Hypeane compressa, Borassus aethiopum, Drypetes natalensis, Mimusops fruticosa,* and *Ficus sycomorus*. The species found most abundantly in *both* forest patches were *Polysphaeria multiflora* and *Lecaniodiscus fraxinifolius.* The relative abundance of other foods varied across sites. Kitere forest patches, however, were more open due to increased human activities. Unlike in Mchelelo, farming along the riverbanks was common, which encouraged crop raiding by primate groups in Kitere study site. In addition, due to anthropogenic disturbances, Kitere riverine forests were characterized by a high number of woodland species, such as *Thespesia danish*, *Cassis abbreviate*, and the invasive *Prosopis juliflora*.

2.2.3 Study subjects & design

I collected field data for 15 months between October 2014 and December 2015. I studied two groups of mangabeys, one in Mchelelo (N = 45 individuals) and the other in Kitere (N = 49 individuals). I recorded data on 12 lactating females, 10 juvenile males, and 9 juvenile females in the Mchelelo group, and 11 lactating females, 12 juvenile males, and 9 juvenile females in the Kitere group. Thus, in total,

I had 63 focal individuals, whereby 23 were lactating females and 40 juveniles. Animals in both groups were habituated seven months before actual data collection started. The Mchelelo group had been followed for over 10 years by previous researchers (Kinnaird, 1992; Wahungu, 1998; Wieczkowski, 2003), while the Kitere group had never been studied before but were habituated by me from March - September 2014. Habituation was to a distance of about 5 meters.
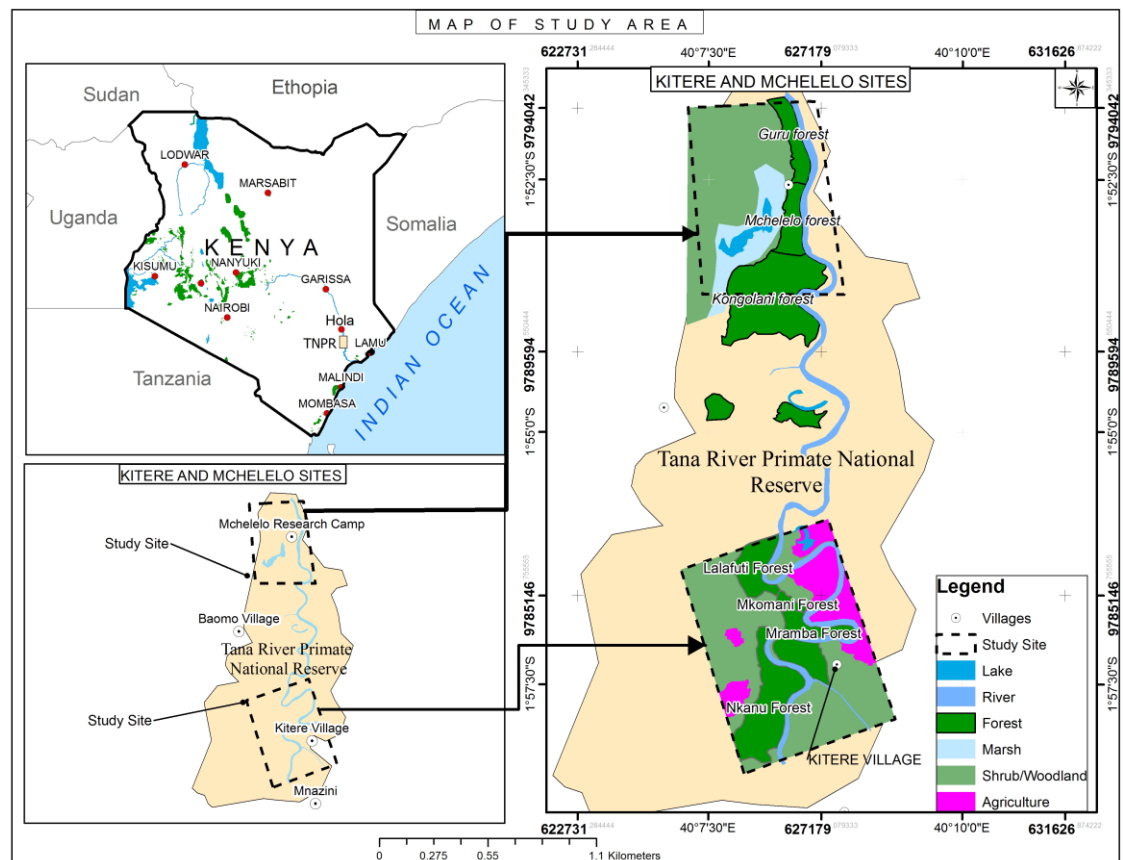
Figure 2.1. Map of the study area in the lower Tana River showing the two study sites (enclosed in the broken line rectangles) within the Tana River Primate National Reserve in the Tana River County, Kenya. Kitere study site is located at the south, while Mchelelo is at the north of the reserve.

2.2.4 Data collection methods

2.2.4.1 Feeding behavior data collection:

I conducted focal animal sampling (Altmann, 1974) throughout the day from 0700h to 1800h. I recorded data continuously for 10-minutes with resting intervals of 5-minutes between focal sessions. During the focal observations, I recorded data on: 1) the activity that the focal animal was performing; 2) the plant species eaten; 3) the exact plant part eaten; 4) the number of units ingested; and 5) the number and duration of feeding bouts. I defined a feeding bout as a discrete unit of feeding time starting when the focal individual made its first physical contact with a food item until the time when it terminated contact for at least 5 seconds or switched to another food item or activity.

In addition, I conducted 5 - minute focal sampling to estimate the food and energy intake rates from different food items eaten by the mangabeys. This was done at the end of the 10 - minute focal session and whenever a focal individual was still feeding or entered into a particular feeding tree that was eaten earlier and captured in the focal observations.

Focal individuals in both cases were randomly scheduled for observations in a manner that no individual was repeated before all other focals were sampled. I collected data for 3 - 5 consecutive days a week from October 2014 to December 2015, depending on the performance of field activities related to data collection.

2.2.4.2 **Vegetation sampling**

To estimate the abundance of the plant foods in the study area I used the nested plots sampling method for vegetation assessment (Ganzhorn et al., 2010). I

established 170 vegetation plots (Mchelelo - 76 plots, Kitere – 94 plots), each of which was 20 m x 20 m. I recorded all trees in the entire plot. For tall shrubs and climbers (including lianas), I focused on measuring half of the plot (10 m x 20 m). I recorded data on short shrubs (1 - 3 m tall) in a quarter plot (5 m x 5 m), while for herbaceous vegetation I used 1 m x 1m plots randomly places in each the four quarters of the plot. I recorded the total number of plant species as well as individuals of each species encountered in the plot as well as the percentage cover of the plot and herbaceous layer. Samples of plants that could not be identified in the field with the help of a botanist were collected and taken to the East African Herbarium, at the National Museums of Kenya, where they were positively identified up to species level where possible.

2.2.4.3 Insect sampling

The mangabeys foraged on insects predominantly on the ground. Thus, I sampled insects in the same plots as where I surveyed vegetation, using quadrant methods, which is effective for sampling ground dwelling insects and has been applied in entomological studies (Kuno, 1991; Zaller et al., 2015). With minimal disturbance, I established four quadrants of 1 m x 5 m from the center of the plot in each of four directions - North, East, South, and West. In each quadrant, I searched for insects under plant debris and dead leaves, and I recorded the type of insects encountered and the total number (Zaller et al., 2015).

2.2.5 Nutritional data

The nutritional data were obtained in two phases: 1) collection and processing of food samples in the field; and 2) subsequent analyses in the laboratory.

2.2.5.1 **Field collection and processing of food samples**

I collected and processed 485 plant food and 150 fecal samples during 15 months of fieldwork. Because of insect attacks and molding before sample milling, I lost about 60 samples, leaving 425 plant samples for analysis. I targeted different plant foods that the mangabeys ate at various times of the year. I recorded all plant foods consumed and usually collected samples immediately after the end of the focal sample period in which I observed the food eaten. Where that was not possible, the individual tree or plant was marked at that time with a red tape, and sample collection occurred later that day or on the following day. Samples were collected within 2 m of the observed feeding spot on a tree, shrub, or the herbaceous layer, except when it was impossible to collect enough samples. For every sample collected I recorded: focal animal identity, age-sex class, time of the day consumed, canopy height at consumption (upper canopy - > 7 m, middle canopy 3- 6 m, lower canopy < 3 m), general habitat type (closed canopy forest – canopy layer continuous with interlocking crowns; open canopy forest – tree canopy layer discontinuous and not interlocking; and open woodland – habitat characterized by dwarf woody shrubs < 7 m tall adjacent to the riverine forest), and specific plant parts eaten (e.g., fruit, leaf, stem, root, bark) . Before drying each sample, I tried to process it in the same way I had observed the subjects prepare the food before ingestion. For

example, if a mangabey discarded the fruit exocarp and ate the seed, I removed the exocarp and only processed the seed. Where individuals consumed one particular food species repeatedly over a period exceeding a month, the food sample was re-sampled until feeding on this food stopped.

To estimate both a unit wet-weight and dry weight intake, I collected between 5 and 50 food units (based on availability) of every species eaten. Wet weight of fresh food units was measured immediately after collection using scientific weighing balance (that measured to the nearest decimal 0.01 grams). Dry weight was measured after completely drying the food units in a dehydrator at 55°C, defined as the constant weight of the dry sample obtained after repeated weighings every 30 minutes during the drying period.

In addition, I collected fecal samples opportunistically for estimation of fiber digestibility of foods. I collected about 50g of feces whenever I observed a focal subject defecate during the focal period. The feces were submerged in 99% ethanol for 24 hours to sterilize them and then dried the same way as the food samples before packaging.

The sample processing, drying, and packaging of unmilled foods was done at the research camp in the field. Since I needed approximately 50g of the dry weight, where possible I collected about 250g of wet weight sample to ensure that I obtained the minimum dry weight required for each sample. I prepared, dried, and determined wet and dry weights of the actual food sample the same way I did for a unit dry weight measurements. Dried food samples were transferred to plastic envelope bags with silica gel and stored in a large plastic container before being

transported to Nairobi. The samples were milled using Willey mill machine with 1 mm sieves based at the Kenya Agricultural and Livestock Research Organization in Muguga, Nairobi. The samples were then stored at room temperature at the Institute of Primate Research.

2.2.5.2 **Laboratory analysis**

Samples were transported from Kenya to the Primate Ecology Laboratory, Hunter College. The goal of the analysis was to assay the nutritional content of plant food samples I collected to estimate the nutrients and total metabolizable energy intake. To achieve this objective I measured: Dry matter, Ash, Neutral Detergent Fiber (NDF), Acid Detergent Fiber (ADF), Acid Detergent Lignin (ADL), Crude Fat, Available Protein (AP), and Acid Detergent Insoluble Nitrogen (ADIN). I followed the standard chemical protocols of Rothman et al. (2012). I calculated the Total Non-structural Carbohydrates (TNC) by subtracting from 100% the percent of ash, NDF, fat, and AP. For the fecal samples, only fibers (NDF, ADF, and ADL) and dry matter were measured. In order to determine the dry matter digestibility, I compared the proportions of ADL in the diet and in the feces, following Rothman et al. (2008b). Finally, I used the conventional methods described by Conklin-Brittain et al. (2006), and also used by Rothman et al. (2012), to determine energy intake in kilocalories per gram (Kcal/g) derived from ingestion of different macronutrients using the following physiological fuel values: available protein – 4 Kcal/g, Total Non-structural Carbohydrates (TNC) – 4 Kcal/g, Fat (lipids) – 9 Kcal/g, and for Neutral Detergent Fiber I used the fiber digestion coefficient of 0.552 that I obtained from the fecal analysis and used a conversion of 4 Kcal/g.

a) Dry matter and total ash

To determine the dry and fresh weight (g) of ingested food that constitutes the nutrient component, I estimated the organic matter (DM) correction coefficient of a field dried sample and grams of organic matter (OM) in fresh food ingested. To obtain the field dry matter correction coefficient of the sample I weighed 0.45 – 0.55 g of field dried sample and dried it in oven at 105°C using dry matter beakers for 3 hours and determined the final dry weight of the sample while hot. To obtain total ash, I burned the sample in ash oven at 550°C. I then weighed the heated sample remains at 100°C to determine the total ash. From these two measures (ash and DM correction coefficient). I calculated the final organic matter (OM) of field-dried sample as:

Equation -2.1: Calculation of organic matter of the field sample

$$OM/g \text{ of Field sample} = (1 - total\ Ash) \times DM\ Correction\ Coefficient)$$

I applied both OM and DM correction coefficients to determine the OM/g of fresh food ingested as:

Equation -2.2: Calculation of organic matter of fresh food sample

$$OM/g\ fresh\ food$$
$$= Field\ DM\ coefficient \times final\ DM\ Correction\ Coefficient$$
$$\times OM\ Correction\ Coefficient$$

b) Crude Fat Analysis

I determined the fat content in the food through petroleum ether extraction process using the ANKOM Fat Analyzer. I weighed 0.45-0.55 g of the food sample and transferred it into a fat extraction filter bag of known weight, which was then sealed using a heat sealer machine. I included one empty control bag and a standard of a commercial food "Duncan Hines Fudge ", which contained 2.87% fat in every set of 18 food sample bags. The sealed filter bags containing the sample were dried in the oven at 105°C for three hours then allowed to cool in a desiccator for 30 minutes, after which I determined the pre-dried weight before fat extraction. I then collected the sample filter bags into a coil, with the control at the middle and suspended in petroleum ether solvent in the fat extractor, and heated for 120 minutes at a temperature of 90°C. I then transferred the samples into the oven and dried them for 8 consecutive hours at 105°C. In cases where it was not possible to dry the samples for 8 hours continuously, drying was divided into two drying sessions, but the samples were kept in a desiccator before completing the drying process. After drying the samples, I allowed them to cool in a desiccator for 30 minutes and I then recorded after-fat extraction weight of the filter bags. I calculated the percentage of crude fat content as follows:

Equation -2.3: *Calculation of crude fat of food sample*

$$\% \, Crude \, Fat \; = \left[\frac{W2 - W3}{W1}\right] \times \; 100$$

where, W1 = Original weight of the sample, W2 = weight of pre-dried sample with filter bag, W3 = weight of the dried sample and filter bag after fat extraction (Rothman et al., 2012).

c) Crude Protein Analysis

Crude protein analysis was done through complete combustion using Leco TruSpec Nitrogen Analyzer. I weighed about 0.10 g of the food sample into a small foil bag and rolled it into a spherical shape. I included one sample of orchid leaf in every 10 samples as a control. The prepared samples were loaded systematically in the open carousel of the analyzer with numbered positions where sample are pushed slowly to the combustion chamber. The carousel positions were displayed on a computer screen connected to the machine where I entered the corresponding weight details of the samples before analysis. I ran at least five blanks and two orchid leaf samples before the start of nitrogen analysis for standardization of the machine. The machine automatically generated the percent crude protein of each food sample after combustion. To estimate the available protein, I determined the Acid Detergent Insoluble Crude Protein (ADICP) in the food samples in order to account for protein bound by fiber and unavailable to the animal as well as what is utilized by gut microbes. I then subtracted the ADICP from the crude protein to obtain available protein (Rothman et al., 2012).

d) Fiber Analysis

Using the ANKOM Fiber Analyzer, I analyzed the food samples and fecal matter for three forms of fiber: Neutral Detergent Fiber (NDF), Acid Detergent Fiber (ADF), and Acid Detergent Lignin (ADL). I calculated the fiber content of the food

and fecal matter in the same way. I performed the analysis of the three fiber types sequentially, meaning I used the same samples for the next type of fiber assay in the order listed above. Samples that had more than 5% fat were first soaked in histological grade acetone for 20 minutes before air-drying for 24 hours prior to fiber analysis. The procedure extracts the fat that could be trapped in the fiber bags, which can distort values.

   i) Neutral Detergent Fiber (NDF): This analysis focused on determining the fiber residue (hemicellulose, cellulose, & lignin) that remains after digesting or heating the food sample in a neutral detergent solution. I weighed 0.45-0.55 g of the food sample, transferred it into a fiber filter bag of known weight, and sealed the bag. One empty fiber bag was sealed and included in every set of 23 fiber sample bags as a control. I collected the sealed sample bags plus the control into a bag suspender then placed them in the boiling chamber of the fiber analyzer. I added 1900 – 2000 ml of neutral detergent solution into the sample chamber, then 4 ml of alpha amylase. After closing the chamber tightly, I agitated and heated the samples at 100°C in this solution mixture for 1 hour 15 minutes. I then removed the samples and rinsed them two times with hot distilled water supplemented with 4 ml of alpha-amylase and then four times with hot distilled water alone. After rinsing, I squeezed excess water from the fiber bags then soaked them for five minutes in histological grade acetone before air-drying them for 24 hours. I transferred the samples into an oven and dried them at 105°C for 30 minutes, then cooled them in a dissector for additional 30 minutes before recording the after fiber analysis (NDF) dry weight. I determined the % NDF as obtained as follows:

Equation -2.4: Calculation of NDF content in food samples

$$\% \; NDF \; = \left[\frac{W3 - (W1 \; \times \; C1)}{W2}\right] \times \; 100$$

where, W1 = bag weight, W2 = sample weight, W3 = dried weight of the fiber bag with the sample, C1 = blank bag correction (control).

To express the percent NDF on dry matter basis, I divided the value obtained above by the dry matter correction coefficient obtained after DM analysis.

ii) Acid Detergent Fiber (ADF): The aim here was to determine cellulose and lignin content by measuring the fiber residue after sample digestion with sulfuric acid and hexadecyltrimethyl ammonium bromide, called the acid detergent solution. I assayed ADF by using the same samples from which I extracted the NDF. I repeated the same procedure for NDF, but this time I used Acid Detergent solution of the same amount, no alpha amylase, and I agitated and heated the samples for 60 minutes and rinsed in hot running water for 30 minutes (instead of hot deionized water as in NDF). I calculated the ADF the same way as NDF but, instead, I used the final dry weight after the ADF analysis.

iii) Acid Detergent Lignin (ADL): The final stage of fiber analysis focused on determining the indigestible component of the fiber in foods. To accomplish this, I analyzed the same samples in the fiber bags that I had extracted NDF and ADF. I collected the sample bags into a 250 ml beaker with a 50 ml Erlenmeyer flask placed on top to counter floatation. I put the beaker with the samples in Pyrex tray filled with deionized water mixed with about 50 ml of sodium bicarbonate to neutralize any spilling sulfuric acid. I then added 72% sulfuric acid to the beaker until the

samples were submerged. I pressed down the samples using the flask for 30 times while flipping them with a spatula after every time I pressed them in order to agitate the samples. I repeated this process after 30 minutes for three hours. I then transferred the samples into a large plastic beaker and rinsed them with hot water for thirty minutes prior to air-drying for 24 hours. After air-drying, the samples were oven dried for 30-minutes to expel the atmospheric moisture. After the samples had been cooled in the desiccator, I recorded the dry weight after lignin analysis. I used the same calculation procedure as in NDF (see above) to obtain the ADL, but I used the dried weight after lignin analysis, instead of dry weight after NDF.

e) Acid Detergent Insoluble Crude Protein (ADICP) Analysis

The protein remaining in the residue after acid detergent fiber analysis represents the protein unavailable to the animals because is bound by fiber. This analysis involved determining the ADF and assessing the protein content of the residue after fiber analysis. I achieved this through running the ADF fiber while skipping the NDF assay using the fiber assay method described above for ADF. After completing the ADF assay and recording the final dry weight of the fiber bags, I opened the fiber bags and processed the sample residue in protein foil bags and performed protein analysis as described for other food samples. After determining the protein content of this sample, I calculated the ADICP as follows,

Equation -2.5*: Calculation of acid detergent insoluble Crude Protein (ADICP)*

$$ADICP\ (DM\ basis) = [\%CP\ \times\ \%ADF(DM\ basis)]/100$$

where %CP = percent CP in ADF residue, %ADF (DM basis) = percent ADF expressed on dry matter basis and calculated using ADF procedure (Rothman et al., 2012).

Fecal analysis: To estimate the fiber digestibility I assayed the fecal samples for fiber (NDF, ADF, and ADL) and dry matter using the same procedures described for food samples. I calculated NDF digestibility coefficient on dry matter (DM) basis using the following equation adopted by Rothman et al. (2008a).

Equation -2.6: *Estimation of neutral detergent fiber (NDF) digestibility coefficient*

$$NDF\ Digestibility(DM)$$

$$= 100 - [100(\%ADL\ in\ diet/\%\ ADL\ in\ feces)$$

$$* (\%\ NDF\ in\ feces/\%\ NDF\ in\ diet)]$$

f) Estimating Metabolizable Energy (ME) Intake

i). Absolute Metabolizable Energy (ME) Intake

Because I obtained fiber digestibility from the fecal samples analysis, I calculated the energy intake by assuming high Metabolizable energy (ME) was derived from neutral detergent fiber fermentation or digestibility. Therefore, I used the fiber digestibility coefficient (0.17), which I multiplied by 3 Kcal (i.e. 0.17*3 = 0.552) and then by NDF content on dry matter basis (g) per food to obtain the ME derived from NDF fermentation. I followed Conklin-Brittain et al. (2006) in calculating the ME intake as:

Equation -2.7: *Calculation of metabolizable energy intake in Kilocalories per gram from macronutrients in foods ingested*

$$Metabolizable\ Energy\ (MEh)\ Kcal/g\ OM$$

$$= \big(4 \times TNC\ (g)\big) + \big(4 \times AP(g)\big) + \big(9 \times Fat\ (g)\big)$$

$$+ \big(0.552 \times NDF\ (g)\big).$$

I calculated the total ME ingested per feeding bout in every focal as the sum of products of grams (g) of each food item consumed and the energy content per gram of that food (Altman, 1998; Conklin-Brittain et al., 2006). I first obtained the total dry weight of the food units ingested by multiplying the total number of units ingested per feeding bout with the field corrected dry matter, then by the energy concentrations of that particular food item. This can be expressed as follows,

Equation -2.8: *Estimation of metabolizable energy consumed from different foods per feeding bout*

$$Total\ ME\ intake\ per\ feeding\ bout$$

$$= \Sigma(No.of\ units\ ingested \times Average\ dry\ matter\ per\ unit$$

$$\times Energy\ concentration\ in\ the\ food\ unit)$$

To obtain ME intake per minute per food item, I divided the total ME intake derived from the food item ingested by the total time (min) spend feeding on that particular food item. To obtain ME intake per feeding bout I divided the total ME ingested from each food item by the number of feeding bouts in each feeding event. I defined a "feeding event" as foraging on any distinct food or class of food from the same food patch, starting when the focal individual make first physical contact with

the food and ending when it stopped feeding or switched to a different food type or class of food within the food patch or completely left the food patch, as modified from Bryso-Morrison et al. (2017).

ii) Relative Metabolizable Energy (Metabolizable Energy per Metabolic Body Mass)

I calculated relative metabolizable energy (ME) intake, by dividing the total ME obtained from each food item consumed during the feeding events by the estimated metabolic body mass ($MBM^{0.75}$) of the focal individuals. I obtained basal MBM as follows:

For the body size of adult female Tana River mangabeys, I used the average body mass of 5.30 kg reported by Gautier-Hion & Gautier (1976). I calculated juvenile body size in the following two-step manner, which involved: (1) assigning a juvenile to one of two age classes, either < 2 years of age or > 2 years of age; and then (2) assigning a body size to each category using a quantitative criterion. For the first step, exact ages were known for juveniles born during my study. For those juveniles whose exact ages were not known because they were born prior to my study, I used the comparative physical characteristics of juveniles of known age to make this age category assignment. This approach elaborated upon a similar system of age assessment used successfully by Homewood (1978) in a study of the same species, where emphasizes are put on body size differences, changes in coat color, and sexual characteristic. The second step of calculating body size was based on the assumption that juveniles less than 2 years would weigh about half the average body mass of adult female while those more than 2 years would weigh about three-quarters of their mass. Thus, the MBM of juveniles less than 2 years was calculated

to be 2.08 kg (i.e., $2.65^{0.75}$ kg) and those more than 2 years was calculated to be 2.82 kg (i.e., $3.98^{0.75}$ kg).

2.2.6 Data Analysis

I collected 5980 10 - minutes focals of behavioral observations, and 4130 5 - minutes focals of nutrient intake estimation. This translated into 996.67 hours of behavior data, 344.17 hours of nutrient intake estimation, and 20,486 feeding events that I used for my analysis. I used results of nutritional analyses of the 394 food samples that I matched with all the feeding events for this analysis. The feeding behavior and nutrient intake data were obtained from a total of 63 focal individuals, of which were 40 juveniles (i.e., 22 males & 18 female juveniles) and 23 were lactating females, in the Mchelelo and Kitere study groups combined. Matching of the feeding observations data with laboratory nutritional data was done in the following manner. First, where multiple food samples of the same item analyzed in the laboratory were collected at different times of the year, the results were matched with feeding data collected at the same time or at the closest period possible. Second, where nutritional samples were missing (either plant part eaten or entire food species), due to spoilage or no collection at all (i.e., about 12%), I used average nutritional scores for other parts analyzed for a particular species (where parts of same species were missing) or the monthly average for all parts and food species eaten during the month of the missed observation (where no nutritional data was available for the food species) (Conklin-Brittain et al., 2006; Rothman et al., 2008a; Vogel et al., 2015).

The analyses focused more on what I designated as "Principal Plant Food Species". These are defined operationally as species that contributed more than 1% of the overall annual diet of mangabeys or the two age classes. This criterion to delineate important plant foods has been adopted previously by other researchers (Fashing et al., 2001; Conklin-Brittain et al., 2006; Rothman et al., 2006). In my study this criterion was useful because the species designated as Principal Plant Food Species in this manner collectively accounted for 90% of the foods ingested by both lactating females and juveniles annually. This suggests that such foods may have more influence of feeding than other foods.

I tested my first prediction (P1) that juveniles had a narrower dietary breadth and higher selectivity of preferred foods than lactating females by calculating the dietary breadth and food preference between the two age classes. First, I compared food preference between juveniles and lactating females using Vanderploeg & Scavia's (1979) Relativized Electivity Index (E*), which is commonly used in ecology (Manly et al., 2002) and has been used I primate studies (Bastian et al., 2010; Vogel et al., 2017). This index utilizes both the relative abundance of food items in the diet and in the environment to measure dietary selectivity. I obtained the monthly and annual percentage of each food species or items in the diet by dividing the total number of times I observed a particular food eaten, by the total number of times I observed all the food species or items being consumed (multiplied by 100). I calculated the relative abundance of the plant foods and insects in the environment by dividing the total number of individuals counted for

each species in all the plots by the total number of individuals counted for all species in all the plots (multiplied by 100).

Several indices have been used to assess dietary preferences in mammals, but a majority suffers from serious shortcomings, such as lack of statistical testability (Lechowicz, 1982). Vanderploeg & Scavia's index has been recommended over other indices as one of the best indices for evaluating dietary preference (Strauss, 1979; Lechowicz, 1982; Manly et al., 2002). This is because the index has most of the desirable characteristics necessary for making meaningful comparisons in diet selection, which include randomness, symmetry, range, linearity, robustness, stability, and statistical testability (Manly et al., 2002). The E* equation is as follows:

Equation -2.9: Vanderploeg & Scavia's Electivity index ($E*$)

$$E* = [Wi - \left(\frac{1}{n}\right)]/[Wi + \left(\frac{1}{n}\right)]$$

$$whereby \; Wi = (\frac{ri}{pi})/\Sigma(\frac{ri}{pi})$$

where, E* = Vanderploeg & Scavia's Electivity Index, Wi = selectivity coefficient, ri = relative abundance of the food resource in the diet, pi = relative abundance of the food resource in the environment (habitat), n = total number of foods items selected or consumed.

The index E* ranges between -1 and +1 where positive values indicate high food preference and negative values low preference or avoidance. Here I operationally define "preferred" foods as those with an index exceeding 0, and "avoided" foods as those with an index below 0. I predicted that juveniles will have a

higher selectivity (E* values) for preferred foods (that easily accessible and high in energy) than the lactating females due to their high energy demands for growth and low foraging efficiency.

I used Wilcoxon signed-rank test to statistically compare the food preferences of juveniles and lactating females for different foods. I calculated E* for juveniles and lactating females for every food resource utilized in each area, then used the paired selectivity scores for the two age classes for statistical comparisons.

Second, I used the standardized Levin's index (B_A) measure of dietary breadth (Levin, 1968) as described by Manly et al. (2002). This index has been used successfully to assess uniformity in the use of resource shared by species, groups or individuals in same habitat (Novakowski et al., 2008; Lyngdoh et al., 2014). These equations are as follows:

Equation -2.10: *Levin's dietary breadth index estimation*

Levin's Dietary Breadth

$$B_A = \frac{B - 1}{n - 1}$$

where, (B_A) = standardized measure of dietary breadth, B = Levin's measure of dietary breadth (and it's the inverse of summation of proportions of food resources utilized by the age class i.e.,$1/\Sigma pij$, where pij = proportion of diet of age class i that is made up of food resource or species j in a diet consisting of n food resources), n = is the total number of food resources (species) eaten by the particular age class. Values of B_A range from 0 to 1, whereby maximum value indicate wider dietary breadth where each resources is utilized in proportion to its abundance (i.e.,

available resources are evenly exploitation) while minimum values suggest narrower dietary breadth where resources are utilized on the least abundant resource state (i.e., available resources are unevenly used) (Hurlbert, 1978; Hadi et al., 2012). I predicted that juveniles will have lower values of B_A than lactating females because the latter are likely to sample more foods but consume them unevenly compared to the former.

To test my (P2) that juveniles will have a higher intake of relative Metabolizable energy (ME) (i.e., intake per Metabolic Body Mass - MBM), evaluating absolute ME intake, and energetic gains from food types, I used Generalized Linear Mixed Models (GLMMs). I performed all the analyses in R statistical software version 3.3.2 (R Core team (2013). Before fitting and running any statistical test or model, data were checked to ensure that all assumptions for generalized linear models or parametric tests were met, especially normal distribution of the data. I used quantile-quantile (q-q) plots and the Shapiro–Wilk test to examine the distribution of my data. Where the assumption of normal distribution was not met, I performed log transformation of the data. For all the statistical analyses I set alpha at 0.05. Also, I selected the best variables and model to test my predictions by first constructing full models including all variables that could have had some effect on dependent or response variables of interest. I then fitted reduce versions of the full model by eliminating a single variable of the full model at a time. I then compared the models using analysis of variance (anova) in R and finally selected any significant model that had the lowest Akaike information criterion (AIC) value as the best model fit for my analysis.

Before testing my second prediction (P2) I examine the energetic contributions from different food species eaten by juveniles and lactating females, the energetic gain obtained by both age classes from these foods, energetic contribution of the Principal Plant Food Species, and the absolute intake (i.e., actual intake without controlling for body mass) of ME between the age classes and study groups. First, to gain more understanding of ME intake, I assessed the energetic gains obtained from consumption of different food types (i.e., fruits, seeds, leaves, mushrooms, stem, gum, insects, and 'others'). For statistical comparisons of these data, I fitted a GLMM with ME intake per feeding bout as my response variable, food type as my fixed effect, and focal ID as my random effect. I proceeded to compare the proportions (%) of energetic intake from these types of foods using a chi-square test. Further, I descriptively evaluated the ME intake derived from consumption of the 20 Principal Plant Food Species as well as time spent feeding on such foods. I statistically compared the energetic contributions (i.e., metabolizable energy per minute and per feeding bout) of all the 96 plant foods consumed by both juveniles and lactating females using paired t- test. Finally, I assessed the absolute ME intake between the age classes and study groups using GLMMs.

I fitted GLMMs to test P2 using the mean relative ME intake in both the per minute and per feeding bout as my response variables (i.e., dependent variables). I included age class and study group as fixed effects (independent variables) and controlled for the focal ID (as the random effect). I first ran the model using absolute mean ME intake both per minute and per feeding bout as my response variable and repeated the test with the mean ME per MBM. I did this to determine the effects of

metabolic body mass on energy intake and how this varied with feeding bout between the age classes.

To understand the energetic contributions of different macronutrients in the foods ingested by juveniles and lactating females, I compared the proportions of ME derived from ingestion of fiber (NDF), fat, available protein (AP), and total non-structural carbohydrates (TNC) in the diet. I focused on ME intake per MBM and how this varied in response to age class and study group. I tested the statistical differences in intake by constructing a GLMM with the per minute mean relative ME intake obtained from the four macronutrients (NDF, Fat, AP, and TNC) as my response variable, age class and study group as fixed effects and focal ID as the random effect.

2.3.0 Results

2.3.1 Diet of the Tana River mangabeys

Before presenting the empirical test of the hypothesis and predictions on dietary breadth, preference, and ME intake in juveniles and lactating females, I provide a general description of the dietary patterns of the Tana River mangabeys and for the two study groups.

***2.3.1.1* Species & Family representation in the diet**

A total of 124 different food items differentiated by species (plants) or by family (animals), were eaten by the Tana River mangabeys during all focal sampling and ad libitum observations (Appendix 2.1). The largest portion of this diet was 110 species of plant foods from 42 families. Of these species, 11 (10%) were human cultivated crops, and 99 (90%) were naturally occurring. The families *Fabaceae* (13.6%), *Poaceae* (10.0%), *Malvaceae* (6.4%), *Sapindaceae* (5.5%), and *Rubiaceae* (5.5%) accounted for the majority of dietary species (41.0%) (Table 2.1). Twenty-one families (Table 2.1) accounted for about 81% of the total number of all plant species consumed.

Trees contributed the highest percentage (40.0%) of plant foods eaten by the Tana River mangabeys, followed by climbers, herbaceous vegetation, and shrubs (Fig. 2.2). Fungi (mushrooms), hemiparasites, and sedges were the least represented, and each contributed only 1% of the plant food life forms.

Table 2.1. List of the plant families in the diet of the Tana River mangabeys.

Family	No. of species eaten	Percent in diet
Fabaceae	15	13.64
Poaceae	11	10.00
Malvaceae	7	6.36
Sapindaceae	6	5.45
Rubiaceae	6	5.45
Phyllanthaceae	4	3.64
Moraceae	4	3.64
Apocynaceae	4	3.64
Arecaceae	3	2.73
Capparaceae	3	2.73
Commelinaceae	3	2.73
Bignoniaceae	3	2.73
Acanthaceae	3	2.73
Anacardiaceae	3	2.73
Vitaceae	2	1.82
Rutaceae	2	1.82
Sterculiaceae	2	1.82
Combretaceae	2	1.82
Euphorbiaceae	2	1.82
Sapotaceae	2	1.82
Cucurbitaceae	2	1.82
Agaricaceae	1	0.91
Cornaceae	1	0.91
Lecythidaceae	1	0.91
Annonaceae	1	0.91
Ulmaceae	1	0.91
Lamiaceae	1	0.91
Burseraceae	1	0.91
Cyperaceae	1	0.91
Ebenaceae	1	0.91
Putranjivaceae	1	0.91
Flagellariaceae	1	0.91
Clusiaceae	1	0.91
Lythraceae	1	0.91
Molluginaceae	1	0.91
Musaceae	1	0.91
Salicaceae	1	0.91
Passifloraceae	1	0.91
Violaceae	1	0.91
Celastraceae	1	0.91
Loranthaceae	1	0.91
Rhamnaceae	1	0.91
Total (N)	**110**	**100**

In the faunal diet, arthropods were exploited most (64.3%), all of which were consumed whole, except for millipedes, whose endoskeletal tissue was sucked out and the exoskeleton discarded (Appendix 2.2). Other faunal components of the diet were amphibians, reptiles, mollusks, and birds, which together with honey, contributed about 35.7% to the faunal diet.
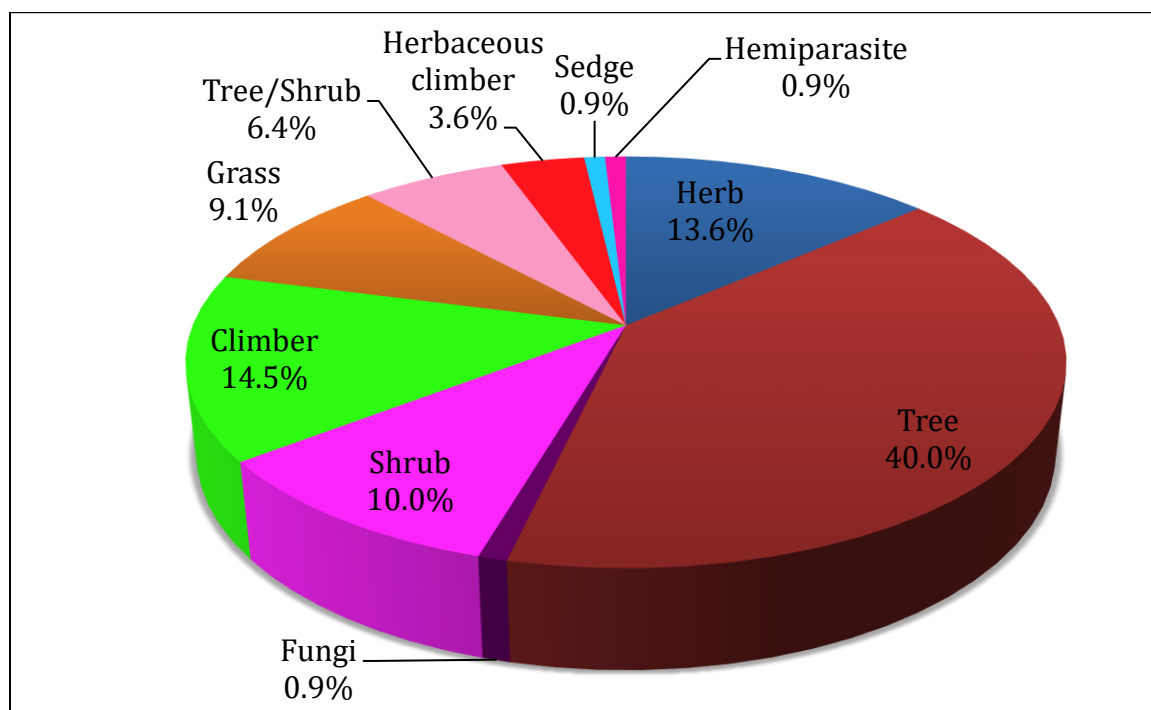
Figure 2.2. Dietary contributions of different life forms represented in the Tana River mangabeys' annual diet.

2.3.1.2 Tana River mangabey diet

Fruits and seeds accounted for the most of the diet, 54.7% and 19.8%, respectively (Fig. 2.3). Mushrooms contributed 5.0% of the diet, nearly as much as

leaves (7.1%). Stems, flowers, bark, exudate, deadwood, subterranean structures (which I operationally is used in this study to collectively refer to all below ground plant parts exploited by mangabeys, since not all were underground storage organs or typical roots), honey, and unidentified foods items were all eaten in smaller proportions and were all combined into the 'others' categories. These items contributed about 2.2% of the species annual diet. The Tana River mangabeys ingested deadwood from *Sorindea madagascariensis*, *Synsepalum msolo*, *Grewia densa*, and *Cordia goetzei* (Appendix 2.1).
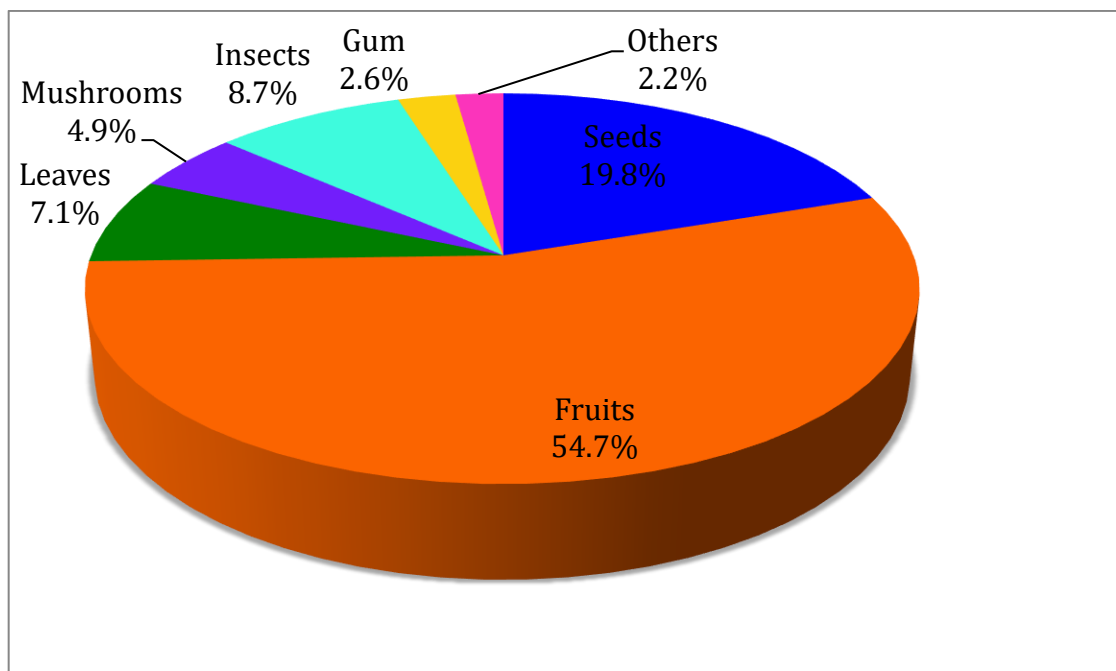
Figure 2.3. Representation of types of food in the diet of the Tana River mangabeys, expressed as a percentage of the total food items observed eaten. The category 'others' comprises stems, flowers, bark, exudates, deadwood, subterranean structures, honey, and unidentified food items. (N = 63, feeding events = 20,486).

2.3.1.3 Diets of mangabeys in Mchelelo and Kitere study groups

Of the 110 plant foods in the total diet, 68 (62%) were present in both study sites and eaten by both groups, while 32 (29%) and 10(9%) were unique to Kitere

and Mchelelo sites, and consumed by the group in each site, respectively (Fig. 2.4). Of all the 11 cultivated plant foods, all were found and eaten in Kitere, but only two (mango, *Mangifera indica,* and lemon, *Citrus limon*) were utilized by the Mchelelo group (Appendix, 2.1).
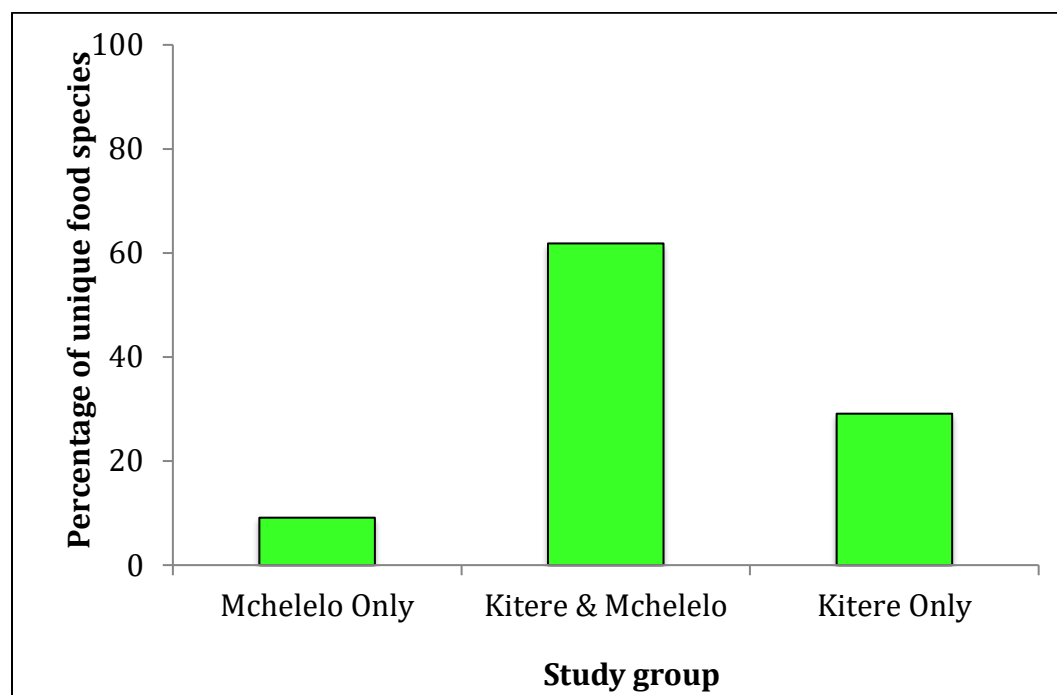
Figure 2.4. Distribution of plant food species (wild and cultivated) eaten by the two mangabey groups across study sites (N = 110 plant foods).

2.3.1.4 Dietary abundance in the habitat and annual diets

Quantitative assessment of each food species' contribution to the annual diet, and calculating of dietary breadth and preference (diet selectivity) required estimation of ingestion rates of each food relative to all other foods available in the habitat. This can only be analyzed from focal sampling data but not with the ad libitum observations, which were important in generating a complete checklist of the species diet. Thus, henceforth, I focus only on focal data for the analysis.

2.3.1.5 Overall food species abundance and contribution in the annual diet

The mangabeys consumed 96 species of plant foods (Appendix 2.3a). Of these species, 18 were designated as Principal Plant Food Species (Table 2.2), but this number varied when data for each study group were considered separately. The two species that were most locally abundant in the habitats were *Polysphaeria multiflora* (22.3%)*,* and *Sorindeia madagascariensis* (9.9%) (Table 2.2). The two species most targeted by mangabeys during foraging (both fruits and seeds), however, were *Phoenix reclinata* (21.1%) and *Ficus sycomorus* (17.7%), which collectively accounted for 38.8% of the diet. The two least consumed plant food species were *Cissus rotundifolia* and *Garcinia livingstonei,* each contributing about 1% to the annual diet. Insects were the most consumed non-plant food resource (5.4%) (Table 2.2).

In summary, among the Principal Plant Food Species *Phoenix reclinata* and *Ficus sycomorus* were the most consumed while *Cissus rotundifolia* and *Garcinia livingstonei* were the least utilized. *Polysphaeria multiflora* and *Sorindeia madagascariensis* were the most abundant in the environment. Insects were a major source of food and ranked fourth in the annual dietary contribution when compared to plant foods.

Table 2.2. The overall dietary composition and relative abundance (%) both in the habitat and annual diet for the 18 Principal Plant Foods Species and insects eaten by the Tana River mangabeys. Relative abundance is expressed as the percentage of either feeding events (in the annual diet) or species occurrences (in the habitat) assigned to particular food species (N = 63 individuals, 20,486 feeding evens & 170 vegetation plots. Totals do not equal to 100 because foods contributing less than 1% are not included.

Species	Relative Abundance (%)	
	Habitat	**Annual Diet**
Phoenix reclinata	8.06	21.11
Ficus sycomorus	0.55	17.66
Vachellia robusta	0.88	9.01
Synsepalum msolo	0.44	4.70
Hyphaene compressa	1.67	4.55
Agaricus sp.	0.04	4.22
Oncoba spinosa	2.99	2.89
Sorindeia madagascariensis	9.87	2.70
Diospyros mespiliformis	2.94	2.66
Grewia densa	2.46	2.65
Polysphaeria multiflora	22.33	2.31
Brachiaria subquadripara	0.40	2.22
Mimusops fruticosa	3.03	1.89
Pavetta sphaerobotrys	2.07	1.52
Alangium salviifolium	1.09	1.42
Mangifera indica	0.05	1.25
Garcinia livingstonei	2.02	1.24
Cissus rotundifolia	0.08	1.19
Insects	1.00	5.40
Total	**61.97**	**90.59**

2.3.2 Diets of the two study groups

2.3.2.1 Dietary composition and abundance in the habitat and annual diet

The Kitere group utilized 76 species of plant foods besides insects, which were eaten as much as some plants (Appendix 2.4). Twenty plant species were considered Principle Plant Food Species for this group. Locally, the most abundant of these species were *Polysphaeria multiflora* (18.8%) and *Lecaniodiscus fraxinifolius*

(14.9%) whereas *Agaricus* sp. and *Mormodica trifoliata* (< 0.1% each) were the least

common. *Phoenix reclinata* (26.3%) and *Ficus sycomorus* (16.9%) constituted the

majority of the annual diet, together accounting for 43.2% of the total annual dietary

composition (Table 2.3).

Table 2.3. Relative abundance (%) of Principal Plant Foods Species plus insects in the habitat and in the annual diet of the Kitere group. Relative abundance is expressed as the percentage of either feeding events (in the annual diet) or species occurrences (in the habitat) assigned to particular food species (N = 32 individuals, 20,486 feeding events, & 94 vegetation plots). Totals do not equal to 100 because foods contributing less than 1% are not included.

	Relative Abundance (%)	
Species	**Habitat**	**Annual Diet**
Phoenix reclinata	8.72	26.26
Ficus sycomorus	0.86	16.93
Synsepalum msolo	0.64	7.86
Vachellia robusta	1.06	4.95
Diospyros mespiliformis	4.11	4.39
Mimusops fruticosa	4.11	3.18
Agaricus sp.	0.03	2.73
Oncoba spinosa	1.20	2.59
Polysphaeria multiflora	18.76	2.57
Grewia densa	2.88	2.52
Mangifera indica	0.12	2.50
Brachiaria subquadripara	0.83	2.44
Lecaniodiscus fraxinifolius	14.90	1.82
Cissus rotundifolia	0.17	1.60
Garcinia livingstonei	2.66	1.41
Momordica trifoliata	0.08	1.27
Sorindeia madagascariensis	5.66	1.20
Alangium salviifolium	0.60	1.19
Antidesma venosum	0.17	1.19
Harrisonia abyssinica	0.71	1.16
Insects	1.20	3.38
Total	**69.47**	**93.14**

Among the Principal Plant Food Species, *Harrisonia abyssinica*, *Antidesma*

venosum, *Alangium salviifolium* and *Sorindeia madagascariensis* were the least

consumed and each contributed approximately 1.2% of the annual diet. Mango (*Mangifera indica*), which is cultivated fruit tree, contributed about 2.50% of the annual diet. Insects contributed about 3.4% of the mangabeys' annual diets, and were the sixth most consumed food resources compared to the Principal Plant Food Species.

The dietary composition of the Mchelelo group included 65 plant species besides insects (Appendix 2.4). Of these plant foods, only 16 species (24.6%) qualified as Principal Plant Food Species (Table 2.4). Among these plant foods, *Polysphaeria multiflora* (25.2%) and *Sorindeia madagascariensis* (13.3%) were the most encountered in the habitat while *Brachiaria subquadripara* and *Agaricus* sp. (<1% each) were the least abundant. *Ficus sycomorus* (18.4%) and *Phoenix reclinata* (16.0%) accounted for the highest percentages of the group's annual diet while *Garcinia livingstonei* (1.0%) and *Saba comorensis* (1.1%) were the least targeted.

Among the plant dietary composition of the Kitere and Mchelelo groups, 20 and 16 species were designated as Principal Plant Food Species for each group respectively. *Phoenix reclinata* and *Ficus sycomorus* had the highest percentage in the diet in both groups while *Polysphaeria multiflora* was the most abundant species in both Kitere and Mchelelo. *Mangifera indica,* which was grown in farmland in Kitere, constituted an important food for the mangabey in the Kitere group.

Table 2.4. Relative abundance (%) of Principal Plant Foods Species plus insects in the habitat and in the annual diet of the Mchelelo group. Relative abundance is expressed as the percentage of either feeding events (in the annual diet) or species occurrences (in the habitat) assigned to particular food species (N = 31 individuals, 20,486 feeding events, & 76 vegetation plots). Totals do not equal to 100 because foods contributing less than 1% are not included.

	Relative Abundance (%)	
Species	**Habitat**	**Annual Diet**
Ficus sycomorus	0.31	18.40
Phoenix reclinata	7.52	15.97
Vachellia robusta	0.73	13.08
Hyphaene compressa	3.01	8.98
Agaricus sp.	0.05	5.71
Sorindeia madagascariensis	13.3	4.21
Oncoba spinosa	4.45	3.19
Pavetta sphaerobotrys	2.86	3.04
Grewia densa	2.13	2.78
Polysphaeria multiflora	25.24	2.05
Brachiaria subquadripara	0.04	1.99
Alangium salviifolium	1.48	1.65
Synsepalum msolo	0.27	1.54
Drypetes natalensis	7.06	1.29
Saba comorensis	0.15	1.14
Garcinia livingstonei	1.49	1.08
Insects	0.83	7.43
Total	**70.92**	**90.53**

2.3.3 Diets and food preference of juveniles and lactating females

To test my prediction **(P1)** on whether dietary selectivity differs between juveniles and lactating females and whether lactating females had a wider dietary breadth than the juveniles, I compared the two age classes concerning: i) dietary composition and preference; and ii) dietary breadth. While the prediction applies to the general juveniles-lactating females differences, I also compare the dietary breadth and food selectivity differences between the age classes in the study groups.

This is important to because it reinforces the findings despite the group differences. Before testing the prediction (P1), first, I evaluate the dietary contributions of different types of foods that constitute the annual diet of juveniles and females.

2.3.3.1 Contribution of different types of foods in diet

Fruits were the predominant component food type of both juveniles (56.9%) and lactating females (52.6%) (Fig. 2.5). Food items lumped in the category 'others' were the least consumed food category by juveniles (1.7%) while gum was the least consumed (2.3%) by lactating females. Among the non-plant foods, insects were the most commonly consumed, contributing 8.1% and 9.3% to the diets of juveniles and lactating females, respectively.
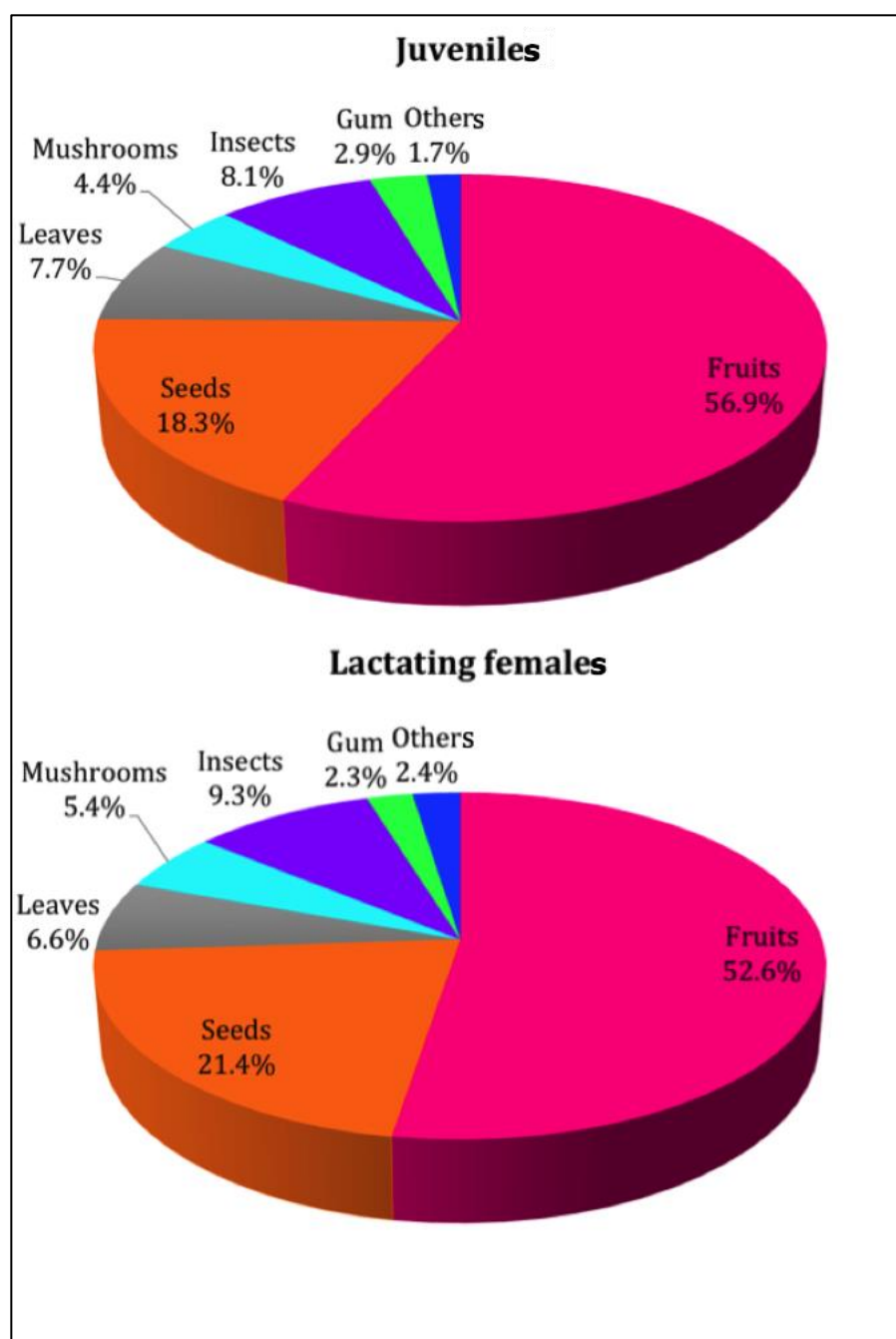
Figure 2.5. Diets of juveniles and lactating females expressed as a percentage of the total food items eaten. The category 'others' comprises stems, flowers, bark, exudate, deadwood, subterranean structures, honey, and unidentified food items (N = 63, feeding events = 20,486).

2.3.3.2 Dietary composition and preference: juveniles versus lactating females

The Principal Plant Food Species, in addition to insects, collectively accounted for about 90% and 92% of the annual diets of the juveniles and lactating females, respectively (Table 2.5, Appendix 2.3b). Overall, seven plant food species and insects were most sought by both juveniles and lactating females (Table 2.5). *Phoenix reclinata* and *Ficus sycomorus* accounted for the highest proportions in the annual diets of juveniles (21.1% & 17.6%, respectively) and lactating females (21.2% & 17.8%, respectively). *Polysphaeria multiflor*a (22.3%) and *Sorindeia madagascariensis* (9.9%) were the most abundant food species in the habitat. The overall plant food E* index demonstrated that *Agaricus* sp. (mushrooms) and *Ficus sycomorus* were the most preferred foods of juveniles (0.93 & 0.81) and lactating females (0.92 & 0.88), respectively. The least preferred plant foods classes were *Polysphaeria multiflor*a and *Sorindeia madagascariensis* (juveniles: E* = -0.93 & -0.85; lactating females: -0.96 & 0.88, respectively) (Table 2.5).

Compared to lactating females, juveniles exhibited higher values of E* for the 18 Principal Plant Food Species and insect components of the diet (Table 2.5; W = -190, p = < 0.0001, N = 19). This result also emerged for the sample based on the larger botanical sample of 96 plant species and insects (Appendix 2.3b, W = -1004, p = 0.0096, N = 97 pairs). In both cases, E* index values for juveniles exceeded those of females for both the preferred species (defined as foods with E* > 0) and the avoided species (E* < 0) (Table 2.5). These results provide support of prediction P1.

Table 2.5. Dietary contribution, abundance in habitat and diet, and Electivity index E* (Vanderploeg & Scavia, 1979) for the 18 Principal Plant Food Species consumed by juveniles (Juv) and lactating females (L. fem), N = 63 individuals, 40 juveniles and 23 lactating females). Dietary contribution is the percentage of feeding events assigned to particular food species (N = 20,486) while relative abundance is the percentage assigned to each food species in the habitat (N = 170 plots). Values in boldface represent preferred food species E* > 0. Totals do not equal to 100 because foods contributing less than 1% are not included.

Species	Relative Abundance (%)			(E*)	
	Habitat	Juv. Diet	L.Fem Diet	Juv	L. Fem
Agaricus sp.	0.04	4.12	4.51	**0.93**	**0.92**
Ficus sycomorus	0.55	17.62	17.82	**0.81**	**0.76**
Mangifera indica	0.05	1.31	1.10	**0.76**	**0.64**
Cissus rotundifolia	0.08	1.21	1.12	**0.65**	**0.53**
Synsepalum msolo	0.44	4.61	4.94	**0.52**	**0.43**
Vachellia robusta	0.88	9.13	8.68	**0.52**	**0.38**
Brachiaria subquadripara	0.40	2.17	2.32	**0.25**	**0.14**
Hyphaene compressa	1.67	4.40	4.95	-0.11	-0.20
Phoenix reclinata	8.06	21.06	21.22	-0.12	-0.25
Alangium salviifolium	1.09	1.39	1.51	-0.44	-0.52
Grewia densa	2.46	2.71	2.49	-0.50	-0.63
Oncoba spinosa	2.99	2.69	3.41	-0.57	-0.59
Diospyros mespiliformis	2.94	2.61	2.78	-0.58	-0.65
Pavetta sphaerobotrys	2.07	1.60	1.30	-0.62	-0.75
Mimusops fruticosa	3.03	1.92	1.80	-0.68	-0.76
Garcinia livingstonei	2.02	1.19	1.38	-0.70	-0.73
Sorindeia madagascariensis	9.87	2.68	2.77	-0.85	-0.88
Polysphaeria multiflora	22.33	2.49	1.82	-0.93	-0.96
Insects	1.00	5.19	6.00	**0.22**	**0.15**
Total	**61.97**	**90.10**	**91.92**	-	-

2.3.3.3 Dietary composition and preference in the two groups: juveniles versus lactating females

Prediction (P1) was also supported when the data for each study group were analyzed separately.

a) Juveniles' and lactating females' diet and preference in Kitere group

Among the 20 Principal Plant Food Species consumed annually by members of the Kitere group, Phoenix reclinata, Ficus sycomorus, and Synsepalum msolo were the most represented, accounting, respectively, for 25.9%, 17.2% & 8.2% of juvenile diets, and 27.1%, 16.2% & 8.2% of female diets (Table 2.6, Appendix 2.4). These three species collectively accounted for 51.0% of the juveniles' and 52.0% of the lactating females' annual diet.

The Electivity values of juveniles exceeded those of lactating females for the 20 Principal Plant Food Species (plus insects) (Table 2.6, $W = -231$, $p < 0.0001$, $N = 21$), as well as for the larger botanical sample of 72 plant species exploited (Appendix 2.4, $W = -1637$, $p < 0.0001$, $N = 72$). Based on E* values, juveniles preferred Agaricus sp. (0.93), Mangifera indica (0.70), and Ficus sycomorus (0.68), while the lactating females focused similarly on Agaricus (0.90) and Ficus sycomorus (0.55), but additionally on Momordica trifoliata (0.56) instead of Mangifera indica (Table 2.6; Appendix 2.4). The least preferred species were Lecaniodiscus fraxinifolius and Polysphaeria multiflora for both juveniles and lactating females. Similar to large botanical samples these results also support my prediction (P1).

Table 2.6. Dietary contribution, abundance in habitat and diet, and Electivity index E* (Vanderploeg & Scavia, 1979) for the 20 Principal Plant Food Species consumed by juveniles (Juv) and lactating females (L. fem) in Kitere group (N = 21 juveniles & 11 lactating females). Dietary contribution is the percentage of feeding events assigned to particular food species (N = 20,486) while relative abundance is the percentage assigned to each food species in the habitat (N = 76 plots). Values in boldface represent preferred food species E* > 0. Totals do not equal to 100 because foods contributing less than 1% are not included.

Species	Relative Abundance (%)			(E*)	
	Habitat	Juv. Diet	L. Fem Diet	Juv	L. Fem
Agaricus sp.	0.03	2.69	2.84	**0.93**	**0.90**
Mangifera indica	0.12	2.62	2.20	**0.70**	**0.53**
Ficus sycomorus	0.86	17.2	16.24	**0.68**	**0.55**
Momordica trifoliate	0.08	1.15	1.56	**0.58**	**0.56**
Synsepalum msolo	0.64	7.71	8.24	**0.52**	**0.40**
Cissus rotundifolia	0.17	1.53	1.78	**0.40**	**0.30**
Antidesma venosum	0.17	1.21	1.14	**0.30**	**0.08**
Vachellia robusta	1.06	4.97	4.90	**0.11**	-0.09
Phoenix reclinata	8.72	25.94	27.08	-0.12	-0.28
Brachiaria subquadripara	0.83	2.25	2.91	-0.16	-0.22
Oncoba spinosa	1.20	2.42	3.02	-0.30	-0.38
Alangium salviifolium	0.60	1.20	1.17	-0.31	-0.48
Harrisonia abyssinica	0.71	1.22	1.00	-0.37	-0.6
Diospyros mespiliformis	4.11	4.31	4.58	-0.56	-0.67
Grewia densa	2.88	2.62	2.27	-0.61	-0.75
Mimusops fruticosa	4.11	3.19	3.16	-0.66	-0.76
Garcinia livingstonei	2.66	1.36	1.53	-0.76	-0.81
Sorindeia madagascariensis	5.66	1.18	1.24	-0.90	-0.92
Polysphaeria multiflora	18.76	2.74	2.13	-0.93	-0.96
Lecaniodiscus fraxinifolius	14.90	1.89	1.63	-0.93	-0.96
Insects	1.20	3.31	3.55	-0.16	-0.31
Total	**69.47**	**92.17**	**94.17**	-	-

b) Juveniles' and lactating females' diet and preference in Mchelelo group

The diet of Mchelelo group consisted was characterized by a fewer number of Principal Plant Food Species compared to Kitere group (Table 2.7, Appendix 2.5). The plant foods that contributed the highest percentages of annual diet of the

Mchelelo group for both juveniles and lactating females were Ficus sycomorus, Phoenix reclinata, and Vachellia robusta (juveniles: 18.0%, 16.2%, & 13.3%; lactating females: 19.4%, 15.4%, & 12.5%, respectively) (Table 2.7). The three species contributed 48% and 47% of the total annual diet of the juveniles and lactating females.

Both the juveniles and lactating females preferred Agaricus sp., Ficus sycomorus, and Brachiaria subquadripara (juveniles: E* = 0.88, 0.81, & 0.77; lactating females: E* = 0.86, 0.77, & 0.65, respectively). The two age classes showed high avoidance of Polysphaeria multiflora, Sorindeia madagascariensis, and Drypetes natalensis (Table 2.7). Nevertheless, juveniles showed higher electivity indices than lactating females (E*) in both the sample of 16 Principal Plant Food Species plus insects (W = -136, p = < 0.0001, N = 17) as well as for the larger sample of 65 plant species eaten plus insects in Mchelelo group (W = -1004, p = < 0.0001, N = 66) (Table 2.7, Appendix 2.5). These results for food electivity values of both Principal Plant Food Species and the large botanical food sample and insects supported my prediction (P1).

In summary, Phoenix reclinata and Ficus sycomorus contributed the highest percentages to the annual diet of both juveniles and lactating females in the two study groups. Juveniles in Kitere, however, showed a high preference for Agaricus sp. and Mangifera indica, while lactating females preferred the former and Momordica trifoliata. In Mchelelo, both juveniles and lactating females showed a high preference for Agaricus sp. and Ficus sycomorus. Juveniles in both study groups had higher electivity indices (E*) for both preferred and avoided foods than

the lactating females. This was reflected in both the Principal Plant Food Species and the entire botanical food composition plus insects utilized by the groups separately and combined, thus, prediction (P1) was supported.

Table 2.7. Dietary contribution, abundance in habitat and diet, and Electivity index E* (Vanderploeg & Scavia, 1979) for the 16 Principal Plant Food Species consumed by juveniles (Juv) and lactating females (L. fem) in the Mchelelo group (N = 12 juveniles & 19 lactating females). Dietary contribution is the percentage of feeding events assigned to particular food species (N = 20,486) while relative abundance is the percentage assigned to each food species in the habitat (N = 94 plots). Values in boldface represent preferred food species E* > 0. Totals do not equal to 100 because foods contributing less than 1% are not included.

Species	Relative Abundance (%)			(E*)	
	Habitat	Juv Diet	L. Fem Diet	Juv	L. Fem
Ficus sycomorus	0.31	18.04	19.4	**0.81**	**0.77**
Agaricus sp.	0.05	5.55	6.18	**0.88**	**0.86**
Brachiaria subquadripara	0.04	2.09	1.73	**0.77**	**0.65**
Vachellia robusta	0.73	13.3	12.46	**0.49**	**0.35**
Saba comorensis	0.15	1.3	0.72	**0.15**	-0.27
Synsepalum msolo	0.27	1.5	1.63	-0.07	-0.16
Hyphaene compressa	3.01	8.71	9.75	-0.37	-0.44
Phoenix reclinata	7.52	16.19	15.35	-0.49	-0.6
Grewia densa	2.13	2.81	2.71	-0.65	-0.73
Pavetta sphaerobotrys	2.86	3.2	2.6	-0.7	-0.8
Alangium salviifolium	1.48	1.58	1.84	-0.71	-0.74
Garcinia livingstonei	1.49	1.02	1.23	-0.8	-0.82
Oncoba spinosa	4.45	2.97	3.79	-0.81	-0.81
Sorindeia madagascariensis	13.3	4.17	4.3	-0.91	-0.92
Drypetes natalensis	7.06	1.3	1.26	-0.94	-0.96
Polysphaeria multiflora	25.24	2.24	1.52	-0.97	-0.99
Insects	0.83	7.06	8.45	**0.15**	**0.1**
Total	**70.92**	**93.03**	**94.92**	**-**	**-**

2.3.4 Dietary breadth of juveniles and lactating females

As I predicted (P1), in each study group individually and for the combined data set, juveniles had a narrower dietary breadth compared to lactating females (Fig. 2.6). The dietary breadth was higher in the Mchelelo group compared to that in

Kitere, and lower in juveniles than in lactating females in both study groups (B_A –

Mchelelo: juveniles = 0.17, lactating female = 0.22; B_A – Kitere: juveniles = 0.11,

lactating = 0.15; B_A – Overall: lactating female = 0.13; Juveniles = 0.11). This

suggested that juveniles consumed various food resources less evenly than lactating

female (Fig. 2.6).
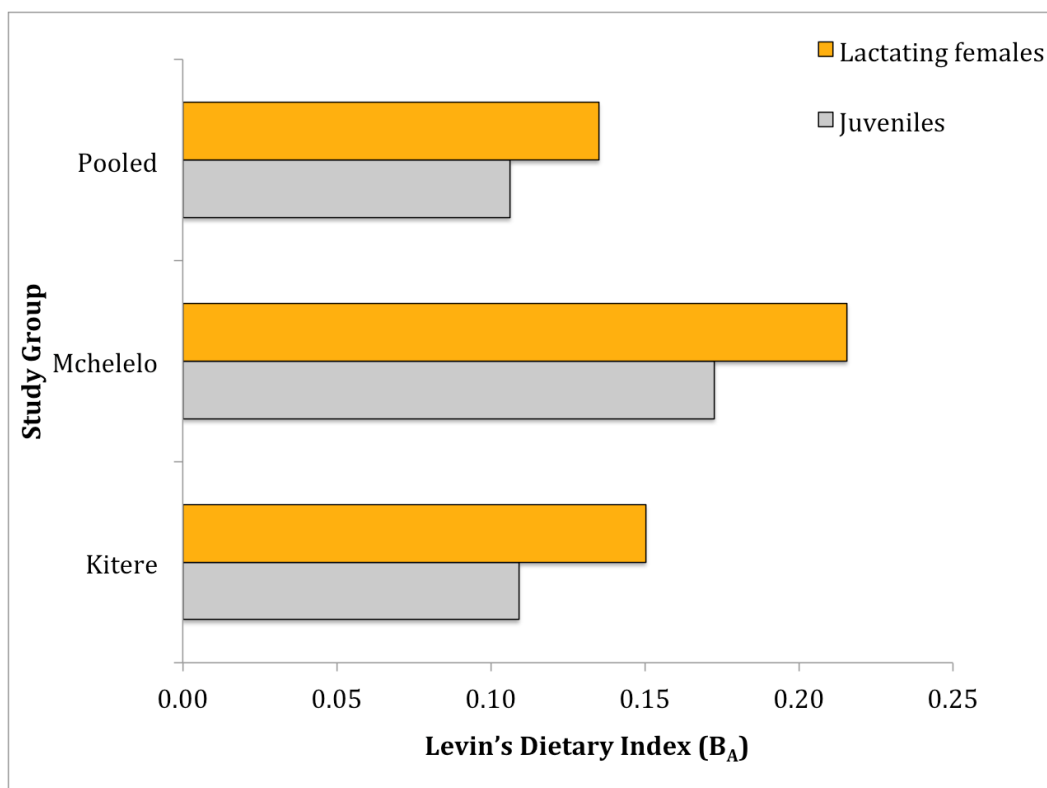
Figure 2.6. Dietary breadth between the juveniles and lactating females in each of the two study groups and in pooled data set (both groups combined) measured using the Levin's dietary index (B_A).

2.3.5 Metabolizable energy (ME) intake

Before testing my prediction **(P2)** on relative ME intake (i.e., ME intake per

metabolic body mass - MBM) between juveniles and lactating females, I first

examine: the energetic gains from different types of foods, plant food species, time

spent feeding on such plant foods, and the differences in absolute ME intake between the age classes and between the two study groups. I focus the analysis on both per minute and per feeding bout intake of ME. Post the hypothesis testing, I present data on ME derived from each of the constituent macronutrients that contribute to total ME ingested, to understand the main source energetic sources.

2.3.5.1 Absolute energetic returns of different types of foods per feeding bout

The mangabeys generally derived more absolute ME per feeding bout from mushrooms, fruits, and gum compared to insects, leaves, seeds, and food category 'others' (Fig. 2.7). The absolute mean ME intake returns per feeding bout were highest in mushrooms (12.23Kcal/feeding bout) and lowest in insects (2.02Kcal/feeding bout). The observed difference in mean ME per feeding bout across the food types varied significantly (F = 548.39, df = 6, p < 0.0001) controlling for focal ID and time spent feeding. Absolute metabolizable energy intake per feeding bout was significantly lower for insects, leaves, seeds, and 'others' (p < 0.0001) than for fruits, gum, and mushrooms.
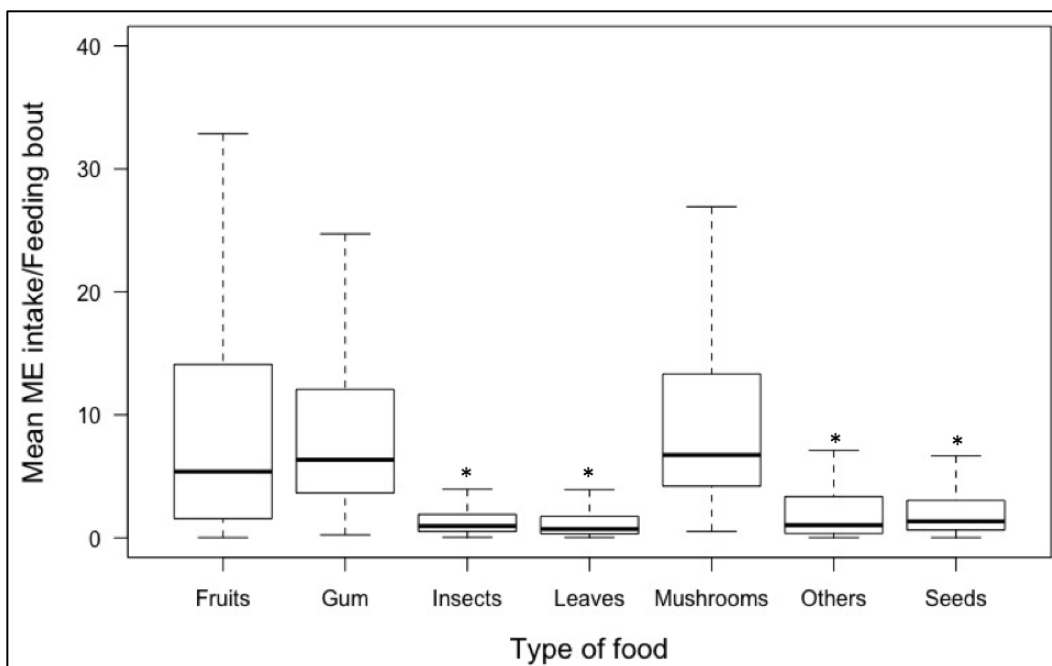
Figure 2.7. Absolute metabolizable energy (ME) returns per feeding bout on dry matter basis obtained from different types of foods eaten by juveniles and lactating females combined in the Tana River mangabeys (N = 63 focal individuals, total feeding events = 20,485, error bars indicate the mean standard deviation).

2.3.5.2 Variation in energetic returns from foods eaten by juveniles and lactating females

Annual energetic contributions of plant foods

Fruits and seeds contributed the highest percentages of the annual diets of juveniles and lactating females as well as of the energetic annual returns (Table 2.8). Fruits accounted for 45.0% of the juvenile diet and 71.8% of the total energy ingested from all food items combined in Kcal/g. Seeds constituted 34.0% of the annual diet and 14.4% of the total energy intake in juveniles. The annual diet of lactating females comprised 45.1% fruits and 34.6% seeds, respectively. Fruits accounted for 74.3% of the total energy ingested while seeds yielded about 14.1%.

The food category 'others' contributed the smallest percentage of both the annual diet and energy returns of the juveniles and lactating females (diet: 1.8% & 1.5%, energy returns: 1.2% & 1.1%, respectively). Fruits and seeds together accounted for about 78.0% and 86.0% of the juveniles' total annual percentage of diet and energetic returns, which was more than three times the annual diet and energetic returns of the remaining categories of food types combined. Similarly, fruits plus seeds combined contributed 80.0% and 88.0% of the annual diet and energetic returns of the lactating females, respectively. This was, again, more than three times the total annual diet and energetic returns obtained by lactating females from all other categories of food types collectively (Table 2.8).

Table 2.8. Annual percentages of different food types and corresponding annual absolute metabolizable energy (ME) intake on dry matter basis obtained from their consumption by juveniles and lactating females in both study groups combined (N =63 focal individuals, total focal observations = 20,486).

	Annual percentages			
	Juveniles		Lactating females	
Food item	Diet	ME intake	Diet	ME intake
Fruits	44.98	71.78	45.13	74.29
Seeds	33.89	14.35	34.59	14.05
Mushrooms	4.17	6.24	4.50	5.64
Gum	2.13	3.30	1.81	2.28
Leaves	7.77	1.85	6.47	1.29
Insects	5.26	1.28	5.98	1.34
Others	1.80	1.19	1.52	1.10
Total	**100.00**	**100.00**	**100.00**	**100.00**

Overall, the observed percentages at which various types of foods were included in the diet (Table 2.8) differed significantly (χ^2 = 22.98, df = 6, p = 0.008). The percentages at which juveniles and lactating females included each type of food in the diet did not differ significantly, however (χ^2 = 0.1597, df = 1, p = 0.689).

2.3.5.3 Absolute energetic gains and time spent feeding Principal Plant Food Species per feeding bout

The mean time spent on feeding and the metabolizable energy obtained from the Principal Plant Food Species per feeding bout showed major variations (Table 2.9). On average, juveniles spent more time feeding per feeding bout on *Diospyros mespiliformis* (2.94 $\pm$ 0.18 Kcal/g) and *Ficus sycomorus* (2.64 $\pm$ 0.05 Kcal/g) compared to other plant species (Table 2.9)*. Lactating females as well spent more time feeding on *Diospyros mespiliformis* (3.22 $\pm$ 0.31 Kcal/g), but not on *Ficus sycomorus*, instead focusing disproportionately on *Hyphaene compressa* (2.73 $\pm$ 0.52 Kcal/g).

Juveniles obtained the highest energetic returns from *Mimusops fruticosa* (30.09 $\pm$ 2.28 Kcal/g) and *Ficus sycomorus* (23.15 $\pm$ 0.48 Kcal/g). Similarly, lactating females gained the highest absolute ME returns from *Mimusops fruticosa* (28.58 $\pm$ 4.47 Kcal/g) and *Oncoba spinosa* (26.66 $\pm$ 1.92 Kcal/g), (Table 2.9, Appendix 2.8). Notably, juveniles and adult females also obtained substantial energetic gains from *Borassus aethiopum* (24.97 $\pm$ 2.05 Kcal/g and 30.55 $\pm$ 3.55 Kcal/g, respectively). Although *Borassus aethiopum* had high energetic returns, it contributed less than 1% of the annual diet of the mangabeys. The mean ME intake per feeding bout from

the food items consumed by both juveniles and lactating females was not statistically different (t = 1.68, df = 96, p = 0.0961, N = 97 food types, 96 plant species and insects).

Table 2.9. Time spent feeding (in minutes ± standard error of the mean - SEM) and absolute metabolizable energy (ME) intake (Kcal/g) per feeding bout on dry matter basis obtained from the important plant foods and insects that are eaten by the juveniles (Juv) and lactating female (L.fem) in Tana River mangabeys (N = 63, total feeding events = 20,486).

Species	Mean ± SEM time spent in feeding (Min)/bout		Mean ± SEM Absolute ME gain (Kcal/g/bout)	
	Juv	L. fem	Juv	L. fem
Mimusops fruticosa	1.97 ± 0.20	2.13 ± 0.33	30.09 ± 2.28	28.58 ± 4.47
Oncoba spinosa	2.23 ± 0.13	2.50± 0.20	20.07 ± 1.16	26.66 ± 1.92
Ficus sycomorus	2.64 ± 0.05	2.52 ± 0.08	23.15 ± 0.48	24.42 ± 0.84
Hyphaene compressa	2.63 ± 0.35	2.73 ± 0.52	15.77 ± 3.21	19.21 ± 5.69
Agaricus sp.	1.37 ± 0.07	1.45 ± 0.11	12.79 ± 0.63	11.37 ± 0.86
Garcinia livingstonei	2.22 ± 0.17	2.36 ± 0.27	6.25 ± 0.55	8.02 ± 1.67
Vachellia robusta	1.61 ± 0.06	1.60 ± 0.06	7.87 ± 0.36	7.78 ± 0.44
Mangifera indica	1.28 ± 0.08	1.10 ± 0.11	5.18 ± 0.42	5.66 ± 0.68
Cissus rotundifolia	1.42 ± 0.12	1.05 ± 0.20	3.38 ± 0.36	4.45 ± 0.81
Phoenix reclinata	2.49 ± 0.05	2.43 ± 0.09	3.49 ± 0.13	3.50 ± 0.20
Alangium salviifolium	1.39 ± 0.10	1.31 ± 0.15	2.63 ± 0.24	3.29 ± 0.51
Sorindeia madagascariensis	1.94 ± 0.14	1.87 ± 0.23	2.76 ± 0.29	2.77 ± 0.54
Synsepalum msolo	2.03 ± 0.09	1.82 ± 0.16	2.59 ± 0.24	2.53 ± 0.40
Diospyros mespiliformis	2.94 ± 0.18	3.22 ± 0.31	2.32 ± 0.20	2.42 ± 0.44
Drypetes natalensis	1.81 ± 0.17	1.60 ± 0.34	2.05 ± 0.26	1.98 ± 0.24
Polysphaeria multiflora	2.05 ± 0.14	2.13 ± 0.27	1.92 ± 0.22	1.88 ± 0.45
Grewia densa	1.91 ± 0.11	1.88 ± 0.18	1.60 ± 0.16	1.39 ± 0.19
Lecaniodiscus fraxinifolius	2.08 ± 0.31	1.16 ± 0.10	2.43 ± 0.39	1.38 ± 0.32
Brachiaria subquadripara	1.50 ± 0.10	1.48 ± 0.16	0.86 ± 0.07	0.94 ± 0.21
Pavetta sphaerobotrys	2.09 ± 0.09	2.12 ± 0.15	0.35 ± 0.03	0.26 ± 0.03
Insects	1.03 ± 0.05	0.97 ± 0.06	1.96 ± 0.13	1.94 ± 0.21

2.3.5.4 Absolute metabolizable energy (ME) intake between age class and study groups

Absolute intake of metabolizable energy was similar for both juveniles and females (Fig. 2.8). The energetic intake did not vary in response to age class for both the per minute analysis (F = 0.09, df =1, p = 0.7710) and per feeding bout analysis (F = 1.06, df = 1, p =0.3068, p = 63). Juveniles and lactating females consumed similar amounts of ME in both per minute (t = 0.29, df =1, p =0.7710, N = 63) and per feeding bout (t = 1.03, df = 62, p = 3070, N = 63).

However, the energetic intake distinction was expressed variably depending upon group identity (Fig 2.8). The absolute ME ingestion differed between the two study groups in both ME intake per minute (F = 84.60, df = 62, p < 0.0001, N = 63) and per feeding bout (F = 18.42, df = 1, p = < 0.0001, p = 63). Compared to Kitere group, Individuals in the Mchelelo group consumed higher absolute ME in both per minute (t = 9.20, df = 62, p < 0.0001, N = 63) and per feeding bout (t = 4.29, df = 1, p < 0.0001, N = 63).

Within both groups, absolute ME intake did not differ between juveniles and lactating females (Fig 2.8). This pattern was true for ME intake per minute in both the Mchelelo group (F =0.08, df = 1, p = 0.7820, t = 0.28, df = 1, p = 7820, N = 31) and the Kitere group (F = 0.24, df = 1, p = 0.6280, N = 32). The analysis of ME intake per feeding bout produced a similar result as there was no difference between Mchelelo (F = 0,64, df = 1, p = 0.4284, t = 0.08, df = 1, p = 0.4280, N = 31) and Kitere groups (F = 1.31, df = 1, 0.2560, t = 1.15 df = 1, p = 0.2560, N = 32).
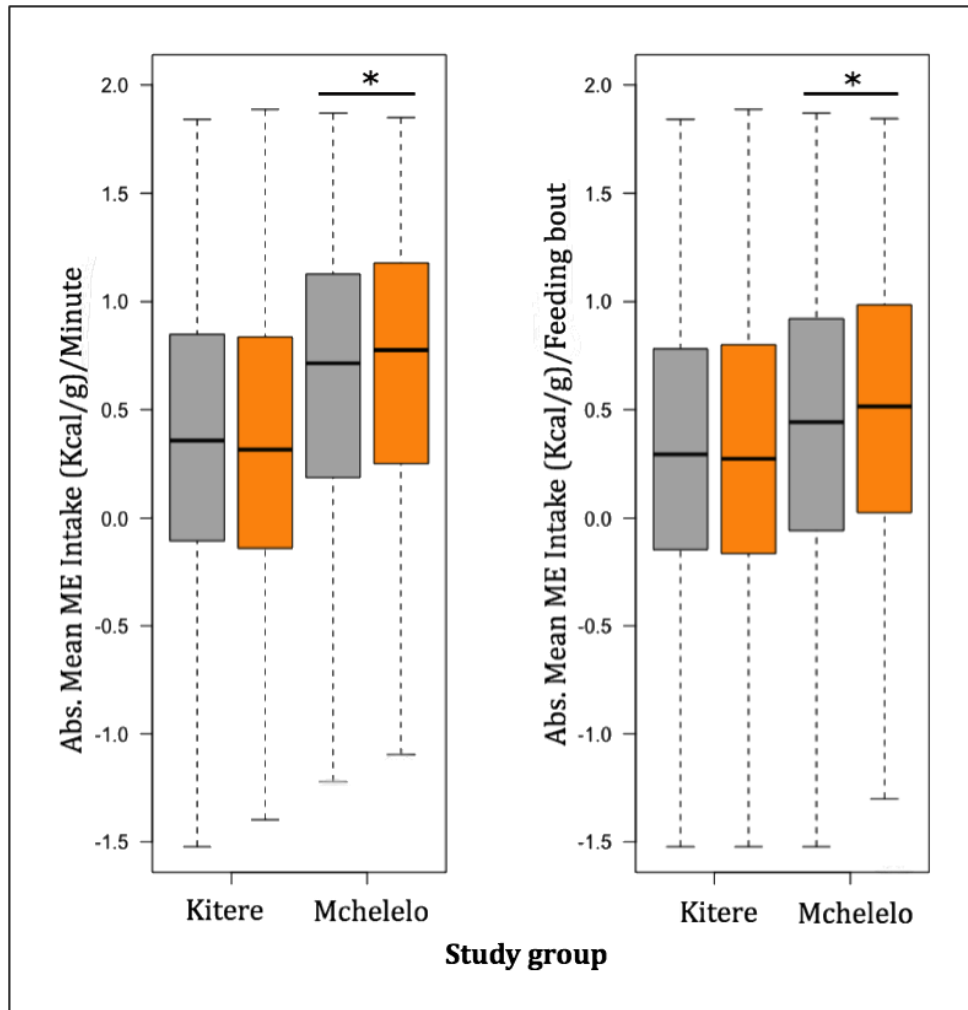
Figure 2.8. Absolute (Abs.) metabolizable energy (ME) intake in Kcal/g on dry matter basis in both per minute and per feeding bout between juveniles (gray bars) and lactating females (orange bars) in Kitere and Mchelelo study groups (data are log transformed and N = 63 focal individuals, error bars indicate mean standard deviation, * shows study group statistical differences, p < 0.05).

In summary, absolute ME intake in either per minute or feeding bout was similar between juveniles and lactating females. However, Mchelelo group had higher energetic intake than the Kitere group.

2.3.6 Metabolizable Energy (ME) Intake per Metabolic Body Mass (MBM)

2.3.6.1 **Relative metabolizable energy (ME) intake between age class and study groups**

The relative ME intake varied significantly in response to age class for both the per minute analysis (F = 38.02, df = 60, p < 0.0001, N = 63) and the per feeding bout analysis (F = 38.09, df = 61, p < 0.0001, N = 63). Juveniles ingested significantly higher ME per MBM than lactating females per feeding minute (t = 6.17, df = 60, p < 0.0001, N = 63) and per feeding bout (t = -6.17, df = 61, p < 0.0001, N = 63) (Fig 2.9).

Relative ME intake per minute also varied significantly as a function of study group identity for both the per minute analysis (F = 85.89, df = 59, p < 0.0001, N = 63) and the per feeding bout analysis (F = 17.54, df = 59, p < 0.0001, N = 63). Compared to the Kitere group, the individuals of Mchelelo group consumed significantly more relative ME per minute (t = 9.268, df = 59, p < 0.0001, N = 63) and per feeding bout t = -6.17, df = 61, p < 0.0001, N = 63) (Fig. 2.9).
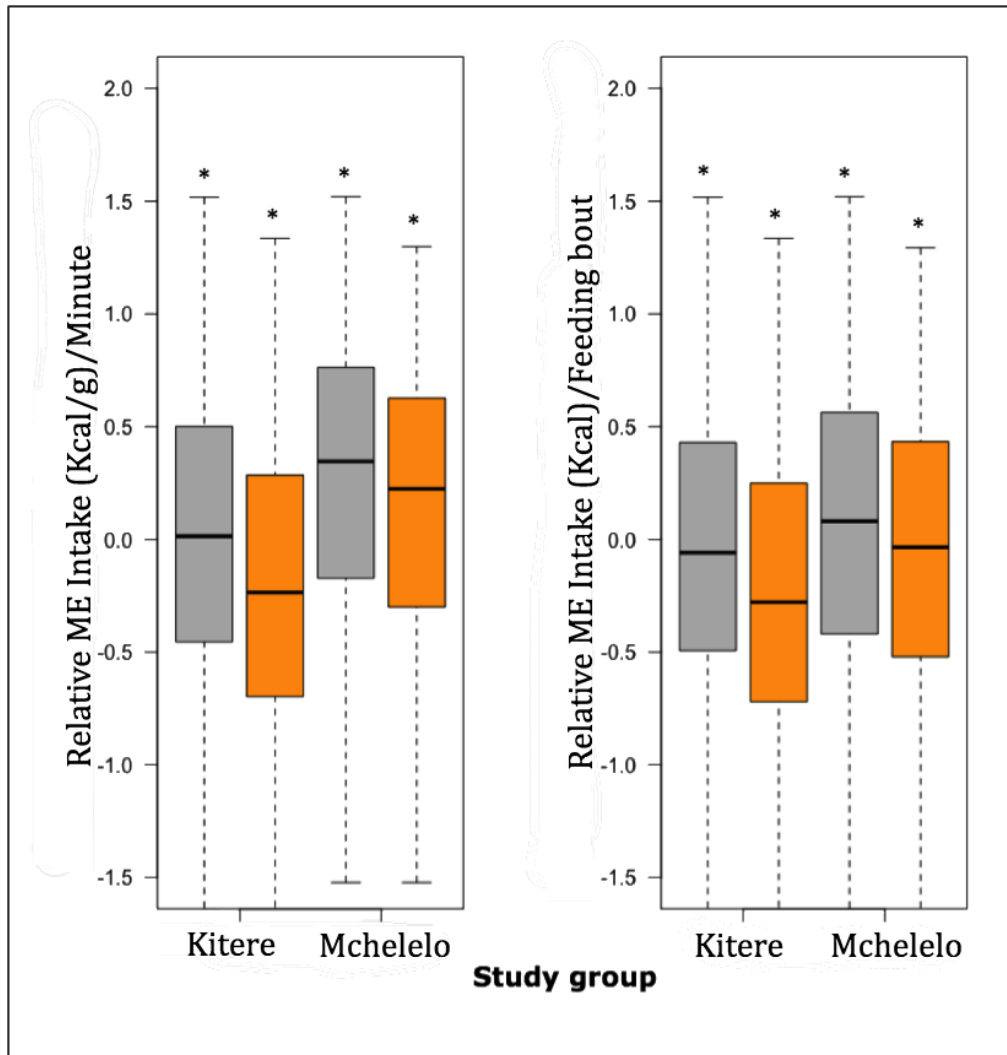
Figure 2.9. Relative metabolizable energy (ME) intake in Kcal/g on dry matter basis in both per minute and per feeding bout between juveniles (grey bars) and lactating females (orange bars) in Kitere and Mchelelo study groups (data are log transformed, N = 63 focal individuals, total feeding events = 20,486, error bars indicate mean standard error, * indicate significant results, p < 0.05).

Within study groups, however, the energetic distinction between age classes was expressed variably depending upon relative ME intake (Fig 2.9). In Mchelelo group, juveniles consumed more relative ME than lactating females in both per minute intake (F =14.09, df = 1, p < 0.0003, t = -3.75, df =1, p < 0.0003, N = 31) and

per feeding bout analysis (F = 25.42, df = 1, p < 0.0001, t = -5.04, df = 1, p < 0.0001, N = 31). The same was true for Kitere group: juveniles ingested higher relative ME than lactating female in per minute analysis (F = 13. 10, df = 1, p = 0.0006, t = -3.62, df = 1, p = 0.0006, N =32) and per feeding bout analysis (F = 26.20, df = 1, p < 0.0001, t = -5.12, df = 1, p < 0.0001, N = 32).

In summary, juveniles consumed more relative ME than lactating females in both pooled data for the two study groups and in each group alone, in both the per minute and per feeding bout intake of ME. The results were consistent with my prediction (P2) that foraging juveniles will seek higher relative intake of ME. In addition, members of the Mchelelo group consumed more ME than those of the Kitere group.

2.3.6.2 **Macronutrients contribution to Metabolizable energy (ME) intake**

To understand the macronutrient contributions to the ingested relative ME, I focus only on the per minute ME intake. This is because relative ME in both per minute and per feeding bout were significant, and any one of these two will provide a true reflection of ME gain from the macronutrients.

Neutral detergent fiber (NDF), fat, available protein (AP), and total non-structural carbohydrates (TNC) are potential sources of metabolizable energy. Relative ME intake (per MBM) from these macronutrients differed significantly between the age classes in the per minute analysis (NDF: F = 33.07, df = 63, p < 0.0001, N = 63, Fat: F = 17.56, df = 63, p < 0.0001, N =s63; AP: F = 28.38, df = 63, p < 0.0001, N = 63, TNC: F = 35.28, df = 63, N = 63) (Fig. 2.11). As predicted (P2), juvenile ME intake per MBM significantly exceeded that of lactating females for ME

sources from NDF (t = 6.28, df = 61, p < 0.0001, N = 63), fat (t = 4.19, df = 62, p < 0.0001, N = 63), available protein (AP), (t = -5.33, df = 61, p < 0.0001, N = 63) and TNC (t = -5.94, df = 61, p = 0.0001, N = 63).

Relative ME intake from these four macronutrients also differed significantly with respect to study group (NDF: F = 39.55, df = 63, p < 0.0001, Fat: F = 55.61, df = 63, p < 0.0001, N = 63, AP: F = 4.80, df = 63, p < 0.0001, TNC: F = 121.81, df = 63, p < 0.0001, N = 63). Both juveniles and lactating females in Mchelelo group had higher intake of ME per MBM than their counterparts in Kitere group from NDF (t = 6.29, df = 59, p < 0.0001, N = 63), Fat (t = 7.457, df = 59, p < 0.0001, N = 63), AP (t = 2.19, df = 59, p < 0.0001, N = 63), and TNC (t = 11.04, df = 59, p < 0.0001).

In summary, juveniles ingested more relative ME per minute from neutral detergent fiber, fat, available protein, and total non-structural carbohydrates than lactating females in both groups. Individuals in Mchelelo group ingested more metabolizable energy from these four macronutrients than the Kitere group while in overall, energy derived from total non-structural carbohydrates and neutral detergent fiber component exceeded that of fat and available proteins.
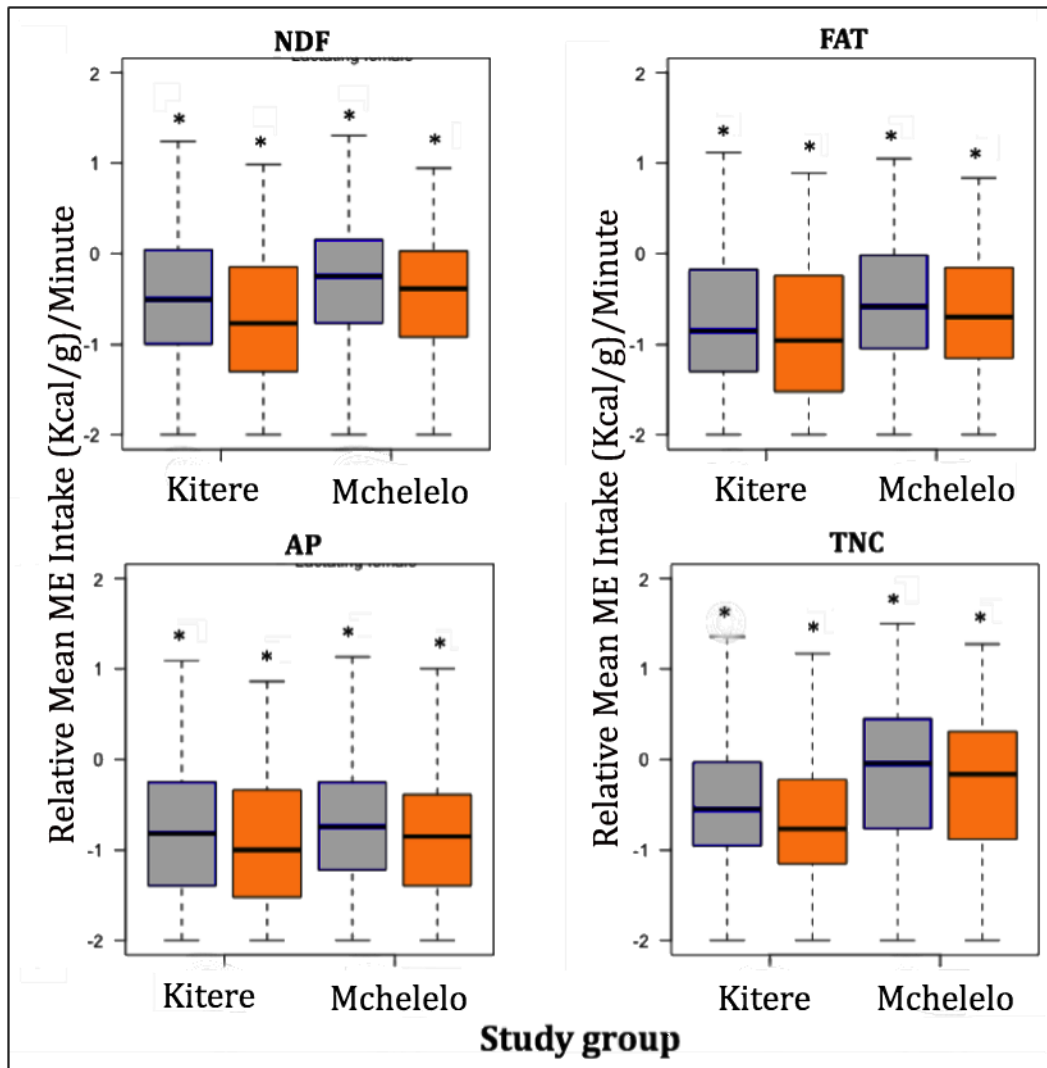
Figure 2.10. Relative metabolizable energy (ME) in Kcal/g on dry matter basis derived from Neutral detergent fiber (NDF), fat, available protein (AP), and total non-structural carbohydrates (TNA) intake per minute by juveniles (gray) and lactating females (orange) between Mchelelo and Kitere study groups. Data are log transformed, N = 63 focal individuals, total feeding events = 20,486, error bars indicate mean standard deviation, * indicate significant results $p < 0.05$).

2.4 Discussion

Dietary composition and food choices in juveniles and lactating females

The overall diets of the juveniles and lactating females in the Tana River mangabeys consisted of 124 different kinds of foods recorded both opportunistically and via systematic sampling of feeding behavior. This diet was comprised of 89% plant and 11% faunal food sources, respectively. Among the plant diet, 90% of the plant foods were natural, while 10% were cultivated plant foods. Based only on focal observations, the Kitere and Mchelelo study groups consumed about 76 and 65 plant species, respectively.

Overall, the dietary composition of the Tana River mangabeys comprised plant foods from 42 plant families. Five families, *Fabaceae, Poaceae, Malvaceae, Sapindaceae, and Rubiaceae,* collectively contributed about 41% of the total number of plant species utilized by the mangabeys (Table 2.1). Trees (40%), climbers (14%), and herbaceous plants (14%) contributed the highest percentages of the plant life forms included in the diet.

Findings from this study suggest that the Tana River mangabeys consumed 14 more plant food species than the highest number of 96 reported previously for this population (Field, 2007; Rowe & Myers, 2015). Homewood (1978) reported that the Tana River mangabeys in Mnazini forest, which is next to Kitere site, consumed about 68 different foods. The Kitere group in this study, which is closest to Mnazini, consumed about 76 different plant species. The plant families and

Principal Plant Food Species recorded in this study, however, are similar to those reported in previous studies on this species (Homewood, 1978; Kinnaird, 1992; Wahungu, 1998; Wieczkowski, 2004).

Variation in dietary composition between the current and previous studies may be explained partly by differences in sampling period. For instance, Homewood (1978) collected data for seven months, which was about half the duration of my study. This implies that several annual plant foods that are available and consumed by the mangabeys within a short period of the year may have been missed. Other reasons for the disparity include changes over time in vegetation diversity and composition, home range size of groups studied, long and irregular patterns of fruiting patterns of certain plant foods, and land use systems (Olupot, 1998; Kinnaird & Wieczkowski, 2008). Kinnaird & Wieczkowski (2008) reported shifts in composition of the plant food species utilized by the mangabeys over a 13-year period. They pointed out that human disturbances, elephant populations, and changes in hydrological cycles following dam construction in upper Tana River about two decades ago were underlying causes of the observed shifts. Similarly, Olupot's (1998) study tracking the dietary changes of grey-cheeked mangabeys reported much variation in the number of plant foods eaten by this species (i.e., from 25 in 1972 to 51 in 1993) in Kibale National Park, Uganda. The changes were attributed to shifts in forest composition, ranging behavior, and fruiting lags in important fruit trees. The same reasons can partly explain the observed dietary differences in the Tana River mangabeys. In addition, a shift in foraging behavior to

include human cultivated crops (as observed mainly in the Kitere group) also contributes to the differences in dietary composition.

The dietary composition reported in this study, however, was lower than that recorded in grey-cheeked mangabeys (*Cercocebus albigena*) in Lopé Reserve in Gabon (155 plant species), but higher than that recorded for the same species in Kibale National Park, Uganda (25 – 91 plant species) (Ham, 1994; Olupot, 1997; Tutin et al., 1997). The Tana River mangabeys also consumed more plant food species than the congeneric sooty mangabeys (*Cercocebus atys*) in Tai (30 plant species) (McGraw et al., 2011), and sanje mangabeys (*Cercocebus sanje*) in Udzungwa mountains, Tanzania (76 plant species) (McCabe et al., 2013). Thus, besides the grey-cheeked mangabeys in Lopé the Tana River subjects have the second most diverse diet of mangabeys.

The three species of mangabeys have similar foraging strategies as the Tana River mangabeys and are adapted to feeding on hard diets (Lambert 2004; McGraw et al., 2011). However, they occupy ecologically distinct habitats that vary in vegetation composition and largely explain the dietary differences. The Sooty, Grey-cheeked, and Sanje mangabeys occur in tropical or tropical-submontane evergreen or deciduous forests (Tutin, et al., 1997; McGraw et al., 2015; McCabe et al., 2013). The Tana River mangabeys occupy the forest galleries that are surrounded by expansive dry savanna woodlands (Njue, 1992). Such ecological variation is likely to influence plant diversity and composition and, subsequently, the feeding strategies of mangabey species.

The local dietary contrasts between the two study groups may be attributed to dietary flexibility driven by anthropogenically caused differences in food availability. Diversification or expansion of dietary breadth has been suggested to be a coping strategy to declining food resources among both frugivorous and folivorous primates (Palombit, 1997; Fashing et al., 2001; Chapman et al., 2010). In addition, according to intermediate disturbance hypothesis (Molino & Sabatier, 2001), moderate habitat disturbances, as occur at Kitere, can increase plant diversity. This implies that more plant foods may be available compared to undisturbed habitats. Findings from my study indicate that the Kitere group consumed more plant foods than Mchelelo group and that unique species eaten in Kitere were almost three times more abundant there than at Mchelelo (Fig. 2.3). Data on food availability and vegetation surveys (presented in chapter 3) indicate that food availability and tree basal area were lower in Kitere forests than in Mchelelo. The forests in Kitere were more heterogeneous, comprising species unique to both its constituent woodland and the riverine habitats, unlike Mchelelo, which was dominated by riverine restricted species. The mangabeys in Kitere included some of the woodland species in their diet, such *Cassia abbreviate* and *Thespesia danish*, which were not common in Mchelelo forest and, consequently, rare in the diet. Crop raiding as a foraging strategy in Kitere group increased the dietary composition compared to Mchelelo group, which did not engage in raiding.

Similar local differences in dietary composition have been reported in other primates. For instance, Mammides et al. (2008) found that disturbance correlated positively with food diversity, availability, and group densities among blue monkeys

(*Cercopithecus mitis*) and black-and-white colobus (*Colobus guereza*) in Kakamega forest Kenya. However, sympatric red-tailed monkeys (*Cercopithecus ascanius*) did not show such pattern suggesting other factors other than disturbance influence dietary selectivity and flexibility. Group dietary differences have been reported among primates even in the absence of anthropogenic influences. For example, Rodgers et al. (2004) found that the dietary composition of the western gorilla, across six sites in Africa, varied widely regarding the number of species eaten and parts included in the diet. Moreover, Rothman et al. (2007) attributed regional differences in dietary composition of two populations of Mountain gorillas occupying similar montane habitats to plant food diversity, distribution, and density. Thus, the same factors as well may explain the observed Tana River mangabeys' group differences in dietary composition. Data from inter- and intra-specific dietary comparison of the sympatric siamang (*Hylobates syndactylus*) and lar gibbons (*Hylobates lar*) provide further evidence on primate groups' dietary differences (Palombit 1997). This study established that frugivory in the two subspecies varied between groups. For instance, the siamangs in Katembe study site included were more frugivorous and also ate higher amounts of non-fig fruits compared to their Malaysian counterparts.

Dietary Breadth

Juveniles from the two study groups had a narrower dietary breadth compared to lactating females (Fig. 2.5), as I predicted (P1). Moreover, both lactating females and juveniles in Mchelelo group had a higher dietary breadth than

their counterparts in Kitere group (Fig. 2.5). The standardized Levin's dietary breadth index suggested that juveniles sampled more food resources but did not consume them evenly compared to lactating females. However, members of the Mchelelo group included fewer species in the diet and utilized them more evenly than Kitere group. These findings partly support the Need-to-Learn hypothesis that juveniles are inefficient foragers, and because they are learning foraging skills, they engage in trial and error feeding strategy, thus, ending up sampling more species than adults (Schuppli et al., 2016). Greater competence in foraging among the lactating females is suggested by their concentrating their feeding on fewer foods that are utilized evenly. This may suggest that lactating females have good knowledge of their dietary profile and do not spend time trying new or unknown plant foods that may have little nutrient value, as juveniles do.

Juvenile-adult differences in foraging competence, energy requirements, as well as site variations in food availability, may explain most of the variations observed in dietary breadth. Data from wild brown capuchin monkeys support this observation (Gunst et al., 2010). This study found that, unlike adults, juveniles have limited skills and ability to exploit tough or hidden foods that require cognitive skills or manual strength such as larvae hidden in bamboo stalks, reducing the number of resources the immatures could efficiently utilize. Comparably, Tana River mangabeys consumed mechanically challenging food species such as *Oncoba spinosa*, *Borassus aethiopum*, and *Hyphaene compressa,* which required extractive foraging skills or adult strength to harvest them (Kivai et al., 2017). Juveniles were, however, restricted in exploiting some of these foods potentially due to lack of

physical strength and skills to break them open or detach the fruits as observed in the field.

Dietary selectivity

The Kitere group showed the highest dietary preference for *Agaricus* sp. and *Mangifera indica* (Table 2.3), while in Mchelelo group, *Agaricus* sp. and *Ficus sycomorus* were the most preferred foods. Other species that were preferred by mangabeys besides these three in both groups were *Brachiaria subquadripara*, *Vachellia robusta,* and *Synsepalum msolo.*

Juveniles in both study groups had higher selectivity index for both the most preferred and the most avoided foods than lactating females. These findings suggest that juveniles consumed the preferred foods as much as those avoided. The two plant foods that constituted the highest percentages of the annual diet of both juveniles and lactating females in both groups were *Ficus sycomorus* and *Phoenix reclinata* while *Polysphaeria multiflora, Sorindeia madagascariensis,* and *Lecaniodiscus fraxinifolius* were the most abundant in habitat, which were also the least preferred foods. The observed dietary patterns may be attributed to differences in food nutritional and mechanical properties, plant secondary metabolites, food distribution and availability, body size and energetic demands, and foraging (Glander, 1982; Milton, 1984; Wendlin et al., 2000; Felton et al., 2009; Lambert & Rothman, 2015; Vogel et al., 2015). For instance, the three most avoided plant foods were easy to exploit, and mangabeys consumed their young leaves, which were available in the riverine forests most parts of the year, suggesting that

their low preference may be linked to chemical deterrents as opposed to mechanical barriers.

The highly preferred foods of *Agaricus* sp*.* and *Ficus sycomorus* had high energetic returns (Table 2.9), as has also been reported in other primate studies (Terborgh, 1986). Caloric returns per minute from *Ficus sycomorus* (24 Kcal/g) ranked third after *Oncoba spinosa* (26 Kcal/g) and *Mimusops fruticosa* (30 Kcal/g). Both juveniles and lactating females need to ingest energy rich foods in order to meet their daily energetic requirements for physiological processes. Juveniles in addition to their smaller bodies are very active and engage more in play and practicing navigation skills on trees, which are energetically demanding (Pereira & Fairbanks, 2002). Similarly, lactating females are faced with increased energetic needs for infant carrying and protection, milk production, and maintaining their bodies as well (Conklin-Brittain et al., 1998; McCabe et al., 2013). This may explain the strong preferences of these species by the two age classes.

Figs, in general, have been found to be keystone food resources to frugivorous forest mammals in Asia and Africa (Terborgh, 1986; Gautier-Hion & Michaloud, 1989). Nutritional analyses of different fig species that are utilized by mammals suggest that figs have high nutritive value (Wendlin et al., 2000). Wendlin et al. (2000) found that figs contain high amounts of important amino acids (valine, leucine, arginine and lysine), numerous micro and macro-minerals, and high percentages of water-soluble carbohydrates, protein, and hemicellulose. *Ficus sycomorus* (24 Kcal/g per minute) ranked third in caloric returns per minute after *Oncoba spinosa* (26 Kcal/g per minute) and *Mimusops fruticosa* (30 Kcal/g per

minute), which were mechanically challenging and seasonally available, respectively. Thus, the nutritional gains and availability of *Ficus sycomorus* in most parts of the year largely explain its high preference. Other factors that may contribute to its selectivity include reduced mechanical constraint since the ripe fruits are very soft and easy to process and ingest.

The annual dietary contributions and abundance of the food species in the habitat in this study agree with data from previous studies on Tana River mangabey dietary ecology (Homewood, 1978; Kinnaird, 1992; Wahungu, 1998; Wieczkowski, 2003). However, those earlier studies never reported the high preferences for mushrooms and mangoes that were observed in this study. *Ficus sycomorus* and *Phoenix reclinata* were the most utilized food resources among the Principal Plant Food Species and constituted the highest percentages of the annual diet of mangabeys, which was consistent with previous studies (Homewood, 1978; Wahungu, 1998; Wieczkowski, 2003). The observed variation in diet selectivity could be explained by long-term temporal changes in the habitat. The majority of these previous studies are over two decades old, and habitat transformation has occurred, especially in Kitere, where mango farming is now more common than in the past. Such habitat changes resulting to variations in species diversity are likely to modify primate dietary patterns as observed in mantled howler monkey (Critoba-Azkarate & Arroyo-Rodriguez, 2007), whereby dietary shifts to include more new species occurred with fragmentation and high population density.

The dietary and nutritional significance of mycophagy in primates is poorly documented. Although the use of fungi (mushrooms) has been reported in more

than 23 primate species (Hanson et al., 2003), these foods typically constitute less than 5% of annual diet and are rarely identified taxonomically. Homewood (1978), however, reported mushrooms consumption in the Tana River mangabeys, but this was not quantified. Findings from my study indicating high preference of mushrooms (fungi) mirrored data from the Sanje mangabeys, whereby fungi was the second most consumed foods item in the species annual diet after fruits (McCabe et al., 2013). This suggests that mushrooms are a significant source of nutrients for mangabeys. In this study Mushrooms contributed about 12.8 and 11.4 Kcal/g of metabolizable energy per feeding bout for juveniles and females, and ranked fifth among Tana River mangabeys' foods with high energetic returns.

Compelling evidence for the nutritional importance of mushrooms in primate diets is provided by research on the small-bodied Goeldi's monkey, *Callimico goeldii*, of South America (Hanson et al., 2003; Porter & Garber, 2010). These monkeys spent about 63% of feeding time consuming different types of fungi, where fungi as food category account for 31 - 34% of the overall species annual diet (Hanson et al., 2003). Mushrooms consumed by Goeldi's monkeys on average contained about 4 Kcal/g of dry matter and between 5.5 - 13.4% crude protein, but some species contained as high as 62% of protein content while others up to 74% of structural carbohydrates (Hanson et al., 2003, 2006). This shows that mushrooms are potentially important sources of both protein and energy for juveniles and lactating females. Similar nutritional value of mushroom was reflected in my study, where mushroom parts ingested by mangabeys contained high protein and also total non-structural carbohydrates (see chapter 3). Moreover, mushrooms are not

mechanically challenging to harvest and process as indicated by low fracture toughness and elastic modulus, which I measured in the field (see chapter 3). This, as well, favors mushroom selectivity, especially for juveniles who have low foraging efficiency and are in the process of learning the foraging strategies.

Cultivated crops have typically high energetic returns compared to wild foods, as documented for crop raiding populations of olive baboons (*Papio anubis*)(Strum, 2010; Warren et al., 2011). The high preference of *Mangifera indica* in Kitere could be attributed to such a nutritional benefit, as well as its accessibility. Mango fruits are individually large compared to other fruits eaten by mangabeys and have high content of simple sugars, especially when ripe (Medlicot & Thompson, 1985). Mango trees are abundant in cultivated and abandoned farmlands around Kitere forests, and thus, are easily accessed by the Kitere group of mangabeys.

Fruits (55%) and seeds (20%) constituted the highest percentages of the mangabeys' diet overall. Juvenile diets were about 57% fruits, while the corresponding figure for lactating females was 53%. Seeds constituted 18% and 21% of the juveniles' and lactating females' diets, respectively. These findings are congruent with previous observations of Tana River mangabeys indicating that fruits generally account for 26 – 62% and seeds 18 - 46% of the two diets (Rowe & Myer, 2015). Young leaves were preferred over mature leaves and constituted about 7% of the annual diet. According to Lambert & Rothman (2015), fruits and seeds are typically high in fat and sugar, moderate in soluble fiber and, low in protein and low secondary metabolites. This profile suggests that fruits and seeds are good sources

of energy since fat and soluble sugars are important sources of energy. On basis of the Tana River mangabeys' dietary composition and preferences, it appears this species heavily relies on high-energy foods (fruits and seeds), which may suggest energy maximization in its foraging strategy. However, this requires detailed data collection and application of the new approaches of geometric framework analysis to ascertain.

Mature leaves generally have relatively high concentrations of plant secondary metabolites and fiber (Glander, 1982; Garber, 1987; Lambert & Rothman, 2015) unlike young leaves, which have high protein-low fiber ratio (Chapman et al., 2004). Thus, mature leaves pose chemical and digestive challenges for primates lacking the anatomical specializations for folivory such as mangabeys (Milton, 1984; Strier, 2015). This factor, likely accounts for the fact that juveniles and lactating females minimize ingestion of mature leaves and focuses more on young leaves to maximize protein intake and minimize indigestible fiber and plant secondary metabolite components (Janzen & Freeland, 1974; Milton, 1984).

Insects in this study contributed about 5.4% to the annual diet of the mangabeys, and had a positive electivity index (0.24), suggesting they were important and preferred food resource. Metabolizable energy intake per minute obtained from ingestion of insects was about 1.96 Kcal/g for juveniles and 1.94 Kcal/g for lactating females, which was low compared to the plant foods. These results are meaningful in the light of recent evidence that insectivory is not restricted to smaller primates, as previously thought and constitute an important source of nutrients (Palombi, 1997; Declawed & Janssen, 2008; Brier et al., 2013;

Isbell et al., 2013; Rothman et al., 2014; Brier et al., 2015). Nutritional evidence by Rothman et al. (2014) shows that, insects are rich in protein and lipids compared to plant foods. Such nutritional incentives attract their consumption by large primates. For instance, patas monkey (*Erythrocebus patas*) and vervet monkeys (*Cholrocebus pygerythrus*) in Laikipia, Kenya were found to obtain about 38 – 60 Kcal/day and 17 – 27 Kcal/day of ME from ants (*Crematogaster mimosae*) hidden in *Acacia drepanolobium* galls (Isbell et al., 2013). The ants contained about 15% ADF, 45% AP, 23% fat, and were significant sources of phosphorus (0.63%), potassium (0.89%), iron (304 ppm), and zinc (150 ppm). Red-tailed monkeys in Kibale National Park, Uganda have also been found to obtain 24% of their daily protein and 14% of energy from insects Bryer et al. (2013). Similarly, chimpanzees and gorillas in Dja Biosphere Reserve, Cameroon, have been found to consume high amounts of *Cubitermes* sp., *Thoracotremes* sp., and *Macrotermes* sp. to meet their daily protein, manganese, and iron requirements (Deblauwe & Jansssens, 2008). Even otherwise heavily frugivorous hylobatids focus as much as 24% of their foraging time on insects in some populations (Palombit, 1997). These studies illustrate the nutritional significance of insects in larger primates.

Despite the nutritional value, insects have chitinous skeleton that is hard to break down and may require specialized adaptations. Evidence from recent studies indicates that larger primates may have the capability to produce digestive enzymes that help digestion of chitin (Janiak, 2016). Thus, it is not surprising given the nutritional benefits, dental adaptations, and possible enzymatic adaptations to handle chitin the Tana River mangabeys include high percentage of insects in their

diet. Typical to majority of primate diets (Lambert & Rothman, 2015), findings of my study indicate that the foods eaten by Tana River mangabeys are generally low in protein and fat. However, given that the two macronutrients are significant sources of ME may explain why insects constitute an important diet to this mangabey species. However, little is currently known about the ability of Tana River mangabeys to digest chitin.

Metabolizable Energy Intake: Contrasts between Juveniles and lactating females

Metabolizable energy (ME) intake per Metabolic Body Mass (MBM) was higher in juveniles than in lactating females (in both the per minute and the per feeding bout) in Kitere and Mchelelo study groups, controlling for food intake and time spent feeding (Fig. 2.10). Moreover, Mchelelo group had higher ME intake compared to Kitere group. These findings supported my second prediction (P2) that compared to lactating females, juvenile would have a higher intake of relative ME. The data reinforce the argument that juveniles require more energy per unit mass than adults to maintain their smaller bodies (Pereira & Fairbanks, 2002). Juveniles also included more of the preferred foods in the diet than did lactating females. The higher energetic returns offered by these foods may explain this preferential feeding among juveniles. Foraging efficiency, however, may be a barrier to juveniles' exploitation of energy-dense foods that are hard to process, such as Hyphaene compressa, Borassus aethiopum, Oncoba spinosa, and Saba comorensis fruits. This idea is supported by data on the energetic returns obtained from consuming different foods (Table 2.9, Appendix 2.8), which suggest that lactating females

obtain higher energetic return in consuming these foods than do the juveniles. However, I observed that juveniles managed to gain access to foods they were unable to process and ingest independently by foraging on the "leftovers" of competent group members. Such findings support the physical maturation hypothesis that suggests lack of strength may limit juveniles foraging efficiency, and potentially higher energy intake in juveniles may result from increased feeding time and intake of more food (Rothman et al., 2008a).

Energy is an important component in nutrition because it powers basal metabolic and physiological functions, including reproduction and lactation (National Research Council, 2003; Chapman et al., 2012). Importantly, basal energy expenditure is a function of body mass area (Kleiber, 1975). Thus, due to their smaller bodies juveniles require more energy per MBM for maintenance than adults (Ausman, 1995). Previous studies have established that mass-specific basal metabolic rates in young and rapidly growing individuals, such as infants and juveniles, are higher than those of adults (Robbins, 2012). The body surface area per unit of body mass has been found to be greater in the young animals with mass-specific basal metabolic rates, surpassing those of adults by 3 - 4 times (Scott, 1986; Robbins, 2012). Thus, given the body size differences between these two age classes, it is clear according to Kleiber's law, that Tana River mangabey juveniles require higher ME intake than lactating females.

Primates require more energy to grow larger brains, compared to other mammals, partly due to the demands of cognitive foraging (Aiello & Wheeler, 1995; Gunst et al., 2010). For instance, anthropoid primates use about 8% of resting

metabolism to support their brains, compared to 3 - 4% in other mammals (Smith & Jungers, 1996). Evidence from other studies shows that energy requirements within primates are high during the juvenile period, particularly before 2 years of age when a rapid growth spurt happens in brains (Leonard & Robertson, 1992). This is also reported by for humans by Holliday (1986), who estimated that a newborn brain consumes twice as much of the resting metabolic rate as a five-year-old child. The Tana River mangabeys, like other primates, are faced with the similar energetic demands to grow big brain and to sustain growth during the juvenile period. Because of the likely cognitive demands underlying extractive foraging in this species and generally, the energetic demands for brain growth are likely to be higher in growing juveniles that are learning foraging skills. These differences in energetic demands to support brain growth as well explain the high relative ME intake in juveniles (which are at a stage of rapid brain development) than in lactating females.

My findings that Mchelelo group had higher intake of relative ME than Kitere group may be a function of habitat differences in quality and food availability, which are regulated by local climatic conditions and river flooding regimes (Kinnaird, 1992; Medley, 1993). Previous phenological and habitat surveys have demonstrated spatial and temporal variability in food resources among the forests occupied by the Tana River mangabeys (Homewood, 1978; Kinnaird, 1992, Wahungu, 1998; Kinnaird & Wieczkowski, 2008). Fruiting patterns greatly vary spatially and temporally (Kinnaird, 1992) resulting in variation in quantity and quality of diet among groups (Homewood, 1978). In addition, forest resource exploitation and

management regimes by humans within the Tana River National Primate Reserve also influence the local primate habitat quality (Medley, 1993; Moinde-Fockler et al., 2007). Areas actively under the protection of Kenya Wildlife Services, such as Mchelelo site, are more intact than forest areas managed by Ndera Community Conservancy or not managed at all, such as the Kitere forests. Consequently, well-managed areas of the reserve offer better food resources than poorly managed areas, and groups of mangabeys in the former areas have better access to food resources (Wieczkowski, 2003). In addition, groups in well-protected forest areas experience reduced food resource competition with humans (Kinnaird, 1992). Thus, Kitere's status as minimally protected and highly utilized by the local communities generates the sparse distribution of food resources and higher human-mangabey encounter rates. Consequently, mangabeys in the Kitere group are more likely to experience an increase in food searching time, low ingestion rates, human disturbances during feeding, and increase in both interspecific and intraspecific competition, compared to Mchelelo group. This scenario may translate to reduced food intake and subsequently low ME intake observed in the Kitere group subjects.

The group differences in ME intake reported here, and the purported underlying causes, are well-supported by evidence from a red-tailed monkey research on nutrient intake between groups utilizing disturbed and undisturbed habitats in Kibale National Park Uganda (Rode et al., 2006). This study established that the quality and quantity of food varied with habitat disturbance and that both variables interacted in influencing nutrient intake. Food availability in undisturbed habitats was three times higher than in disturbed habitats. Red-tailed monkey

groups in undisturbed habitats experienced higher ingestion rates, spent more time feeding, and less time in food searching than groups in disturbed habitats. Consequently, groups utilizing the intact habitats had higher nutrient intake particularly, NDF, crude protein, lipids, and minerals. Given that ME is an abstraction calculated from NDF, protein, lipids, and TNC, these results implies that the groups occupying undisturbed habitat also have higher intake of ME. This argument conforms to my findings that Mchelelo group, which utilizes a more protected habitat, had higher intake of ME obtained from NDF, fat, AP, and TNC (Fig. 2.11).

In conclusion, I found significant differences between juveniles and lactating females in dietary breadth preference, and relative metabolizable energy (ME) intake (i.e., intake per metabolic body mass-MBM). As I predicted (P1) juveniles had a narrower dietary breadth whose constituent foods were consumed less evenly than the lactating females. Juveniles sampled more food resources than lactating females but did not consume them evenly implying inexperience in foraging or use of trial and error strategy of feeding. Juveniles showed high selectivity of both preferred as well as for avoided foods than the lactating female. The majority of the preferred foods by both age classes, such as Ficus sycomorus and Agaricus sp., had high energetic returns. Thus, a high preference for preferred foods was attributed to the need to ingest more energy (i.e., energy maximization), while for avoided foods to lack of foraging experience. These findings are in line with the Need-to-Learn and Nutritional Constraint hypotheses that are have been suggested to explain sources of juvenile-adult foraging differences.

Metabolizable energy intake per MBM was higher in juveniles than in lactating females in both Kitere and Mchelelo groups. The findings supported my second prediction that due to higher energetic needs to support smaller bodies and to sustain growth, juveniles ingest more relative ME than lactating females in one group (Mchelelo) and ingested more relative ME than their counterparts in Kitere group. I attributed the group differences largely to variation in quantity and quality of the available foods primarily due to anthropogenically induced habitat disturbances in one site.

Appendices

Appendix 2.1. A checklist of the dietary composition of the Tana River mangabeys including all plant and faunal diets eaten by the two groups in Mchelelo and Kitere study sites (Life forms: T –tree, S –shrub, H –herb, G – grass, HP –hemi-parasite, C – climber, T-H – tree-shrub; Part consumed: LF – leaf, FR – fruit, FL – flower, SD – seed, SH –shoot, ST – stem, B – bark, RT –subterranean structures, DW –dead-wood, PT –Pith, PL –petiole, GM – gum, SS –stem sap, EX –exudate, NW –nut water, CR - crown)

Species	Family	Life form	Part eaten	Site
Abutilon mauritianum	Malvaceae	H	FL, FR, SD	Kitere & Mchelelo
Abutilon pannosum	Malvaceae	H	FL, FR, SD	Kitere
Afzelia quanzensis	Fabaceae	T	SD	Kitere & Mchelelo
Agaricus sp.	Agaricaceae	F	CR, ST	Kitere & Mchelelo
Alangium salviifolium	Cornaceae	T	LF, SD, FR	Kitere & Mchelelo
Albizia glaberrima	Fabaceae	T	LF, SD	Kitere & Mchelelo
Albizia gummifera	Fabaceae	T	SD	Kitere & Mchelelo
Antidesma venosum	Phyllanthaceae	T	LF, SH, FR, SD	Kitere & Mchelelo
Antidesma vogelianum	Phyllanthaceae	S	LF, SH, FR, SD	Kitere & Mchelelo
Aporrhiza paniculata	Sapindaceae	C	SD	Mchelelo
Barringtonia racemosa	Lecythidaceae	T	FL, FR	Kitere
Blighia unijugata	Sapindaceae	T	FR	Kitere & Mchelelo
Borassus aethiopum	Arecaceae	T	FR	Kitere & Mchelelo
Brachiaria subquadripara	Poaceae	G	LF, SD,	Kitere & Mchelelo
Cajanus cajan	Fabaceae	S	SD	Kitere
Capparis tomentosa	Capparaceae	C	LF	Kitere & Mchelelo
Carica papaya	Annonaceae	T, S	FR	Kitere
Cassia abbreviate	Fabaceae	T	SD	Kitere
Cassia afrofistula	Fabaceae	S	SD	Kitere & Mchelelo
Capparis erythrocarpus	Capparaceae	C	LF	Kitere

Species	Family	Life form	Part eaten	Site
Celtis philippensis	Ulmaceae	T	FR	Mchelelo
Chyntranthus obliquinervis	Sapindaceae	T	LF, FR, SH, SD, PT	Kitere & Mchelelo
Cissus petiolata	Vitaceae	Cr	LF, FR, SH, PT,	Kitere
Cissus rotundifolia	Vitaceae	C	LF, FR, SH, PT,	Kitere & Mchelelo
Citrus limon	Rutaceae	T, S	FR	Kitere & Mchelelo
Clerodendrum acerbianum	Lamiaceae	S	FR	Kitere
Cola clavata	Sterculiaceae	T	SD	Kitere
Combretum constrictum	Combretaceae	T, S	PT	Kitere
Commelina Africana	Commelinaceae	H	LF, FL, ST, RT	Kitere & Mchelelo
Commelina benghalensis	Commelinaceae	H	LF, FL, ST, RT	Kitere & Mchelelo
Commelina forskaolii	Commelinaceae	H	LF, FL, ST, RT	Kitere & Mchelelo
Commiphora campestris	Burseraceae	T, -S	LF	Kitere
Cordia goetzei	Bignoniaceae	T	FR, LF, PT, SH, B, DW	Kitere & Mchelelo
Cordia sinensis	Bignoniaceae	T	LF, FR	Kitere & Mchelelo
Croton menyhartii	Euphorbiaceae	S	FR	Kitere
Cynometra lukei	Fabaceae	T	LF, SD	Kitere & Mchelelo
Cyperus rotundus	Cyperaceae	S	LF	Kitere & Mchelelo
Digitaria velutina	Poaceae	G	FL	Kitere & Mchelelo
Diospyros mespiliformis	Ebenaceae	T	LF, FR, SD	Kitere & Mchelelo
Drypetes natalensis	Putranjivaceae	T	LF, FR, SD	Kitere & Mchelelo
Ficus bubu	Moraceae	T	FR	Kitere & Mchelelo
Ficus bussei	Moraceae	T	ST, FR	Kitere & Mchelelo
Ficus natalensis	Moraceae	T	FR	Kitere
Ficus sycomorus	Moraceae	T	FR, B, EX	Kitere & Mchelelo
Flagellaria guineensis	Flagellariaceae	C	LF, FR, SH, RT	Kitere & Mchelelo

Species	Family	Life form	Part eaten	Site
Flueggea virosa	Phyllanthaceae	S	LF	Kitere & Mchelelo
Garcinia livingstonei	Clusiaceae	T	FR, SD	Kitere & Mchelelo
Geophila repens	Rubiaceae	H	FT	Mchelelo
Grewia bicolor	Malvaceae	C	FR, LF	Kitere
Grewia densa	Malvaceae	C	FR, LF	Kitere & Mchelelo
Harrisonia abyssinica	Rutaceae	C	LF, FR, DW, RT	Kitere & Mchelelo
Hibiscus micranthus	Malvaceae	H	FR, FL, SD	Kitere & Mchelelo
Hunteria zeylanica	Apocynaceae	T	LF, SD, SH	Kitere & Mchelelo
Hyphaene compressa	Arecaceae	T	FR, NW, FL,	Kitere & Mchelelo
Hypoestes aristata	Acanthaceae	H	Lf, FL, FR	Kitere & Mchelelo
Indigofera schimperi	Fabaceae	S	LF	Kitere
Ipomea sp*.*	Euphorbiaceae	C	LF, SH	Mchelelo
Ixora narcissodora	Rubiaceae	S	B	Kitere
Justicia flava	Acanthaceae	H	LF, FR, FL	Kitere & Mchelelo
Keetia zanzibarica	Rubiaceae	C	LF, FR, SH	Kitere & Mchelelo
Kigelia africana	Bignoniaceae	T	LF	Kitere
Landolphia watsoniana	Apocynaceae	T- S	LF	Kitere & Mchelelo
Lannea schweinfurthii	Anacardiaceae	T	FR	Kitere & Mchelelo
Lawsonia inermis	Lythraceae	T-S	FR	Kitere
Lecaniodiscus fraxinifolius	Sapindaceae	T	LF, FR, SD,	Kitere & Mchelelo
Maerua calantha	Capparaceae	C	LF	Mchelelo
Majidea zanguebarica	Sapindaceae	T	SD	Kitere & Mchelelo
Mangifera indica	Anacardiaceae	T	LF, FR, FL, SD	Kitere
Mimusops fruticosa	Sapotaceae	T	FR	Kitere & Mchelelo
Mollugo nudcaulis	Molluginaceae	H	SD	Mchelelo
Momordica friesiorum	Cucurbitaceae	C	LF, FR, SD	Kitere & Mchelelo

Species	Family	Life form	Part eaten	Site
Momordica rostrata	Cucurbitaceae	C	FR, SD, PL	Kitere
Musa acuminata	Musaceae	H	FR	Kitere & Mchelelo
Oncoba spinosa	Salicaceae	T	LF, FR, FL, SD	Kitere & Mchelelo
Oryza sativa	Poaceae	G	SD	Kitere
Panicum trichocladum	Poaceae	G	LF, FL	Kitere
Passiflora foetida	Passifloraceae	C	FR	Mchelelo
Paullinia pinnata	Sapindaceae	C	FR, SD, PT	Kitere & Mchelelo
Pavetta sphaerobotrys	Rubiaceae	T	LF, FR	Kitere & Mchelelo
Phoenix reclinata	Arecaceae	T	LF, FR, ST, SD, SS, RT	Kitere & Mchelelo
Phyllanthus ovalifolius	Phyllanthaceae	S	LF	Kitere & Mchelelo
Polysphaeria multiflora	Rubiaceae	T	FR, LF, SD	Kitere & Mchelelo
Rauvolfia mombasiana	Apocynaceae	T	FR	Kitere & Mchelelo
Rhynchosia minima	Fabaceae	C	SD	Kitere
Rinorea elliptica	Violaceae	T-S	LF	Kitere & Mchelelo
Ruellia patula	Acanthaceae	H	FR, LF, SD	Kitere & Mchelelo
Rytigynia celastroides	Rubiaceae	S	LF	Kitere
Saba comorensis	Apocynaceae	C	FR, FL, LF, SD	Kitere & Mchelelo
Saccharum officinarum	Poaceae	G	ST	Kitere
Salacia erecta	Celastraceae	C	LF	Kitere & Mchelelo
Senegalia rovumae	Fabaceae	T	SD, GM	Mchelelo
Senna occidentalis	Fabaceae	S	SD	Kitere
Setaria verticillata	Poaceae	H	LF, FL	Kitere & Mchelelo
Sida ovate	Malvaceae	H	FR	Kitere & Mchelelo
Panicum trichocladum	Poaceae	G	ST	Kitere
Sorghum bicolor	Poaceae	G	SD	Kitere
Sorindeia madagascariensis	Anacardiaceae	T	LF, FR, FL, SD, DW	Kitere & Mchelelo

Species	Family	Life form	Part eaten	Site
Sporobolus sp.	Poaceae	G	LF, FL	Kitere & Mchelelo
Stenotaphrum dimidiatum	Poaceae	G	LF, FL	Kitere & Mchelelo
Sterculia appendiculata	Sterculiaceae	T	SD	Mchelelo
Synsepalum msolo	Sapotaceae	T	FR, SD, DW	Kitere & Mchelelo
Tamarindus indica	Fabaceae	T	LF, FR, FL	Kitere & Mchelelo
Tapinanthus zanzibarensis	Loranthaceae	HP	FR, FL	Kitere
Terminalia brevipes	Combretaceae	T	FR	Kitere & Mchelelo
Thespesia danis	Malvaceae	T	FR	Kitere & Mchelelo
Vachellia robusta	Fabaceae	T	LF, SD, FL, GM	Kitere & Mchelelo
Vigna radiata	Fabaceae	H	LF, SD	Kitere
Vigna unguiculata	Fabaceae	C	LF, SD	Kitere
Zea mays	Poaceae	G	SD	Kitere
Ziziphus pubescens	Rhamnaceae	T	FR, PT	Kitere & Mchelelo

Appendix 2.2: List of non-plant foods included in the diet of the Tana River mangabeys.

Organism/Food	Class/Order	Group	Study Site
Termites	Isoptera	Insect	Kitere & Mchelelo
Stingless honey bees larvae	Hymenoptera	Insect	Kitere & Mchelelo
Silver worms	Haplotaxida	Insect	Kitere & Mchelelo
Crickets	Orthoptera	Insect	Kitere & Mchelelo
Butterflies	Lepidoptera	Insect	Kitere & Mchelelo
Grasshoppers	Orthoptera	Insect	Kitere & Mchelelo
Black ants	Hymenoptera	Insect	Kitere & Mchelelo
Black Beetles	Coleoptera	Insect	Kitere & Mchelelo
Millipede	Spirobolida	Insect	Kitere & Mchelelo
Snails	Gastropod	Mollusk	Kitere & Mchelelo
Frogs	Anura	Amphibian	Kitere & Mchelelo
Lizards	Squamata	Reptile	Kitere & Mchelelo
Birds	Aves	Bird	Kitere & Mchelelo
Honey (bee product)	N/A	N/A	Kitere & Mchelelo

Appendix 2.3a: Overall dietary selectivity index among the Tana River mangabeys calculated from the annual relative abundance of food items in the diet and the abundance in the habitat using the Vanderploeg & Scavia's Electivity Index (E*) (data for both sites and age classes combined).

| Species | Relative Abundance (%) | | (E*) |
	Habitat	Diet	
Phoenix reclinata	8.06	21.11	-0.08
Ficus sycomorus	0.55	17.66	0.82
Vachellia robusta	0.88	9.01	0.54
Insects	1.00	5.40	0.27
Synsepalum msolo	0.44	4.70	0.55
Hyphaene compressa	1.67	4.55	-0.07
Agaricus sp.	0.04	4.22	0.94
Oncoba spinosa	2.99	2.89	-0.53
Sorindeia madagascariensis	9.87	2.70	-0.84
Diospyros mespiliformis	2.94	2.66	-0.55
Grewia densa	2.46	2.65	-0.48
Polysphaeria multiflora	22.33	2.31	-0.94
Brachiaria subquadripara	0.40	2.22	0.29
Mimusops fruticosa	3.03	1.89	-0.67
Pavetta sphaerobotrys	2.07	1.52	-0.62
Alangium salviifolium	1.09	1.42	-0.41
Mangifera indica	0.05	1.25	0.76
Garcinia livingstonei	2.02	1.24	-0.67
Cissus rotundifolia	0.08	1.19	0.66
Drypetes natalensis	5.66	0.97	-0.90
Lecaniodiscus fraxinifolius	10.62	0.95	-0.94
Saba comorensis	0.16	0.70	0.18
Momordica trifoliata	0.04	0.63	0.66
Antidesma venosum	0.08	0.63	0.42
Harrisonia abyssinica	0.47	0.60	-0.42
Borassus aethiopum	0.58	0.56	-0.52
Ficus natalensis	0.07	0.51	0.42
Thespesia danis	1.71	0.34	-0.88
Cordia goetzei	1.06	0.32	-0.82
Cordia sinensis	0.28	0.32	-0.46
Cassia abbreviate	0.08	0.27	0.05
Flagellaria guineensis	0.54	0.26	-0.73
Tamarindus indica	0.10	0.24	-0.13
Chytranthus obliquinervis	2.90	0.22	-0.95
Ficus bubu	0.02	0.18	0.52
Keetia zanzibarica	0.77	0.15	-0.88

	Relative Abundance (%)		
Species	**Habitat**	**Diet**	**(E*)**
Albizia gummifera	0.64	0.15	-0.86
Hunteria zeylanica	2.92	0.15	-0.97
Lannea schweinfurthii	0.07	0.11	-0.32
Flueggea virosa	0.49	0.07	-0.91
Ruellia patula	0.02	0.07	0.09
Paullinia pinnata	0.04	0.06	-0.34
Commelina forskaolii	0.09	0.06	-0.63
Setaria verticillata	0.15	0.06	-0.76
Rauvolfia mombasiana	0.16	0.06	-0.78
Sterculia appendiculata	0.05	0.06	-0.41
Justicia flava	0.07	0.05	-0.58
Ziziphus pubescence	0.99	0.05	-0.97
Commelina africana	0.05	0.03	-0.62
Hibiscus macranthus	0.36	0.03	-0.95
Kigelia africana	0.04	0.03	-0.58
Cissus petiolata	0.13	0.02	-0.88
Rhynchosia minima	0.01	0.02	0.15
Ficus bussei	0.00	0.02	-1.00
Apporrhiza paniculata	0.05	0.02	-0.72
Baragtonia racemosa	0.00	0.02	-1.00
Panicum trichocladum	0.01	0.02	0.03
Cassia afrofistula	0.07	0.02	-0.84
Cynometra lukei	0.04	0.01	-0.80
Antidesma vogelianum	0.28	0.01	-0.97
Abutilon mauritianum	0.11	0.01	-0.92
Afzelia quanzensis	0.06	0.01	-0.86
Indigofera schimperi	0.34	0.01	-0.97
Majedia zanguebarica	0.12	0.01	-0.93
Mollugo nudcaulis	0.00	0.01	-1.00
Commiphora campestris	0.01	0.01	-0.58
Stenotaphrum dimidiatum	0.02	0.01	-0.76
Terminalia brevipes	0.84	0.01	-0.99
Commelina bangalensis	0.01	0.01	-0.31
Passiflora foetida	0.02	0.01	-0.70
Capparis tomentosa	0.24	0.01	-0.97
Citrus limon	0.01	0.01	-0.59
Ocimum americanum	0.01	0.01	-0.59
Phyllanthus ovalifolius	0.22	0.01	-0.97
Senegalia rovumae	0.01	0.01	-0.32
Abutilon pannosum	0.13	0.00	-0.98
Blighia unijugata	0.37	0.00	-0.99

| Species | Relative Abundance (%) | | (E*) |
	Habitat	Diet	
Calcasia orietntalis	0.27	0.00	-0.99
Capparis erythrocarpus	0.22	0.00	-0.99
Cassia orientalis	0.00	0.00	-1.00
Clerodendrum acerbianum	0.44	0.00	-0.99
Cola clavata	1.72	0.00	-1.00
Combretum botryiosum	0.00	0.00	-1.00
Combretum brevipes	0.05	0.00	-0.94
Grewia stulhmanii	0.14	0.00	-0.98
Lawsonia inermis	0.11	0.00	-0.97
Rytigynia celastroides	0.00	0.00	-1.00
Sida ovate	0.01	0.00	-0.76
Sporobolus helvolus	0.01	0.00	-0.58
Tapanensis sasimbariensis	0.00	0.00	-1.00
Celtis philippensis	0.20	0.00	-0.99
Croton meyhartii	0.19	0.00	-0.98
Cyperus rotundus	0.20	0.00	-0.98
Ipomea sp.	0.01	0.00	-0.77
Landolphia uatsoniana	0.01	0.00	-0.77
Maerua cantha	0.08	0.00	-0.96
Sporobolus sp.	0.00	0.00	-1.00

Appendix 2.3b: General age class dietary selectivity index among the Tana River mangabeys calculated from the annual relative abundance of foods in the diet and the abundance in the habitat using the Vanderploeg & Scavia's Electivity Index (E*).

Species	Relative Abundance (%)			(E*)	
	Habitat	Juv. Diet	L.Fem diet	Juv	L. Fem
Phoenix reclinata	8.06	21.06	21.22	-0.12	-0.25
Ficus sycomorus	0.55	17.62	17.82	0.81	0.76
Vachellia robusta	0.88	9.13	8.68	0.52	0.38
Insects	1.00	5.19	6.00	0.22	0.15
Synsepalum msolo	0.44	4.61	4.94	0.52	0.43
Hyphaene compressa	1.67	4.40	4.95	-0.11	-0.20
Agaricus sp.	0.04	4.12	4.51	0.93	0.92
Oncoba spinosa	2.99	2.69	3.41	-0.57	-0.59
Sorindeia madagascariensis	9.87	2.68	2.77	-0.85	-0.88
Diospyros mespiliformis	2.94	2.61	2.78	-0.58	-0.65
Grewia densa	2.46	2.71	2.49	-0.50	-0.63
Polysphaeria multiflora	22.33	2.49	1.82	-0.93	-0.96
Brachiaria subquadripara	0.40	2.17	2.32	0.25	0.14
Mimusops fruticosa	3.03	1.92	1.80	-0.68	-0.76
Pavetta sphaerobotrys	2.07	1.60	1.30	-0.62	-0.75
Alangium salviifolium	1.09	1.39	1.51	-0.44	-0.52
Mangifera indica	0.05	1.31	1.10	0.76	0.64
Garcinia livingstonei	2.02	1.19	1.38	-0.70	-0.73
Cissus rotundifolia	0.08	1.21	1.12	0.65	0.53
Drypetes natalensis	5.66	1.00	0.90	-0.90	-0.93
Lecaniodiscus fraxinifolius	10.62	1.00	0.82	-0.94	-0.97
Saba comorensis	0.16	0.78	0.47	0.20	-0.19
Momordica trifoliate	0.04	0.58	0.78	0.61	0.61
Antidesma venosum	0.08	0.65	0.59	0.40	0.22
Harrisonia abyssinica	0.47	0.64	0.50	-0.42	-0.61
Borassus aethiopum	0.58	0.58	0.52	-0.54	-0.67
Ficus natalensis	0.07	0.49	0.54	0.39	0.30
Thespesia danis	1.71	0.38	0.23	-0.87	-0.94
Cordia goetzei	1.06	0.38	0.18	-0.80	-0.93
Cordia sinensis	0.28	0.36	0.21	-0.44	-0.70
Cassia abbreviate	0.08	0.31	0.18	0.08	-0.32
Flagellaria guineensis	0.54	0.28	0.21	-0.73	-0.84
Tamarindus indica	0.10	0.29	0.12	-0.07	-0.57
Chytranthus obliquinervis	2.90	0.20	0.27	-0.96	-0.96
Ficus bubu	0.02	0.20	0.11	0.54	0.15

Species	Relative Abundance (%)			(E*)	
	Habitat	Juv. Diet	L.Fem diet	Juv	L. Fem
Keetia zanzibarica	0.77	0.18	0.09	-0.87	-0.95
Albizia gummifera	0.64	0.15	0.14	-0.87	-0.90
Hunteria zeylanica	2.92	0.18	0.07	-0.96	-0.99
Lannea schweinfurthii	0.07	0.13	0.09	-0.31	-0.57
Flueggea virosa	0.49	0.06	0.09	-0.93	-0.92
Ruellia patula	0.02	0.08	0.04	0.14	-0.38
Paullinia pinnata	0.04	0.06	0.07	-0.38	-0.45
Commelina forskaolii	0.09	0.03	0.14	-0.80	-0.47
Setaria verticillata	0.15	0.07	0.05	-0.76	-0.85
Rauvolfia mombasiana	0.16	0.07	0.04	-0.76	-0.90
Sterculia appendiculata	0.05	0.08	0.02	-0.34	-0.84
Justicia flava	0.07	0.05	0.05	-0.60	-0.69
Ziziphus pubescence	0.99	0.05	0.05	-0.97	-0.98
Commelina Africana	0.05	0.01	0.09	-0.84	-0.41
Hibiscus macranthus	0.36	0.03	0.02	-0.94	-0.98
Kigelia Africana	0.04	0.03	0.02	-0.55	-0.80
Cissus petiolata	0.13	0.03	0.02	-0.87	-0.94
Rhynchosia minima	0.01	0.03	0.00	0.27	-1.00
Ficus bussei	0.00	0.03	0.02	-1.00	-1.00
Apporrhiza paniculata	0.05	0.03	0.00	-0.66	-1.00
Baragtonia racemosa	0.00	0.01	0.04	-1.00	-1.00
Panicum trichocladum	0.01	0.03	0.00	0.17	-1.00
Cassia afrofistula	0.07	0.03	0.00	-0.79	-1.00
Cynometra lukei	0.04	0.01	0.02	-0.82	-0.82
Antidesma vogelianum	0.28	0.01	0.02	-0.97	-0.97
Abutilon mauritianum	0.11	0.02	0.00	-0.90	-1.00
Afzelia quanzensis	0.06	0.02	0.00	-0.82	-1.00
Indigofera schimperi	0.34	0.01	0.02	-0.98	-0.98
Majedia zanguebarica	0.12	0.02	0.00	-0.91	-1.00
Mollugo nudcaulis	0.00	0.01	0.04	-1.00	-1.00
Commiphora campestris	0.01	0.00	0.04	-1.00	-0.20
Stenotaphrum dimidiatum	0.02	0.01	0.00	-0.70	-1.00
Terminalia brevipes	0.84	0.01	0.00	-0.99	-1.00
Commelina bangalensis	0.01	0.01	0.00	-0.19	-1.00
Passiflora foetida	0.02	0.01	0.00	-0.63	-1.00
Capparis tomentosa	0.24	0.01	0.00	-0.97	-1.00
Citrus limon	0.01	0.01	0.00	-0.51	-1.00
Ocimum americanum	0.01	0.01	0.02	-0.72	-0.49
Phyllanthus ovalifolius	0.22	0.01	0.02	-0.98	-0.96
Senegalia rovumae	0.01	0.01	0.02	-0.51	-0.19

Species	Relative Abundance (%)			(E*)	
	Habitat	Juv. Diet	L.Fem diet	Juv	L. Fem
Abutilon pannosum	0.13	0.00	0.02	-1.00	-0.94
Blighia unijugata	0.37	0.01	0.00	-0.99	-1.00
Calcasia orietntalis	0.27	0.01	0.00	-0.98	-1.00
Capparis erythrocarpus	0.22	0.01	0.00	-0.98	-1.00
Cassia orientalis	0.00	0.01	0.00	-1.00	-1.00
Clerodendrum acerbianum	0.44	0.01	0.00	-0.99	-1.00
Cola clavata	1.72	0.01	0.00	-1.00	-1.00
Combretum botryiosum	0.00	0.01	0.00	-1.00	-1.00
Combretum brevipes	0.05	0.01	0.00	-0.93	-1.00
Grewia stulhmanii	0.14	0.01	0.00	-0.97	-1.00
Lawsonia inermis	0.11	0.00	0.02	-1.00	-0.93
Rytigynia celastroides	0.00	0.01	0.00	-1.00	-1.00
Sida ovate	0.01	0.01	0.00	-0.70	-1.00
Sporobolus helvolus	0.01	0.00	0.02	-1.00	-0.20
Tapanensis sasimbariensis	0.00	0.01	0.00	-1.00	-1.00
Celtis philippensis	0.20	0.01	0.00	-0.98	-1.00
Croton meyhartii	0.19	0.01	0.00	-0.98	-1.00
Cyperus rotundus	0.20	0.01	0.00	-0.98	-1.00
Ipomea sp.	0.01	0.01	0.00	-0.72	-1.00
Landolphia uatsoniana	0.01	0.01	0.00	-0.72	-1.00
Maerua canthi	0.08	0.00	0.02	-1.00	-0.90
Sporobolus sp.	0.00	0.01	0.00	-1.00	-1.00

Appendix 2.4. Habitat and dietary profile of Kitere study group: Relative abundance of food species in the habitat (% of total number of individuals of each species relative to individuals of all species encountered) and in diet (% of number of times each species was eaten relative total number of times all the species were eaten) of the juvenile and lactating females and (E* is the Vanderploeg & Scavia's Electivity Index).

Species	Abundance in the Habitat & in Diet (%)			Electivity Index (E*)	
	Habitat	Juv	L.Fem	Juv	L. Fem
Phoenix reclinata	8.72	25.94	27.08	-0.12	-0.28
Ficus sycomorus	0.86	17.20	16.24	0.68	0.55
Synsepalum msolo	0.64	7.71	8.24	0.52	0.40
Vachellia robusta	1.06	4.97	4.90	0.11	-0.09
Diospyros mespiliformis	4.11	4.31	4.58	-0.56	-0.67
Mimusops fruticose	4.11	3.19	3.16	-0.66	-0.76
Agaricus sp.	0.03	2.69	2.84	0.93	0.90
Oncoba spinose	1.20	2.42	3.02	-0.30	-0.38
Polysphaeria multiflora	18.76	2.74	2.13	-0.93	-0.96
Grewia densa	2.88	2.62	2.27	-0.61	-0.75
Mangifera indica	0.12	2.62	2.20	0.70	0.53
Brachiaria subquadripara	0.83	2.25	2.91	-0.16	-0.22
Lecaniodiscus fraxinifolius	14.90	1.89	1.63	-0.93	-0.96
Cissus rotundifolia	0.17	1.53	1.78	0.40	0.30
Garcinia livingstonei	2.66	1.36	1.53	-0.76	-0.81
Momordica trifoliate	0.08	1.15	1.56	0.58	0.56
Sorindeia madagascariensis	5.66	1.18	1.24	-0.90	-0.92
Alangium salviifolium	0.60	1.20	1.17	-0.31	-0.48
Antidesma venosum	0.17	1.21	1.14	0.30	0.08
Harrisonia abyssinica	0.71	1.22	1.00	-0.37	-0.60
Thespesia danis	3.63	0.77	0.46	-0.89	-0.96
Drypetes natalensis	3.93	0.70	0.53	-0.91	-0.95
Cordia goetzei	1.48	0.64	0.36	-0.80	-0.92
Cassia abbreviate	0.15	0.61	0.36	0.05	-0.39
Cordia sinensis	0.60	0.60	0.36	-0.58	-0.81
Flagellaria guineensis	1.19	0.54	0.43	-0.78	-0.88
Borassus aethiopum	1.28	0.46	0.60	-0.83	-0.84
Chytranthus obliquinervis	2.53	0.24	0.32	-0.95	-0.96
Saba comorensis	0.16	0.26	0.21	-0.39	-0.61
Albizia gummifera	0.01	0.22	0.25	0.63	0.54
Lannea schweinfurthii	0.05	0.25	0.18	0.11	-0.25
Tamarindus indica	0.08	0.58	0.25	0.32	-0.28

Species	Abundance in the Habitat & in Diet (%)			Electivity Index (E*)	
	Habitat	Juv	L.Fem	Juv	L. Fem
Paullinia pinnata	0.08	0.13	0.14	-0.42	-0.52
Flueggea virosa	0.86	0.10	0.18	-0.94	-0.93
Hyphaene compressa	0.03	0.10	0.14	-0.02	-0.02
Commelina forskaolii	0.01	0.04	0.21	-0.09	0.48
Justicia flava	0.12	0.08	0.04	-0.69	-0.90
Hibiscus macranthus	0.52	0.07	0.04	-0.93	-0.98
Kigelia Africana	0.08	0.07	0.04	-0.63	-0.85
Cissus petiolate	0.01	0.06	0.04	0.05	-0.35
Commelina Africana	0.08	0.01	0.14	-0.91	-0.52
Ficus natalensis	0.09	0.04	0.07	-0.79	-0.76
Rhynchosia minima	0.00	0.07	0.00	-1.00	-1.00
Setaria verticillata	0.13	0.06	0.04	-0.80	-0.91
Baragtonia racemosa	0.00	0.03	0.07	-1.00	-1.00
Keetia zanzibarica	0.86	0.06	0.00	-0.97	-1.00
Panicum trichocladum	0.01	0.06	0.00	0.05	-1.00
Cassia afrofistula	0.16	0.04	0.00	-0.87	-1.00
Ruellia patula	0.01	0.04	0.00	-0.09	-1.00
Commiphora campestris	0.03	0.00	0.07	-1.00	-0.35
Cynometra lukei	0.04	0.03	0.00	-0.69	-1.00
Ficus bubu	0.01	0.03	0.00	-0.29	-1.00
Ficus bussei	0.00	0.01	0.04	-1.00	-1.00
Hunteria zeylanica	0.58	0.03	0.00	-0.97	-1.00
Stenotaphrum dimidiatum	0.04	0.03	0.00	-0.69	-1.00
Terminalia brevipes	1.31	0.03	0.00	-0.99	-1.00
Abutilon pannosum	0.12	0.00	0.04	-1.00	-0.90
Antidesma vogelianum	0.17	0.00	0.04	-1.00	-0.93
Apporrhiza paniculata	0.00	0.01	0.00	-1.00	-1.00
Blighia unijugata	0.39	0.01	0.00	-0.98	-1.00
Calcasia orietntalis	0.52	0.01	0.00	-0.99	-1.00
Capparis erythrocarpus	0.44	0.01	0.00	-0.98	-1.00
Cassia orientalis	0.00	0.01	0.00	-1.00	-1.00
Clerodendrum acerbianum	0.99	0.01	0.00	-0.99	-1.00
Cola clavata	3.77	0.01	0.00	-1.00	-1.00
Combretum brevipes	0.08	0.01	0.00	-0.91	-1.00
Commelina bangalensis	0.00	0.01	0.00	-1.00	-1.00
Grewia stulhmanii	0.16	0.01	0.00	-0.96	-1.00
Lawsonia inermis	0.07	0.00	0.04	-1.00	-0.83
Combretum botryiosum	0.00	0.01	0.00	-1.00	-1.00

Species	Abundance in the Habitat & in Diet (%)			Electivity Index (E*)	
	Habitat	Juv	L.Fem	Juv	L. Fem
Passiflora foetida	0.04	0.01	0.00	-0.83	-1.00
Rauvolfia mombasiana	0.01	0.01	0.00	-0.57	-1.00
Rytigynia celastroides	0.00	0.01	0.00	-1.00	-1.00
Sida ovata	0.03	0.01	0.00	-0.76	-1.00
Sporobolus helvolus	0.01	0.00	0.04	-1.00	-0.35
Tapanensis sasimbariensis	0.00	0.01	0.00	-1.00	-1.00
Abutilon mauritianum	0.16	0.00	0.00	-1.00	-1.00
Afzelia quanzensis	0.00	0.00	0.00	-1.00	-1.00
Capparis tomentosa	0.29	0.00	0.00	-1.00	-1.00
Celtis philippensis	0.00	0.00	0.00	-1.00	-1.00
Citrus limon	0.03	0.00	0.00	-1.00	-1.00
Croton meyhartii	0.43	0.00	0.00	-1.00	-1.00
Cyperus rotundus	0.01	0.00	0.00	-1.00	-1.00
Indigofera schimperi	0.72	0.00	0.00	-1.00	-1.00
Ipomea sp.	0.01	0.00	0.00	-1.00	-1.00
Landolphia uatsoniana	0.01	0.00	0.00	-1.00	-1.00
Maerua canthi	0.17	0.00	0.00	-1.00	-1.00
Majedia zanguebarica	0.01	0.00	0.00	-1.00	-1.00
Mollugo nudcaulis	0.00	0.00	0.00	-1.00	-1.00
Ocimum americanum	0.03	0.00	0.00	-1.00	-1.00
Pavetta sphaerobotrys	1.11	0.00	0.00	-1.00	-1.00
Phyllanthus ovalifolius	0.47	0.00	0.00	-1.00	-1.00
Senegalia rovumae	0.01	0.00	0.00	-1.00	-1.00
Sporobolus sp.	0.00	0.00	0.00	-1.00	-1.00
Sterculia appendiculata	0.01	0.00	0.00	-1.00	-1.00
Ziziphus pubescence	0.05	0.00	0.00	-1.00	-1.00
Ziziphus pubescence	0.05	0.00	0.00	0.00	0.00
Insects	1.20	3.31	3.55	-0.16	-0.31

Appendix 2.5: Habitat and dietary profile of Mchelelo study group: Relative abundance of food species in the habitat (% of total number of individuals of each species relative to individuals of all species encountered) and in diet (% of number of times each species was eaten relative total number of times all the species were eaten) of the juvenile and lactating females and (E*, the Vanderploeg & Scavia's Electivity Index).

Species	Abundance in the Habitat & in Diet (%)			Electivity Index (E*)	
	Habitat	Juv	L.Fem	Juv	L.Fem
Ficus sycomorus	0.31	18.04	19.40	0.81	0.77
Phoenix reclinata	7.52	16.19	15.35	-0.49	-0.60
Vachellia robusta	0.73	13.30	12.46	0.49	0.35
Hyphaene compressa	3.01	8.71	9.75	-0.37	-0.44
Agaricus sp.	0.05	5.55	6.18	0.88	0.86
Sorindeia madagascariensis	13.30	4.17	4.30	-0.91	-0.92
Oncoba spinosa	4.45	2.97	3.79	-0.81	-0.81
Pavetta sphaerobotrys	2.86	3.20	2.60	-0.70	-0.80
Grewia densa	2.13	2.81	2.71	-0.65	-0.73
Polysphaeria multiflora	25.24	2.24	1.52	-0.97	-0.99
Brachiaria subquadripara	0.04	2.09	1.73	0.77	0.65
Alangium salviifolium	1.48	1.58	1.84	-0.71	-0.74
Synsepalum msolo	0.27	1.50	1.63	-0.07	-0.16
Drypetes natalensis	7.06	1.30	1.26	-0.94	-0.96
Saba comorensis	0.15	1.30	0.72	0.15	-0.27
Garcinia livingstonei	1.49	1.02	1.23	-0.80	-0.82
Ficus natalensis	0.04	0.95	1.01	0.55	0.47
Diospyros mespiliformis	2.00	0.91	0.98	-0.87	-0.89
Cissus rotundifolia	0.00	0.88	0.47	-1.00	-1.00
Borassus aethiopum	0.01	0.70	0.43	0.82	0.65
Mimusops fruticosa	2.15	0.65	0.43	-0.91	-0.95
Ficus bubu	0.02	0.38	0.22	0.46	0.09
Hunteria zeylanica	4.83	0.32	0.14	-0.98	-0.99
Keetia zanzibarica	0.70	0.30	0.18	-0.87	-0.94
Chytranthus obliquinervis	3.21	0.17	0.22	-0.98	-0.98
Sterculia appendiculata	0.08	0.16	0.04	-0.51	-0.89
Rauvolfia mombasiana	0.28	0.13	0.07	-0.86	-0.94

Species	Abundance in the Habitat & in Diet (%)			Electivity Index (E*)	
	Habitat	Juv	L.Fem	Juv	L.Fem
Cordia sinensis	0.01	0.12	0.07	0.26	-0.11
Ruellia patula	0.02	0.12	0.07	-0.08	-0.43
Ziziphus pubescence	1.75	0.10	0.11	-0.98	-0.99
Cordia goetzei	0.71	0.12	0.00	-0.95	-1.00
Antidesma venosum	0.01	0.09	0.04	0.14	-0.43
Lecaniodiscus fraxinifolius	7.12	0.10	0.00	-1.00	-1.00
Setaria verticillata	0.16	0.08	0.07	-0.86	-0.90
Albizia gummifera	1.16	0.08	0.04	-0.98	-0.99
Apporrhiza paniculata	0.09	0.05	0.00	-0.83	-1.00
Commelina forskaolii	0.15	0.03	0.07	-0.95	-0.89
Harrisonia abyssinica	0.27	0.05	0.00	-0.94	-1.00
Justicia flava	0.02	0.03	0.07	-0.68	-0.43
Abutilon mauritianum	0.08	0.04	0.00	-0.85	-1.00
Afzelia quanzensis	0.11	0.04	0.00	-0.89	-1.00
Ficus bussei	0.00	0.04	0.00	-1.00	-1.00
Indigofera schimperi	0.02	0.03	0.04	-0.68	-0.67
Majedia zanguebarica	0.21	0.04	0.00	-0.94	-1.00
Mollugo nudcaulis	0.00	0.01	0.07	-1.00	-1.00
Antidesma vogelianum	0.36	0.03	0.00	-0.98	-1.00
Capparis tomentosa	0.20	0.03	0.00	-0.96	-1.00
Citrus limon	0.00	0.03	0.00	-1.00	-1.00
Commelina Africana	0.02	0.01	0.04	-0.83	-0.67
Flueggea virosa	0.19	0.03	0.00	-0.96	-1.00
Ocimum americanum	0.00	0.01	0.04	-1.00	-1.00
Phyllanthus ovalifolius	0.01	0.01	0.04	-0.68	-0.43
Senegalia rovumae	0.00	0.01	0.04	-1.00	-1.00
Cassia afrofistula	0.00	0.01	0.00	-1.00	-1.00
Celtis philippensis	0.37	0.01	0.00	-0.99	-1.00
Commelina bangalensis	0.01	0.01	0.00	-0.68	-1.00
Croton meyhartii	0.00	0.01	0.00	-1.00	-1.00
Cynometra lukei	0.04	0.00	0.04	-1.00	-0.82
Cyperus rotundus	0.35	0.01	0.00	-0.99	-1.00
Flagellaria guineensis	0.01	0.01	0.00	-0.68	-1.00
Ipomea sp.	0.01	0.01	0.00	-0.68	-1.00
Landolphia uatsoniana	0.01	0.01	0.00	-0.68	-1.00
Maerua canthi	0.00	0.00	0.04	-1.00	-1.00
Passiflora foetida	0.00	0.01	0.00	-1.00	-1.00
Sporobolus sp.	0.00	0.01	0.00	-1.00	-1.00

Species	Abundance in the Habitat & in Diet (%)			Electivity Index (E*)	
	Habitat	Juv	L.Fem	Juv	L.Fem
Abutilon pannosum	0.14	0.00	0.00	-1.00	-1.00
Baragtonia racemosa	0.00	0.00	0.00	-1.00	-1.00
Blighia unijugata	0.36	0.00	0.00	-1.00	-1.00
Calcasia orietntalis	0.07	0.00	0.00	-1.00	-1.00
Capparis erythrocarpus	0.03	0.00	0.00	-1.00	-1.00
Cassia abbreviate	0.02	0.00	0.00	-1.00	-1.00
Cassia orientalis	0.00	0.00	0.00	-1.00	-1.00
Cissus petiolata	0.22	0.00	0.00	-1.00	-1.00
Clerodendrum acerbianum	0.00	0.00	0.00	-1.00	-1.00
Cola clavata	0.04	0.00	0.00	-1.00	-1.00
Combretum botryiosum	0.00	0.00	0.00	-1.00	-1.00
Combretum brevipes	0.03	0.00	0.00	-1.00	-1.00
Commiphora campestris	0.00	0.00	0.00	-1.00	-1.00
Grewia stulhmanii	0.13	0.00	0.00	-1.00	-1.00
Hibiscus macranthus	0.23	0.00	0.00	-1.00	-1.00
Kigelia Africana	0.00	0.00	0.00	-1.00	-1.00
Lannea schweinfurthii	0.09	0.00	0.00	-1.00	-1.00
Lawsonia inermis	0.14	0.00	0.00	-1.00	-1.00
Mangifera indica	0.00	0.00	0.00	-1.00	-1.00
Momordica trifoliate	0.01	0.00	0.00	-1.00	-1.00
Panicum trichocladum	0.00	0.00	0.00	-1.00	-1.00
Paullinia pinnata	0.01	0.00	0.00	-1.00	-1.00
Rhynchosia minima	0.01	0.00	0.00	-1.00	-1.00
Rytigynia celastroides	0.00	0.00	0.00	-1.00	-1.00
Sida ovate	0.00	0.00	0.00	-1.00	-1.00
Sporobolus helvolus	0.00	0.00	0.00	-1.00	-1.00
Stenotaphrum dimidiatum	0.01	0.00	0.00	-1.00	-1.00
Tamarindus indica	0.12	0.00	0.00	-1.00	-1.00
Tapanensis sasimbariensis	0.00	0.00	0.00	-1.00	-1.00
Terminalia brevipes	0.46	0.00	0.00	-1.00	-1.00
Thespesia danis	0.14	0.00	0.00	-1.00	-1.00
Insects	0.83	7.06	8.45	0.15	0.10

Appendix 2.6. Figures showing the normality test of the log transformed data used in GLMMs to evaluate ME intake between juveniles and lactating females in the two study sites. Tests were with the data in model 1 before using the data in all other models.
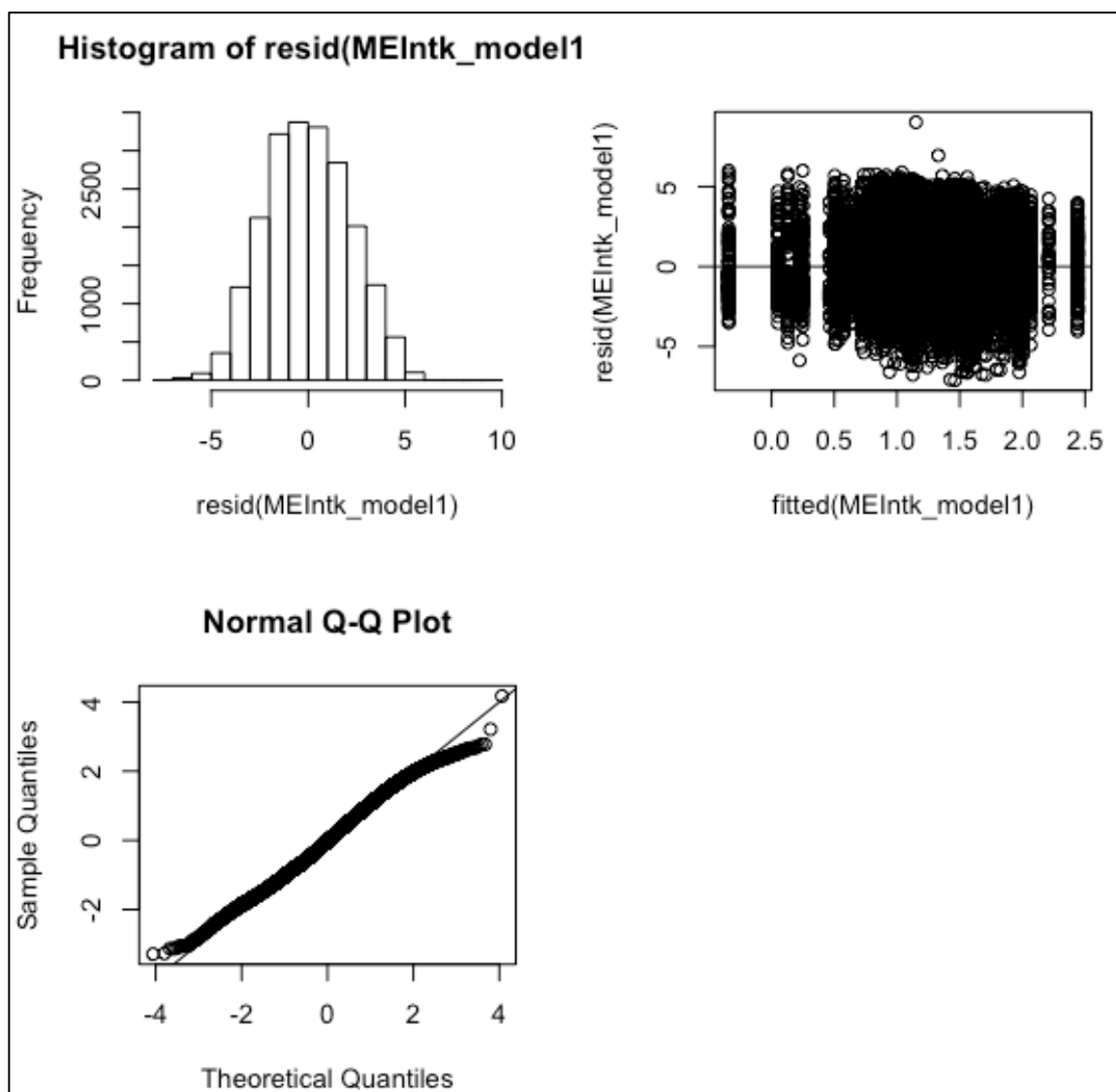
Figures of Log-transformed data of the Metabolizable energy used for analysis of the ME intake.

Appendix 2.7. Mean time spent feeding (Min) and mean Metabolizable energy (ME) gained (Kcal/g) per feeding bout for both plant and faunal diets of the juveniles (Juv) and lactating females (L.fem) in Kitere and Mchelelo study groups combined.

Species	Mean time spent in feeding (Min)/bout				Mean ME gain (Kcal/g)/bout			
	Juv.	SEM	L. fem	SEM	Juv.	SEM	L. fem	SEM
Phoenix reclinata	2.49	0.05	2.43	0.09	3.49	0.13	3.50	0.20
Ficus sycomorus	2.64	0.05	2.52	0.08	23.15	0.48	24.42	0.84
Vachellia robusta	1.61	0.06	1.60	0.09	7.87	0.36	7.78	0.44
Insects	1.03	0.05	0.97	0.06	1.96	0.13	1.94	0.21
Synsepalum msolo	2.03	0.09	1.82	0.16	2.59	0.24	2.53	0.40
Hyphaene compressa	2.63	0.35	2.73	0.52	15.77	3.21	19.21	5.69
Agaricus sp.	1.37	0.07	1.45	0.11	12.79	0.63	11.37	0.86
Grewia densa	1.90	0.11	1.88	0.18	1.60	0.16	1.39	0.19
Oncoba spinosa	2.23	0.13	2.50	0.20	20.07	1.16	26.66	1.92
Sorindeia madagascariensis	1.94	0.14	1.87	0.23	2.76	0.29	2.77	0.54
Diospyros mespiliformis	2.94	0.18	3.22	0.31	2.32	0.20	2.42	0.44
Polysphaeria multiflora	2.05	0.14	2.13	0.27	1.92	0.22	1.88	0.45
Brachiaria subquadripara	1.50	0.10	1.48	0.16	0.86	0.07	0.94	0.21
Mimusops fruticosa	1.97	0.20	2.13	0.33	30.09	2.28	28.58	4.47
Pavetta sphaerobotrys	2.08	0.09	2.12	0.15	0.35	0.03	0.26	0.03
Alangium salviifolium	1.39	0.10	1.31	0.15	2.63	0.24	3.29	0.51
Mangifera indica	1.28	0.08	1.10	0.11	5.18	0.42	5.66	0.68
Cissus rotundifolia	1.42	0.12	1.05	0.20	3.38	0.36	4.45	0.81
Garcinia livingstonei	2.22	0.17	2.36	0.27	6.25	0.55	8.02	1.67
Lecaniodiscus fraxinifolius	2.08	0.31	1.16	0.10	2.43	0.39	1.38	0.32
Drypetes natalensis	1.81	0.17	1.60	0.34	2.05	0.26	1.98	0.24
Saba comorensis	2.64	0.34	3.49	0.57	9.69	2.69	7.14	1.84
Antidesma venosum	3.79	0.76	1.27	0.19	1.36	0.53	0.85	0.21
Harrisonia abyssinica	1.56	0.42	0.77	0.09	2.66	0.48	1.27	0.24
Borassus aethiopum	4.44	0.42	4.18	0.58	24.97	2.05	30.55	3.55
Momordica trifoliata	0.83	0.08	1.01	0.11	8.19	0.81	7.33	0.94
Ficus natalensis	2.35	0.69	1.79	0.54	1.48	0.28	1.40	0.43
Thespesia danis	0.64	0.08	0.77	0.18	1.49	0.20	2.12	0.69
Cordia goetzei	2.05	0.59	0.63	0.23	1.01	0.24	0.65	0.21
Cordia sinensis	2.95	0.62	2.83	0.88	1.06	0.32	0.64	0.29
Cassia abbreviata	1.50	0.12	1.50	0.37	1.16	0.27	1.20	0.25
Tamarindus indica	0.54	0.07	0.79	0.23	3.40	1.05	0.30	0.08
Flagellaria guineensis	1.43	0.09	1.06	0.13	1.28	0.04	0.27	0.05
Chytranthus obliquinervis	1.32	0.26	1.31	0.30	1.63	0.65	1.08	0.29
Ficus bubu	3.04	0.33	1.82	0.57	11.52	1.69	8.13	2.55
Keetia zanzibarica	2.32	0.55	1.17	0.31	1.37	0.25	0.80	0.16

Species	Mean time spent in feeding (Min)/bout				Mean ME gain (Kcal/g)/bout			
	Juv.	SEM	L. fem	SEM	Juv.	SEM	L. fem	SEM
Hunteria zeylanica	2.07	0.70	0.78	0.50	1.69	0.76	0.53	0.08
Albizia gummifera	1.99	0.60	1.68	0.21	5.53	1.47	5.00	2.15
Lannea schweinfurthii	0.74	0.15	0.75	0.21	3.24	0.59	1.66	0.42
Ruellia patula	3.26	0.95	0.90	0.70	0.78	0.33	0.23	0.05
Sterculia appendiculata	2.14	0.36	2.30	0.00	4.25	1.16	1.60	0.00
Rauvolfia mombasiana	0.83	0.19	1.34	0.50	1.35	0.09	0.37	0.19
Setaria verticillata	0.79	0.20	0.76	0.30	0.54	0.31	0.44	0.11
Paullinia pinnata	0.87	0.18	1.01	0.32	0.15	0.07	0.15	0.03
Flueggea virosa	2.27	0.78	0.94	0.26	0.71	0.35	0.91	0.34
Justicia flava	1.65	0.58	1.23	0.06	0.88	0.45	0.30	0.02
Ziziphus pubescence	1.19	0.21	1.56	0.54	6.37	1.59	3.62	1.52
Hibiscus macranthus	1.09	0.23	0.66	0.00	0.11	0.03	0.02	0.00
Kigelia africana	1.92	0.82	0.42	0.00	0.42	0.22	1.70	0.00
Rhynchosia minima	1.33	0.31	0.00	0.00	0.08	0.02	0.00	0.00
Commelina forskaolii	1.20	0.65	2.11	0.88	0.26	0.08	0.17	0.09
Apporrhiza paniculata	2.03	0.37	0.00	0.00	1.71	1.06	0.00	0.00
Cissus petiolata	0.70	0.25	0.33	0.00	2.35	1.47	1.09	0.00
Panicum trichocladum	0.98	0.72	0.00	0.00	2.17	0.71	0.00	0.00
Cassia afrofistula	1.38	0.68	0.00	0.00	0.51	0.02	0.00	0.00
Ficus bussei	3.10	0.91	1.56	0.00	15.02	6.06	1.40	0.00
Abutilon mauritianum	0.85	0.41	0.00	0.00	1.25	0.24	0.00	0.00
Afzelia quanzensis	2.68	0.63	0.00	0.00	9.48	0.70	0.00	0.00
Majedia zanguebarica	0.50	0.05	0.00	0.00	13.56	9.53	0.00	0.00
Baragtonia racemosa	0.09	0.00	0.23	0.00	2.03	0.68	2.13	0.00
Cynometra lukei	0.22	0.01	0.14	0.00	2.37	1.35	3.65	0.00
Stenotaphrum dimidiatum	0.18	0.12	0.00	0.00	2.75	2.25	0.00	0.00
Terminalia brevipes	0.72	0.38	0.00	0.00	11.22	10.45	0.00	0.00
Commelina africana	2.73	0.00	0.86	0.21	0.05	0.00	0.12	0.01
Commelina bangalensis	0.54	0.00	0.00	0.00	0.79	0.00	0.00	0.00
Passiflora foetida	0.68	0.00	0.00	0.00	1.45	0.00	0.00	0.00
Others	0.87	0.00	0.00	0.00	23.24	0.00	0.00	0.00
Antidesma vogelianum	0.23	0.01	0.08	0.00	0.21	0.06	0.23	0.00
Capparis tomentosa	0.56	0.03	0.00	0.00	0.47	0.07	0.00	0.00
Citrus limon	0.25	0.10	0.00	0.00	14.11	5.78	0.00	0.00
Indigofera schimperi	0.53	0.10	1.66	0.00	0.19	0.00	0.12	0.00
Blighia unijugata	1.49	0.00	0.00	0.00	0.05	0.00	0.00	0.00
Calcasia orietntalis	0.26	0.00	0.00	0.00	0.58	0.00	0.00	0.00
Capparis erythrocarpus	0.20	0.00	0.00	0.00	0.52	0.00	0.00	0.00
Clerodendrum acerbianum	0.85	0.00	0.00	0.00	3.71	0.00	0.00	0.00

Species	Mean time spent in feeding (Min)/bout				Mean ME gain (Kcal/g)/bout			
	Juv.	SEM	L. fem	SEM	Juv.	SEM	L. fem	SEM
Cola clavata	0.61	0.00	0.00	0.00	10.81	0.00	0.00	0.00
Combretum botryiosum	1.28	0.00	0.00	0.00	1.53	0.00	0.00	0.00
Grewia stulhmanii	0.57	0.00	0.00	0.00	0.69	0.00	0.00	0.00
Honey	1.01	0.00	1.92	0.00	0.50	0.00	0.46	0.00
Sida ovate	0.81	0.00	0.00	0.00	5.08	0.00	0.00	0.00
Tapanensis sasimbariensis	0.63	0.00	0.00	0.00	0.43	0.00	0.00	0.00
Celtis philippensis	0.73	0.00	0.00	0.00	0.12	0.00	0.00	0.00
Croton meyhartii	2.77	0.00	0.00	0.00	0.06	0.00	0.00	0.00
Cyperus rotundus	0.22	0.00	0.00	0.00	0.10	0.00	0.00	0.00
Ipomea sp.	0.23	0.00	0.00	0.00	0.93	0.00	0.00	0.00
Landolphia uatsoniana	0.44	0.00	0.00	0.00	0.10	0.00	0.00	0.00
Mollugo nudcaulis	0.85	0.00	0.58	0.16	1.60	0.00	1.51	0.13
Ocimum americanum	1.00	0.00	2.23	0.00	0.09	0.00	0.15	0.00
Phyllanthus ovalifolius	1.59	0.00	0.35	0.00	0.26	0.00	1.59	0.00
Lizard	0.54	0.00	0.00	0.00	0.18	0.00	0.00	0.00
Senegalia rovumae	0.07	0.00	0.52	0.00	6.42	0.00	1.66	0.00
Abutilon pannosum	0.00	0.00	0.18	0.00	0.00	0.00	3.05	0.00
Commiphora campestris	0.00	0.00	0.31	0.06	0.00	0.00	0.62	0.12
Lawsonia inermis	0.00	0.00	0.28	0.00	0.00	0.00	0.45	0.00
Maerua cantha	0.00	0.00	0.56	0.00	0.00	0.00	0.27	0.00
Sporobolus helvolus	0.00	0.00	0.24	0.00	0.00	0.00	0.34	0.00
Bird eggs	0.00	0.00	0.59	0.08	0.00	0.00	1.29	0.59

Appendix 2.8: Percentages of the annual contribution of Metabolizable energy (ME) acquire from ingested each different plant and faunal diet of the juveniles and lactating females.

Food species	Percent annual ME Intake	
	Juvenile	Lactating female
Ficus sycomorus	45.18	45.56
Vachellia robusta	9.09	8.14
Phoenix reclinata	7.46	6.80
Hyphaene compressa	6.81	7.38
Agaricus sp.	6.24	5.64
Oncoba spinosa	5.93	9.33
Mimusops fruticosa	4.86	4.01
Borassus aethiopum	1.54	1.63
Mangifera indica	1.43	1.30
Insects	1.28	1.34
Synsepalum msolo	1.02	0.98
Momordica trifoliate	1.00	1.19
Sorindeia madagascariensis	0.83	0.84
Garcinia livingstonei	0.83	1.15
Saba comorensis	0.75	0.44
Diospyros mespiliformis	0.69	0.74
Polysphaeria multiflora	0.53	0.36
Grewia densa	0.47	0.36
Cissus rotundifolia	0.45	0.49
Alangium salviifolium	0.43	0.57
Ficus bubu	0.40	0.18
Lecaniodiscus fraxinifolius	0.30	0.24
Drypetes natalensis	0.27	0.22
Harrisonia abyssinica	0.23	0.13
Tamarindus indica	0.21	0.01
Brachiaria subquadripara	0.21	0.21
Antidesma venosum	0.17	0.05
Pavetta sphaerobotrys	0.13	0.07
Thespesia danis	0.12	0.10
Albizia gummifera	0.09	0.09
Ficus natalensis	0.09	0.09
Lannea schweinfurthii	0.09	0.03
Cassia abbreviate	0.08	0.04
Sterculia appendiculata	0.08	0.01
Ziziphus pubescence	0.08	0.04
Ficus bussei	0.06	0.01
Majedia zanguebarica	0.06	0.00

Food species	Percent annual ME Intake	
	Juvenile	Lactating female
Cordia sinensis	0.05	0.01
Cordia goetzei	0.05	0.02
Afzelia quanzensis	0.04	0.00
Citrus limon	0.04	0.00
Chytranthus obliquinervis	0.04	0.03
Others	0.03	0.00
Terminalia brevipes	0.03	0.00
Hunteria zeylanica	0.03	0.01
Keetia zanzibarica	0.03	0.01
Cola clavata	0.02	0.00
Flagellaria guineensis	0.01	0.01
Cissus petiolata	0.01	0.00
Rauvolfia mombasiana	0.01	0.00
Panicum trichocladum	0.01	0.00
Senegalia rovumae	0.01	0.01
Apporrhiza paniculata	0.01	0.00
Stenotaphrum dimidiatum	0.01	0.00
Sida ovata	0.01	0.00
Cynometra lukei	0.01	0.01
Ruellia patula	0.01	0.00
Justicia flava	0.01	0.00
Baragtonia racemosa	0.01	0.02
Abutilon mauritianum	0.01	0.00
Clerodendrum acerbianum	0.01	0.00
Setaria verticillata	0.00	0.00
Flueggea virosa	0.00	0.02
Kigelia Africana	0.00	0.01
Mollugo nudcaulis	0.00	0.01
Combretum botryiosum	0.00	0.00
Passiflora foetida	0.00	0.00
Paullinia pinnata	0.00	0.00
Capparis tomentosa	0.00	0.00
Ipomea sp.	0.00	0.00
Cassia afrofistula	0.00	0.00
Commelina bangalensis	0.00	0.00
Grewia stulhmanii	0.00	0.00
Commelina forskaolii	0.00	0.00
Calcasia orietntalis	0.00	0.00
Hibiscus macranthus	0.00	0.00
Capparis erythrocarpus	0.00	0.00
Honey	0.00	0.00

Food species	Percent annual ME Intake	
	Juvenile	**Lactating female**
Tapanensis sasimbariensis	0.00	0.00
Antidesma vogelianum	0.00	0.00
Indigofera schimperi	0.00	0.00
Rhynchosia minima	0.00	0.00
Phyllanthus ovalifolius	0.00	0.01
Lizard	0.00	0.00
Celtis philippensis	0.00	0.00
Cyperus rotundus	0.00	0.00
Landolphia uatsoniana	0.00	0.00
Ocimum americanum	0.00	0.00
Croton meyhartii	0.00	0.00
Blighia unijugata	0.00	0.00
Commelina Africana	0.00	0.00
Abutilon pannosum	0.00	0.01
Commiphora campestris	0.00	0.00
Lawsonia inermis	0.00	0.00
Maerua canthi	0.00	0.00
Sporobolus helvolus	0.00	0.00
Bird eggs	0.00	0.01

Appendix 2.9. Annual dietary percentages and Metabolizable energy (ME) returns obtained from consumption of different types of foods (both plant and faunal) by juveniles and lactating females. The table includes a detailed list of food types categories (N = 63 Focal Ids, 20,486 feeding events)

	Annual Percentages			
	Juvenile		**Lactating female**	
Food item	**% in Diet**	**% ME Intake**	**% in Diet**	**% ME Intake**
Fruits	44.98	71.78	45.13	74.29
Seeds	33.89	14.35	34.59	14.05
Mushrooms	4.17	6.24	4.50	5.64
Gum	2.13	3.30	1.81	2.28
Leaves	7.77	1.85	6.47	1.29
Insects	5.26	1.28	5.98	1.34
Bark	0.18	0.41	0.18	0.46
Stems	0.96	0.34	0.64	0.23
Flowers	0.49	0.33	0.47	0.22
Deadwood	0.07	0.09	0.07	0.17
Subterranean structures	0.05	0.02	0.04	0.01
Exudate	0.04	0.01	0.11	0.01
Honey	0.01	0.00	0.02	0.00
Reptiles	0.01	0.00	0.00	0.00

2.5 References

Aiello, Leslie C., & Peter Wheeler. "The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution." *Current anthropology* 36.2 (1995): 199-221.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49(3), 227-267.

Altmann, J., & Alberts, S. C. (2005). Growth rates in a wild primate population: ecological influences and maternal effects. *Behavioral Ecology and Sociobiology*, *57*(5), 490-501.

Altmann, S.A., (1998). *Foraging for survival: yearling baboons in Africa*. Chicago: University of Chicago Press.

Ausman, L. M., Powell, E. M., Mercado, D. L., Samonds, K. W., el Lozy, M., & Gallina, D. L. (1982). Growth and developmental body composition of the cebus monkey (*Cebus albifrons*). *American Journal of Primatology*, *3*(1-4), 211-227.

Barton, R. A. (1990). *Foraging strategies, diet and competition in olive baboons* (Doctoral dissertation, University of St Andrews).

Barton, R. A., & Whiten, A. (1994). Reducing complex diets to simple rules: food selection by olive baboons. *Behavioral Ecology and Sociobiology*, *35*(4), 283-293.

Bastian, M. L., Zweifel, N., Vogel, E. R., Wich, S. A., & van Schaik, C. P. (2010). Diet traditions in wild orangutans. *American Journal of Physical Anthropology*, 143, 175–187.

Bentley-Condit, V. K. (2009). Food choices and habitat use by the Tana River yellow baboons (*Papio cynocephalus*): a preliminary report on five years of data. *American journal of primatology*, *71*(5), 432-436.

Boyer, D., Ramos-Ferna´ndez, G Miramontes, O., Mateos, J. L., Cocho1, I. G., Larralde, H., Ramos H. & Rojas, F. (2006). Scale-free foraging by primates emerges from their interaction with a complex environment. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*(1595), 1743-1750.

Bryer, M. A., Chapman, C. A., & Rothman, J. M. (2013). Diet and polyspecific associations affect spatial patterns among redtail monkeys (*Cercopithecus ascanius*). *Behaviour*, *150*(3-4), 277-293.

Bryer, M. A., Chapman, C. A., Raubenheimer, D., Lambert, J. E., & Rothman, J. M. (2015). Macronutrient and energy contributions of insects to the diet of a frugivorous monkey (*Cercopithecus ascanius*). *International Journal of Primatology*, *36*(4), 839-854.

Butynski, T. M., & Mwangi, G. (1994). Conservation status and distribution of the Tana River red colobus and crested mangabey for Zoo Atlanta. *Kenya Wildlife Service, National Museums of Kenya, Institute of Primate Research, and East African Wildlife Society*, *68*.

Chalk, J., Wright, B. W., Lucas, P. W., Schuhmacher, K. D., Vogel, E. R., Fragaszy, D., Visalberghi, E., Izar, P. & Richmond, B. G. (2016). Age-related variation in the mechanical properties of foods processed by *Sapajus libidinosus*. *American journal of physical anthropology*, *159*(2), 199-209.

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

Chapman, C. A., Chapman, L. J., Naughton-Treves, L., Lawes, M. J., & Mcdowell, L. R. (2004). Predicting folivorous primate abundance: validation of a nutritional model. *American Journal of Primatology*, *62*(2), 55-69.

Chapman, C. A., Struhsaker, T. T., Skorupa, J. P., Snaith, T. V., & Rothman, J. M. (2010). Understanding long-term primate community dynamics: implications of forest change. *Ecological Applications*, *20*(1), 179-191.

Chapman, C. A., Rothman, J. M., & Lambert J. E. (2012). Socialization and Development of Behavior. In*: Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.), *The evolution of primate societies* (pp. 245-268). Chicago: University of Chicago Press.

Chivers, D. J., & Hladik, C. M. (1984). Diet and gut morphology in primates. In *Food acquisition and processing in primates* (pp. 213-230). Springer US.

Chivers, D. J., Wood, B. A., & Bilsborough, A. (2013). *Food acquisition and processing in primates*. Springer Science & Business Media.

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

Clements, Kendall D., David Raubenheimer, and J. Howard Choat. "Nutritional ecology of marine herbivorous fishes: ten years on." *Functional Ecology* 23, no. 1 (2009): 79-92.

Conklin-Brittain, N. L., Knott, C. D., & Wrangham, R. W. (2006). Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. *Cambridge Studies in Biological and Evolutionary Anthropology*, *1*(48), 445-472.

Cork, S. J., & Foley, W. J. (1991). Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forests. *Plant defenses against mammalian herbivory*, 133-166.

Cowlishaw, G. & Dunbar, R.I.M. (2000). *Primate Conservation Biology*. The University of Chicago Press, Chicago, IL.

Cristóbal-Azkarate, J., & Arroyo-Rodríguez, V. (2007). Diet and activity pattern of howler monkeys (Alouatta palliata) in Los Tuxtlas, Mexico: effects of habitat fragmentation and implications for conservation. *American Journal of Primatology*, *69*(9), 1013-1029.

Davenport, T. R., De Luca, D. W., Bracebridge, C. E., Machaga, S. J., Mpunga, N. E., Kibure, O., & Abeid, Y. S. (2010). Diet and feeding patterns in the kipunji (*Rungwecebus kipunji*) in Tanzania's Southern Highlands: a first analysis. *Primates*, *51*(3), 213-220.

Davies, A., Bennett, E. L., & Waterman, P. G. (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*(1), 33-56.

Dearing, M. D., Foley, W. J., & McLean, S. (2005). The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annu. Rev. Ecol. Evol. Syst.*, *36*, 169-189.

Deblauwe, I., & Janssens, G. P. (2008). New insights in insect prey choice by chimpanzees and gorillas in southeast Cameroon: the role of nutritional value. *American Journal of Physical Anthropology*, *135*(1), 42-55.

Di Fiore, A., Link, A. & Dew, J.L. (2008). Diets of wild spider monkeys. *SpiderMonkeys: Behavior, Ecology and Evolution of the Genus Ateles* (ed. C.J. Campbell), pp. 81–137. Cambridge University Press, Cambridge.

Eadie, E. C. (2015). Ontogeny of foraging competence in capuchin monkeys (*Cebus capucinus*) for easy versus difficult to acquire fruits: a test of the needing to learn hypothesis. *PloS one*, *10*(9), e0138001.

Estrada, A., & Coates Estrada, R. (1984). Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Mexico. *American Journal of Primatology*, *6*(2), 77-91.

Fashing, P. J. (2001). Feeding ecology of guerezas in the Kakamega Forest, Kenya: the importance of Moraceae fruit in their diet. *International Journal of Primatology*, *22*(4), 579-609.

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

Felton, A. M., Felton, A., Wood, J. T., & Lindenmayer, D. B. (2008). Diet and feeding ecology of *Ateles chamek* in a Bolivian semi humid forest: the importance of Ficus as a staple food resource. *International Journal of Primatology*, *29*(2), 379-403.

Field, L. P. (2003). *Mangabeys Cercocebus and Lophocebus, North American Regional Studbook*. Sacramento, CA.

Foley, W. J., & McArthur, C. (1994). The effects and costs of allelochemicals for mammalian herbivores: an ecological perspective. *The digestive system in mammals: Food, form and function*, 370-391.

Fragaszy, D. M. (1986). Time budgets and foraging behavior in wedge-capped capuchins (*Cebus olivaceus*): age and sex differences.

Fragaszy, D. M., & Boinski, S. (1995). Patterns of individual diet choice and efficiency of foraging in wedge-capped capuchin monkeys (*Cebus olivaceus*). *Journal of Comparative Psychology*, *109*(4), 339.

Freeland, W. J., & Janzen, D. H. (1974). Strategies in herbivory by mammals: the role of plant secondary compounds. *The American Naturalist*, *108*(961), 269-289.

Frias, A. E., Morgan, T. K., Evans, A. E., Rasanen, J., Oh, K. Y., Thornburg, K. L., & Grove, K. L. (2011). Maternal high-fat diet disturbs uteroplacental hemodynamics and increases the frequency of stillbirth in a nonhuman primate model of excess nutrition. *Endocrinology*, *152*(6), 2456-2464.

Garber, P. A. (1987). Foraging strategies among living primates. *Annual review of Anthropology*, *16*(1), 339-364.

Garber, P. A., Righini, N., & Kowalewski, M. M. (2015). Evidence of alternative dietary syndromes and nutritional goals in the genus Alouatta. In *Howler Monkeys* (pp. 85-109). Springer New York.

Gautier-Hion, A., & Gautier, J. P. (1976). Croissance, maturité sexuelle et sociale, reproduction chez les cercopithécinés forestiers africains. *Folia Primatologica*, *26*(3), 165-184.

Gautier-Hion, A., Duplantier, J. M., Quris, R., Feer, F., Sourd, C., Decoux, J. P., Dubost, G, Emmons, L., Erard, C., Hecketsweiler, H., Roussilhon, C., Tliiollay, J.M & Moungazi, A. (1985). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia*, *65*(3), 324-337.

Gautier-Hion, A., & Michaloud, G. (1989). Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology*, *70*(6), 1826-1833.

Glander, K. E. (1982). The impact of plant secondary compounds on primate feeding behavior. *American Journal of Physical Anthropology*, *25*(S3), 1-18.

Gunst, N., Boinski, S., & Fragaszy, D. M., (2008). Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour*, *145*(2), 195-229.

Gunst, N., Leca, J.B., Boinski, S., & Fragaszy, D., (2010). The ontogeny of handling hard-to-process food in wild brown capuchins (*Cebus apella apella*): evidence from foraging on the fruit of *Maximiliana maripa*. *American journal of primatology*, *72*(11), 960-973.

Hadi, S., Ziegler, T., Waltert, M., Syamsuri, F., Mühlenberg, M., & Hodges, J. K. (2012). Habitat use and trophic niche overlap of two sympatric colobines, *Presbytis potenziani* and *Simias concolor*, on Siberut Island, Indonesia. *International Journal of Primatology*, *33*(1), 218-232.

Ham, R. M. (1994). Behaviour and ecology of grey-cheeked mangabeys (*Cercocebus albigena*) in the Lope Reserve, Gabon. Ph.D. dissertation, University of Stirling.

Hanson, A. M., Hall, M. B., Porter, L. M., & Lintzenich, B. (2006). Composition and nutritional characteristics of fungi consumed by Callimico goeldii in Pando, Bolivia. *International journal of primatology*, *27*(1), 323.

Hanson, A. M., Hodge, K. T., & Porter, L. M. (2003). Mycophagy among primates. *Mycologist*, *17*(1), 6-10.

Harvey, P. H., & Clutton-Brock, T. H. (1981). Primate home-range size and metabolic needs. *Behavioral Ecology and Sociobiology*, *8*(2), 151-155.

Hemingway, C. A. (1998). Selectivity and variability in the diet of Milne-Edwards' sifakas (*Propithecus diadema edwardsi*): Implications for folivory and seed-eating. *International Journal of Primatology*, *19*(2), 355-377.

Hill, R. A., & Dunbar, R. I. M. (2002). Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary ecology*, *16*(6), 579-593.

Holliday, M. A. (1986). Body composition and energy needs during growth. In *Postnatal Growth Neurobiology* (pp. 101-117). Springer US.

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

Hurlbert, S. H. (1978). The measurement of niche overlap and some relatives. *Ecology*, *59*(1), 67-77.

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral ecology*, *2*(2), 143-155.

Isbell, L. A., Pruetz, J. D., & Young, T. P. (1998). Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. *Behavioral Ecology and Sociobiology*, *42*(2), 123-133.

Janiak, M. C. (2016). Digestive enzymes of human and nonhuman primates. *Evolutionary Anthropology: Issues, News, and Reviews*, *25*(5), 253-266.

Janson C. & van Schaik C. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira M.E. & Fairbanks L.A., (Eds.), *Juvenile primates: life history, development, and behavior* (pp. 57 – 76). New York: Oxford University Press.

Janson, C. H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella. Animal Behaviour*, *55*(5), 1229-1243.

Janson, C. H., & Boinski, S. (1992). Morphological and behavioral adaptations for foraging in generalist primates: the case of the cebines. *American Journal of Physical Anthropology*, *88*(4), 483-498.

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

Janzen, D. H. (1983). Dispersal of seeds by vertebrate guts. *Coevolution*, 232-262.

Kinnaird, M. F. (1990). Behavioral and demographic responses to habitat change by the Tana River crested mangabey (*Cercocebus galeritus galeritus*). (Doctoral dissertation, University of Florida, Florida)

Kinnaird, M. F. (1992). Phenology of flowering and fruiting of an East African riverine forest ecosystem. *Biotropica,* 24 (2), 187–194.

Kivai S. M, Erin E. R. Rothman J.M. Kivasu C. M. & Palombit, R. A. (2017). Extractive foraging in wild Tana River Mangabeys, *Cercocebus galeritus*: Implication of Different Physical Properties of Foods. *Abstract, presented in the 86th Annual Meeting of the American Association of Physical Anthropologists (2017)*. American Association of Physical Anthropologists.

Kivai, S. (2013). Predation on an Endemic and Endangered Tana River Mangabey (*Cercocebus galeritus*) by a Sympatric Yellow Baboon (*Papio cynocephalus*) in Tana River National Primate Reserve, Kenya. *African Primates* 8, 59-62.

Knott, C. (2005). Energetic responses to food availability in the great apes: implications for hominin evolution. *In*; Brockly, D & van Schaik, P.C (eds), *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates.* Cambridge University Press.

Krishnamani, R., & Mahaney, W. C. (2000). Geophagy among primates: adaptive significance and ecological consequences. *Animal behaviour*, *59*(5), 899-915.

Kuno, E. (1991). Sampling and analysis of insect populations. *Annual review of entomology*, *36*(1), 285-304.

Lambert J.E. (2005). The ecomorphology of anterior dentition: an analysis of food handling and processing in a community of African cercopithecoids. *Am J Primatol* 66, 136.

Lambert, J. E. (1998). Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology: Issues, News, and Reviews*, *7*(1), 8-20.

Lambert, J. E. (2002). Resource switching and species coexistence in guenons: a community analysis of dietary flexibility. *In: The Guenons: Diversity and Adaptation in African Monkeys.* Glenn, M. E., and Cords, M. (eds.), Kluwer Academic/Plenum Press, New York. pp. 309-323.

Lambert, J. E. (2010). Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In: Campell, C., Fuentes, A., Mackinnon, K. C., Panger, M., and Beadner, S. (Eds), *Primates in perspective* (pp. 482-495). Oxford: Oxford University Press.

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

Lechowicz, M. J. (1982). The sampling characteristics of electivity indices. *Oecologia*, 52(1), 22-30.

Leonard, W. R., & Robertson, M. L. (1992). Nutritional requirements and human evolution: a bioenergetics model. *American Journal of Human Biology*, *4*(2), 179-195.

Lonsdorf, E.V., & Ross, S.R., (2012). Socialization and Development of Behavior. In*: Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.), *The evolution of primate societies* (pp. 245-268). Chicago: University of Chicago Press.

Lonsdorf, E.V., Eberly, L.E., & Pusey, A. E., (2004). Sex differences in learning in chimpanzees. *Nature*, *428*(6984), 715-716.

Lyngdoh, S., Shrotriya, S., Goyal, S. P., Clements, H., Hayward, M. W., & Habib, B. (2014). Prey preferences of the snow leopard (*Panthera uncia*): regional diet specificity holds global significance for conservation. *PLoS One*, *9*(2), e88349.

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

MacKinnon, K. C. (2006). Food choice by juvenile capuchin monkeys (*Cebus capucinus*) in a tropical dry forest. In *New perspectives in the study of Mesoamerican primates* (pp. 349-365). Springer US.

Mammides, C., Cords, M., & Peters, M. K. (2009). Effects of habitat disturbance and food supply on population densities of three primate species in the Kakamega Forest, Kenya. *African Journal of Ecology*, *47*(1), 87-96.

Manly, B. F. L., McDonald, L., Thomas, D., McDonald, T. L., & Erickson, W. P. (2007). *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & Business Media.

Marsh, C.M. (1981). Ranging behavior and its relation to diet selection in Tana River red colobus. *J. Zool.,* 195, 473-492

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

Matsuda, R. (2013). *Morphology and evolution of the insect abdomen: with special reference to developmental patterns and their bearings upon systematics*. Elsevier.

Mattson Jr, W. J. (1980). Herbivory in relation to plant nitrogen content. *Annual review of ecology and systematics*, *11*(1), 119-161.

Mbora, D. N., Wieczkowski, J., & Munene, E. (2009). Links between habitat degradation, and social group size, ranging, fecundity, and parasite prevalence in the Tana River mangabey (*Cercocebus galeritus*). *American Journal of Physical Anthropology*, *140*(3), 562-571.

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

McGraw, W. S., Vick, A. E., & Daegling, D. J. (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*(1), 140-153.

McGraw, W. S., Vick, A. E., & Daegling, D. J. (2014). Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): Implications for fallback foods and dental adaptation. *American journal of physical anthropology*, *154*(3), 413-423.

McKey, D. B., Gartlan, J. S., Waterman, P. G. & Choo, G. M. (1981). Food selection by black colobus monkeys (*Colobus satanus*) in relation to plant chemistry. *Biological Journal of the Linnean Society*, *16*(2), 115-146.

Medley, K. E. (1993). Extractive forest resources of the Tana River National Primate Reserve, Kenya. *Economic Botany*, *47*(2), 171-183.

Medlicott, A. P., & Thompson, A. K. (1985). Analysis of sugars and organic acids in ripening mango fruits (*Mangifera indica* L. var Keitt) by high performance liquid chromatography. *Journal of the Science of Food and Agriculture*, *36*(7), 561-566.

Milton, K. (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *The American Naturalist*, *114*(3), 362-378.

Milton, K. (1980). *The Foraging Strategy of Howler Monkeys*. New York: Columbia University Press.

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

Milton, K. (1984). The role of food-processing factors in primate food choice. *Adaptations for foraging in nonhuman primates*, 249-279.

Milton, K. (1999). Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us?. *Nutrition*, *15*(6), 488-498.

Milton, K. (2003). Micronutrient intakes of wild primates: are humans different?. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *136*(1), 47-59.

Min, B. R., Barry, T. N., Attwood, G. T., & McNabb, W. C. (2003). The effect of condensed tannins on the nutrition and health of ruminants fed fresh temperate forages: a review. *Animal Feed Science and Technology*, *106*(1), 3-19.

Moinde-Fockler, N. N., Oguge, N. O., Karere, G. M., Otina, D., & Suleman, M. A. (2007). Human and natural impacts on forests along lower Tana river, Kenya: implications towards conservation and management of endemic primate species and their habitat. *Biodiversity and conservation*, *16*(4), 1161-1173.

Molino, J. F., & Sabatier, D. (2001). Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science*, *294*(5547), 1702-1704.

Morellato, L. P. C., Camargo, M. G. G., Fernanda, F. D., Luize, B. G., Mantovani, A., & Hudson, I. L. (2010). *The influence of sampling method, sample size, and frequency of observations on plant phenological patterns and interpretation in tropical forest trees* (pp. 99-121). Springer Netherlands.

National Research Council. (2003). *Nutrient requirements of nonhuman primates*. National Academies Press.

Njue, A. (1992). *The Tana river floodplain forest, Kenya: hydrologic and edaphic factors as determinants of vegetation structure and function* (Doctoral dissertation, University of California, Davis.).

Norconk, M. A., Wright, B. W., Conklin-Brittain, N. L., & Vinyard, C. J. (2009). Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In *South American Primates* (pp. 279-319). Springer New York.

Novakowski, G. C., Hahn, N. S., & Fugi, R. (2008). Diet seasonality and food overlap of the fish assemblage in a pantanal pond. *Neotropical Ichthyology*, *6*(4), 567-576.

O'Brien, T.G., Margaret F. Kinnaird, M.F., Dierenfeld, E.S., Conklin-Brittain, L.N., Wrangham, R. W & Silver, C.S (1998). Fruit-eating animals regularly prefer to eat figs even when other food is abundant. We propose that high calcium levels contribute to the desirability of figs as food for many forest animals. *Nature*, *392*(6677), 668.

O'mara, M. T. (2015). Ecological risk aversion and juvenile ring-tailed lemur feeding and foraging. *Folia Primatologica*, *86*(1-2), 96-105.

Oates, J. F. (1978). Water-plant and soil consumption by guereza monkeys (*Colobus guereza*): a relationship with minerals and toxins in the diet? *Biotropica*, 10(4), 241-253.

Oates, J. F., Swain, T., & Zantovska, J. (1977). Secondary compounds and food selection by colobus monkeys. *Biochemical systematics and Ecology*, *5*(4), 317-321.

Olupot, W. (1998). Long-term variation in mangabey (*Cercocebus albigena* Johnston Lydekker) feeding in Kibale National Park, Uganda. *African Journal of Ecology*, *36*(1), 96-101.

Palombit, Ryne A. "Inter-and intraspecific variation in the diets of sympatric siamang (Hylobates syndactylus) and lar gibbons (Hylobates lar)." *Folia Primatologica* 68, no. 6 (1997): 321-337.

Pereira, M.E., Fairbanks, L.A., (2002). *Juvenile Primates: Life history, Development and Behavior*. New York: Oxford University Press.

Porter, L. M., & Garber, P. A. (2010). Mycophagy and its influence on habitat use and ranging patterns in *Callimico goeldii*. *American journal of physical anthropology*, *142*(3), 468-475.

Raubenheimer, D., Machovsky-Capuska, G. E., Chapman, C. A., & Rothman, J. M. (2015). Geometry of nutrition in field studies: an illustration using wild primates. *Oecologia*, *177*(1), 223-234.

Raubenheimer, D., & Simpson, S. J. (2004). Organismal stoichiometry: quantifying non-independence among food components. *Ecology*, *85*(5), 1203-1216.

Raubenheimer, D., Simpson, S. J., & Mayntz, D. (2009). Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology*, *23*(1), 4-16.

Reynolds, A. M. (2012). Fitness-maximizing foragers can use information about patch quality to decide how to search for and within patches: optimal Lévy walk searching patterns from optimal foraging theory. *Journal of The Royal Society Interface,* 9(72) 1568-157*.*

Robbins, C. (2012). *Wildlife feeding and nutrition*. Elsevier.

Robbins, C.T. 1993. Energy requirements for maintenance. Pp. 114-174 in Wildlife Feeding and Nutrition. San Diego: Academic Press, Inc.

Robbins, M. M., & Hohmann, G. (2006). Primate feeding ecology: an integrative approach. *Feeding Ecology of Apes and other Primates.* G. Hohmann, M. M. Robbins & C. Boesch (eds.)*. Cambridge University Press, Cambridge. 523pp.*, 1-13.

Rode, K. D., Chapman, C. A., McDowell, L. R., & Stickler, C. (2006). Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*) *Biotropica*, *38*(5), 625-634.]

Rogers, E., Cipolleta, C., Doran, D., Mcfarland, K., Nishihara, T., Remis, M., & Tutin, C. E (2004). Western gorilla diet: a synthesis from six sites. *American Journal of Primatology*, *64*, 173-192.

Rothman, J. M., Chapman, C. A., & Pell, A. N. (2008b). Fiber-bound nitrogen in gorilla diets: implications for estimating dietary protein intake of primates. *American Journal of Primatology*, *70*(7), 690-694.

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

Rothman, J. M., Dierenfeld, E. S., Hintz, H. F., & Pell, A. N. (2008a). Nutritional quality of gorilla diets: consequences of age, sex, and season. *Oecologia*, *155*(1), 111-122.

Rothman, J. M., Dierenfeld, E. S., Molina, D. O., Shaw, A. V., Hintz, H. F., & Pell, A. N. (2006). Nutritional chemistry of foods eaten by gorillas in Bwindi Impenetrable National Park, Uganda. *American Journal of Primatology*, *68*(7), 675-691.

Rothman, J. M., Plumptre, A. J., Dierenfeld, E. S., & Pell, A. N. (2007). Nutritional composition of the diet of the gorilla (*Gorilla beringei*): a comparison between two montane habitats. *Journal of Tropical Ecology*, *23*(06), 673-682.

Rothman, J. M., Raubenheimer, D., Bryer, M. A., Takahashi, M., & Gilbert, C. C. (2014). Nutritional contributions of insects to primate diets: Implications for primate evolution. *Journal of Human Evolution*, *71*, 59-69.

Rowe, N., & Myers, M. (2015). All the world's primates. *Primate Conservation Inc. Charlestown RI.*

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

Sato, H., Santini, L., Patel, E. R., Campera, M., Yamashita, N., Colquhoun, I. C., & Donati, G. (2016). Dietary flexibility and feeding strategies of Eulemur: a comparison with Propithecus. *International Journal of Primatology*, *37*(1), 109-129.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual review of ecology and systematics*, *2*(1), 369-404.

Scott, M. L. 1986. Energy: requirements, sources, and metabolism. Pp. 12-78 in Nutrition in Humans and Selected Animal Species. New York: John Wiley & Sons.

Shah, N.F. (2003). Foraging strategies in two sympatric mangabey species (*Cercocebus agilis* and *Lophocebus albigena*). (*Ph.D. dissertation thesis, Stony Brook University, Stony Brook, NY)*

Simpson, S. J., Batley, R., & Raubenheimer, D. (2003). Geometric analysis of macronutrient intake in humans: the power of protein?. *Appetite*, *41*(2), 123-140.

Simpson, S. J., Le Couteur, D. G., & Raubenheimer, D. (2015). Putting the balance back in diet. *Cell*, *161*(1), 18-23.

Sinclair, A. R., Fryxell, J., & Caughley, G. (2011). *Wildlife ecology, conservation and management*. Wiley. com.

Smith, R. J., & Jungers, W. L. (1997). Body mass in comparative primatology. *Journal of Human evolution*, *32*(6), 523-559.

Sorensen, J. S., McLister, J. D., & Dearing, M. D. (2005). Plant secondary metabolites compromise the energy budgets of specialist and generalist mammalian herbivores. *Ecology*, *86*(1), 125-139.

Stevenson, P. R., Pineda, M., & Samper, T. (2005). Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) at Tinigua Park, Colombia. *Oikos*, *110*(3), 435-440.

Strait, S. G. (1993). Differences in occlusal morphology and molar size in frugivores and faunivores. *Journal of Human Evolution*, *25*(6), 471-484.

Strauss, R. E. (1979). Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society*, *108*(4), 344-352.

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

Strier, K. B. (2015). *Primate behavioral ecology*. Routledge.

Strier, K. B. (2016). *Primate behavioral ecology 4th Edition*. Routledge, New York.

Strum, S. C. (2010). The development of primate raiding: implications for management and conservation. *International Journal of Primatology*, *31*(1), 133-156.

Sussman, R. W. (1987). Species-specific dietary patterns in primates and human dietary adaptations. *The evolution of human behavior: primate models. Albany:* State University of New York Press, pp. 151-179.

Terborgh, J. (1986). Keystone plant resources in the tropical forest. In; Conservation biology: the Science of scarcity and diversity (Ed. Soule, M.E). Sinauer Associates, Sunderland, Massachusetts, USA.

Twinomugisha, D., Chapman, C. A., Lawes, M. J., Worman, C. O. D., & Danish, L. M. (2006). How Does the Golden Monkey of the Virungas Cope in a Fruit-Scarce Environment?. In *Primates of Western Uganda* (pp. 45-60). Springer New York.

Van Doorn, A. C., O'Riain, M. J., & Swedell, L. (2010). The effects of extreme seasonality of climate and day length on the activity budget and diet of semi-commensal chacma baboons (*Papio ursinus*) in the Cape Peninsula of South Africa. *American Journal of Primatology*, *72*(2), 104-112.

van Noordwijk, M. A., & van Schaik, C. P. (2005). Development of ecological competence in Sumatran orangutans. *American Journal of Physical Anthropology*, *127*(1), 79-94.

Vanderploeg, H. A., & Scavia, D. (1979). Two electivity indices for feeding with special reference to zooplankton grazing. *Journal of the Fisheries Board of Canada*, *36*(4), 362-365.

Visalberghi, E., & Fragaszy, D. M. (1990). Do monkeys ape. *Language" and intelligence in monkeys and apes:* In *Comparative developmental perspectives*, (pp. 247-273). Cambridge University press.

Visalberghi, E., & Néel, C. (2003). Tufted capuchins (*Cebus apella*) use weight and sound to choose between full and empty nuts. *Ecological Psychology*,*15*(3), 215-228.

Vogel, E. R., Alavi, S. E., Utami-Atmoko, S. S., van Noordwijk, M. A., Bransford, T. D., Erb, W. M., Zulfa, A., Sulistyo, F., Farida, W.R. & Rothman, J. M. (2017). Nutritional ecology of wild Bornean orangutans (Pongo pygmaeus wurmbii) in a peat swamp habitat: Effects of age, sex, and season. *American journal of primatology*, *79*(4), 1-20.

Vogel E.R, Kivai S. M. & Alavi S. (2016). Foraging strategies. *International Encyclopedia of Primatology*. In Press

Vogel, E. R., Haag, L., Mitra-Setia, T., van Schaik, C. P., & Dominy, N. J. (2009). Foraging and ranging behavior during a fallback episode: *Hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. *American Journal of Physical Anthropology*, *140*(4), 716-726.

Vogel, E. R., Harrison, M. E., Zulfa, A., Bransford, T. D., Alavi, S. E., Husson, S., Morrog-Bernard, H., Firtsman, T., Utami-Atmoko, S.S., van Noordwijk, M.A. & Farida, W. R. (2015). Nutritional differences between two orangutan habitats: implications for population density. *PloS one*, *10*(10), e0138612.

Vogel, E.R., Knott, C., Crowley, B.E, Blakely, M.D, Larsen, D.M and Dominy, N.J (2012). Bornean orangutans on the brink of protein bankruptcy. *Biology letters*, *8*(3), 333-336.

Wahungu, G. (1998). Diet and habitat overlap in two sympatric primate species, the Tana crested mangabey *Cercocebus galeritus* and yellow baboon *Papio cynocephalus*. *African Journal of Ecology*, *36*(2), 159-173.

Wallace, B.R. (2008). The Influence of Feeding Patch Size and Relative Fruit Density on the Foraging Behavior of the Black Spider Monkey *Ateles chamek*. *Biotropica*, *40*(4), 501-506.

Waser, P. M. (1982). Primate polyspecific associations: do they occur by chance? *Animal Behaviour*, *30*(1), 1-8.

Waterman, P. G., Ross, J. A., Bennett, E. L., & Davies, A. (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), 1-32.

Wendeln, M. C., Runkle, J. R., & Kalko, E. K. (2000). Nutritional Values of 14 Fig Species and Bat Feeding Preferences in Panama. *Biotropica*, *32*(3), 489-501.

Whiten, A., Byrne, R. W., Barton, R. A., Waterman, P. G., Henzi, S. P., Hawkes, K., Widdowson, E.M., Altmann, S.A., Milton, K & Dunbar, R. I. M. (1991). Dietary and foraging strategies of baboons and discussion. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *334*(1270), 187-197.

Wieczkowski J. (2003). *Aspects of the ecological flexibility of the Tana mangabey (Cercocebus galeritus) in its fragmented habitat, Tana River, Keny*a. Ph.D. dissertation thesis. Athens, GA: University of Georgia.

Wieczkowski, J. (2004). Ecological correlates of abundance in the Tana mangabey (*Cercocebus galeritus*). *American Journal of Primatology*, *63*(3), 125-138.

Wieczkowski, J. (2009). Brief communication: Puncture and crushing resistance scores of Tana River mangabey (*Cercocebus galeritus*) diet items. *American journal of physical anthropology*, *140*(3), 572-577.

Wieczkowski, J., & Kinnaird, M. (2008). Shifting forest composition and primate diets: a 13-year comparison of the Tana River mangabey and its habitat. *American Journal of Primatology*, *70*(4), 339-348.

Wieczkowski, J., McGraw, W. S., & Butynski, T. M. (2012). Inferred African Crowned Eagle (*Stephanoaetus coronatus*) Predation on a Tana River Mangabey (*Cercocebus galeritus*). *African Primates*, *7*(2), 218-223.

Wieczkowski, J., T. Butynski. (2007). *Cercocebus galeritus*. T Butynski, J Kingdon, J Kalina, eds. *Mammals of Africa*.

Warren, Y., Higham, J. P., Maclarnon, A. M., & Ross, C. (2011). Crop-raiding and commensalism in olive baboons: the costs and benefits of living with humans. In *Primates of Gashaka* (pp. 359-384). Springer New York.

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

Wrangham, R. W., & Waterman, P. G. (1981). Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. *The Journal of Animal Ecology*, *50*(3), 715-731.

CHAPTER THREE: FOOD NUTRITIONAL PROPERTIES AND NUTRIENT INTAKE IN JUVENILE TANA RIVER MANGABEYS, *CERCOCEBUS GALERITUS.*

Abstract

For animals with lengthy periods of immaturity, variation in the ability of juveniles to ingest enough food to meet their nutritional requirements is likely to have important long-term consequences for individual fitness. Juveniles are expected to be less efficient and less competent foragers than adults, due to incompletely developed physical, behavioral, and cognitive capabilities. Consequently, they are potentially faced with significant challenges in acquiring nutrients and are also likely to suffer the effects of nutritional stress more than adults because of the nutritional requirements of growth. Data focusing on the nutritional ecology of juvenile primates are very limited, and little is known, in particular, about juvenile-adult differences in nutritional strategies. To redress this empirical gap, I investigated juvenile nutrient intake and the chemical properties of foods among Tana River mangabeys (*Cercocebus galeritus*), using adult lactating female group-mates as a control. I tested two hypotheses. First, (H1) juveniles' nutritional needs differ from those of lactating females because of their different metabolic requirements and foraging capabilities. I predicted that, compared to lactating females, juveniles would have a higher relative intake (per metabolic body mass) of protein and minerals. Second, (H2) because of the potential negative consequences of plant secondary metabolites, the monkeys will organize foraging to minimize intake of these compounds. I predicted that mangabeys will forage selectively to avoid foods high in condensed tannins.

To test these hypotheses and predictions, I collected behavioral data using focal animal sampling and nutritional data via samples of foods consumed. I used the

generalized linear mixed models (GLMMs) to determine the effects of age class and month on nutrient intake and used the standard laboratory protocols for nutritional analyses and the acid-butanol assay method to assess condensed tannin presence/absence in mangabey foods. Relative available protein intake per minute varied in response to age class and was significantly higher in juveniles than in lactating females (F = 171.69, df = 1, p < 0.0001, t = 13.37, df = 1, p < 0.0001, N = 63 individuals). Moreover, available protein also varied in response to season of fruit availability (F = 56.40, df = 14, p < 0.0001, N = 2 seasons of fruit availability). Intake of available protein was significantly higher during high fruit availability compared to low fruit availability (t = -4.74, df = 1, p <0.0001). Juveniles showed higher relative consumption of both macro-minerals (calcium, potassium, phosphorus, magnesium, and sodium) and micro-minerals (iron, zinc, copper, manganese, and molybdenum) than did lactating females (p < 0.0001). Although foods containing some condensed tannins were generally more common in the diet than foods with little or none of these secondary compounds (χ^2 = 18.27, df = 7, p = 0.0322), the mangabeys avoided ingesting that subset of foods characterized by high concentrations of condensed tannins (χ^2 = 18.27, df = 4, p = < 0. 0001). These findings supported H1 and partly H2.

In conclusion, juvenile Tana River mangabeys ingested more available protein and micro- and macro-minerals, relative to body mass than did conspecific adult females, which I interpret as reflecting juveniles' increased nutritional demands to support growth. Also, mangabeys appeared to regulate the intake of condensed tannins by including in their diet many foods with some amount of these secondary compounds, but selectively foraging to avoid those items that are high in condensed tannins.

3.1 Introduction

3.1.1 Background

The foraging efficiency of primates is predicted primarily by the ability to access, process and ingest enough resources to fulfill an individual's nutritional requirements at minimal negative consequences (Norconk et al., 2009; Constantino et al., 2012; Lambert & Rothman, 2015). The mechanical properties of food constitute a major source of such costs, through risks of dental wear, tooth loss, dislocation of the jaw tissues, and indigestibility, which not only impair food acquisition and processing but are potentially life threatening (Yamashita et al., 2012; Lucas et al., 2013). From the nutritional perspective, however, such costs can also derive from inadequate and imbalanced nutrient concentrations and high levels of plant secondary compounds in plant foods (Milton, 1984). Primate feeding adaptations should overcome these mechanical and nutritional challenges to allow individuals to meet their daily nutritional requirement for growth, reproduction, and survival (Altmann, 1998; Rothman et al., 2008a; Chapman et al 2012; Vogel et al., 2017). Juveniles are likely to suffer the negative effects of such feeding challenges more than adults because of the demands of growth as well as reduced competency in feeding. Variation in the inability to acquire adequate nutrients as a juvenile, for example, is associated with long-term reproductive success, and in extreme cases, premature mortality (Altmann, 1998; Chapman et al., 2012).

Foraging competence in primates is potentially impeded by myriad factors besides the mechanical and nutritional problems such as limited cognitive skills,

intraspecific competition, predation risks, and spatial and temporal distribution of food resources (Pereira & Fairbank, 2002). These factors, together with chemical and mechanical properties of foods, may operate independently or synergistically to select for dietary strategies. Although, it is relatively clear that chemical properties of foods constrain adult primate foraging efficiency, however, the effects on juveniles are less studied. A handful studies focusing on juveniles have explored the effects of nutritional properties of food (Altmann, 1998; Pereira & Fairbanks, 2002; Rothman et al., 2008a) but there is a need for more data to understand how juveniles meet their nutritional requirements given the chemical problems presented by foods and foraging competency. Here I investigate the nutritional properties of Tana River mangabey foods and examine how this influences the juvenile nutrient intake.

3.1.2 Nutritional Properties of Primate Foods and Ecological Implications

3.1.2.1 Nutritional ecology: advances and conceptual framework

Despite several decades of research on primate feeding, it is only relatively recently that major progress has been made in the field of primate nutrition ecology (Freeland & Janzen, 1974; Milton, 1979, 1980, 1999; Raubenheimer et al., 1997; Altmann, 1998; Chapman et al., 2004; Simpson et al., 2003, Rothman et al., 2006, 2008b, 2012; Felton et al., 2008, 2009; Altman, 2009; Raubenheimer et al., 2014; Rothman et al., 2014, Vogel et al., 2016; Righini, 2017). Methodological advances and innovations (Rothman et al., 2012; Felton et al., 2009; Raubenheimer, 2011) have spurred much of this rapid growth in research. Nevertheless, of studies of

nutritional ecology in juveniles remain scanty. Redressing this empirical deficiency is not only important for advancing our understanding the evolutionary significance of nutrition, but also for informing the conservation of primate species, which face a greater extinction risk than other mammalian orders do (Estrada et al., 2017).

3.1.2.2 Components of primate nutritional ecology and their implications

Primate diets notably encompass a diverse array of food items, ranging from plant vegetative and reproductive parts, to fungi, and fauna (Garber, 1987; Vogel et al., 2016). Analysis of the diets of 131 primate species suggests that individuals in 90% of them eat fruits, 79% consume soft vegetative and reproductive plant parts, 69% mature leaves, invertebrates 65%, seeds 41%, and 37% consume other animal foods (Harding, 1981; Oftedal et al., 1991). Primates are choosy in what they eat (Milton, 1984), and potential causes of food selectivity include: body size, energy requirements, food chemistry, anatomical or morphological constraints, resource availability, and competition (Janson, 1988; Oftedal et al., 1991).

Food items vary in available metabolizable energy (Garber et al., 2015). Consequently, primates must regulate food intake to maintain an optimal balance of nutrient intake. It is worth noting that not all food that is consumed is fully broken down to obtain energy since potentially available nutrients come packaged with impurities of several kinds (Lambert & Rothman, 2015). For instance, fiber, which is common in the plant foods consumed by primates, as well as the chitin making up insects exoskeletons, are generally hard to digest. With the help of enzymes, fermentation, and gut microorganisms, however, digestion of both fiber and chitin

can be enhanced. The chemical constituents of fiber are intricate and range from components that can be digested readily (such as pectin), partially (e.g., cellulose & hemicellulose) or not at all (e.g., polyphenolic compounds such as lignin) (Oftedal et al., 1991). Adaptations facilitating fiber breakdown, which include shredding molars and hind- or fore-gut fermentation are fundamental in primate utilization of diets high in fiber.

The ability to digest fiber varies across primate species, but folivores are well adapted for fiber break down compared to frugivorous primates (Milton, 1979; Power, 1991; Chapman et al., 2004; Rothman et al., 2008b). Thus, regulation of fiber intake is expected to play a pivotal role in primate feeding strategies. This has been demonstrated in both captive and field studies. For instance, when experimentally fed a diet containing 15 - 25% of fiber, black and white colobus, or guereza monkeys (*Colobus guereza*), digested 68 - 81% of the fiber, while chimpanzee efficiency was 51 - 71% (Oftedal et al., 1982; Milton & Demment, 1988). Mantled howler monkeys *(Alouatta palliata)* fed on natural leaves and fruits digested 24 - 42% of the dietary fiber (Milton et al., 1980). Finally, Mountain gorillas (*Gorilla beringei*) in Bwindi forest, Uganda, have been found to digest between 41 - 59% of the fiber in their diet (Rothman et al., 2008b) while orangutans have been suggested to digest about 54% of dietary fiber (Knott, 1998). These differences illustrate clearly how the digestibility of fiber varies across species.

Plant secondary metabolites that function as chemical defenses to herbivory are common in a majority of primate foods. These include digestibility reducing

compounds and toxins. An example of the former is a group of tannins, which may occur in condensed form (CT) as in many leguminous forage, or as hydrolyzable forms (HT) such as is encountered frequently in in leaves, fruit pods, and plant galls (Glander, 1982; Freeland & Janzen, 1974; Oftedal et al., 1991; Min et al., 2003). In both forms, tannins bind to protein making it unavailable to the consumers (Robbins et al., 1987; Min et al., 2003).

Interestingly, recent studies have suggested that intake of such compounds may also be beneficial to consumers by suppressing parasites, neutralizing other harmful chemical compounds that come with ingested foods or reducing blood loss through hemorrhaging associated with parturition (Mueller- Harvey, 2006; Rothman et al., 2009). These claims are substantiated by evidence from ruminant studies, which have demonstrated that diets containing more than $400\mu g$ CT/ml maximize inhibition of proteolysis as well as the growth of several bacteria species in the gut (Min et al., 2003). Thus, although current evidence establishes that plant secondary metabolites such as condensed tannins generally play a significant role in shaping feeding strategies of primates, the precise nature of interactive positive and negative effects remains relatively unclear, particularly as they relate to immature individuals.

Data on the nutritional requirements for individuals in the wild remain limited for most primate species due to the challenges of in-situ experiments. Researchers continue to use adjusted nutritional estimates from humans or captive populations in analyses (Oftedal et al., 1991), which may under- or over-estimate

the exact values for free ranging primates. . There is a general consensus that the nutrient prioritized by the majority of primates, particularly those that are frugivorous, is protein, thereby highlighting its important in food selection (Milton, 1979; Mattson, 1980; Glander, 1982; Robbins et al., 2007; Felton et al., 2008, 2009). This is unsurprising since proteins play a fundamental role in growth, immunity, and essential body physiological processes (Mattson, 1980; Felton et al., 2009). Primate need about 7 - 11% protein in their diet for growth and maintenance and about 14% for reproduction (Waterman & Kool, 1994). Leaves contain 12 - 16% protein (Glander, 1982) and so may be a good source of this nutrient, but not all of this is available via fermentation, partly because of binding by tannins and partly because of utilization by symbiotic gut microbes.

There is evidence that primates forage selectively to include leaves, seeds, fruits, or insects that are rich in protein content. McKey et al. (1981) found that seed preference of black colobus (*Colobus satanus*) is correlated positively with the protein content of the seeds, while leaf choice in mantled howler monkeys also targeted those with high protein content (Milton, 1979). In addition, studies in Kibale forest in Uganda by Chapman et al. (2005) established that the guereza monkeys mostly selected leaves with a high protein-low fiber ratio.

Energy maximization, acquisition of limited micro- and macro-minerals, and balancing of nutrients are also important in determining primates' feeding strategies (Felton et al., 2009). The theory of optimal feeding strategies posits that foraging goals are geared toward maximizing energy returns per unit feeding time

or maximizing time investment in foraging (Schoener, 1971; Stevensons et al., 2005). Among the handful of such studies conducted in primates, mixed findings have emerged, with some supporting energy maximization as an underlying factor while others reject this idea (Strier, 1992; Felton et al., 2009). Strier (1992) suggested that foraging Peruvian spider monkey (*Ateles chamek*) maximize energy intake, and indeed the fast gut passage rates, large territories, fluid social structure and consumption of fruit rich in sugars and lipids that characterize this species are generally associated with energy maximizers (Dew, 2005; Di Fiore et al., 2008). Findings from a recent nutritional study on the mantled howler monkey similarly indicated that the species forages in a manner to maximize energy ingestion especially in periods of low food abundance (Amato et al., 2014). Despite this set of evidence, further studies on *Ateles chamek* indicate that the species' nutritional goal is to meet a certain amount of protein ingestion as opposed to the maximization of energy (Felton et al., 2009). These conflicting results projecting the Peruvian spider monkeys as both an energy maximizers and protein prioritizer call for more detailed analyses to understand the nutritional goals in different species.

Minerals are elements as opposed to organic molecules and exist in chemical complexes once consumed. Minerals are fundamental because they play significant roles in primates such as tissue support, constituting structural components of enzymes and proteins, maintenance of osmotic gradients for nervous impulse transmission and muscle contraction, and promoting good health (National Research Council, 2003; Irwin et al., 2017). Primates and other mammals require minerals in small quantities and typically occur in very small concentration in

majority of food types (Rode et al., 2003; Chapman et al., 2012). However, shortfalls or overshooting mineral intake may lead to health complications (e.g., weak bones, osteoporosis, rickets, blindness), toxicity and difficulties in their excretion from the body (Irwin et al., 2017).

Due to the essential functional roles of minerals in primate physiology, they potentially influence diet selectivity of the traditional foods (i.e., foods, leaves, flower) and shape the primate foraging goals (Felton et al., 2009). For instance, primatologists have reported different foraging strategies among primates that are believed to promote mineral intake such as chewing decaying wood, eating soil or clay, visiting salt licks, taking urine and mud puddles (Oates, 1978; Krishnamani & Mahaney, 2000; Magliocca & Gautier-Hion, 2002; Rode et al., 2006; Fashing et al., 2007). Consequently, primate's effort to meet their daily mineral intake requirements potentially promotes dietary diversity since primates ingest different complementary foods sources for specific minerals (Cancelliere et al., 2014). In addition, the need to meet mineral requirements may impact of primates population growth, daily ranging patterns, home range, and habitat choices (Rode et al., 2006; Chapman et al., 2012; Irwin et al., 2017).

Previous primate studies have reported some simple generalizations on mineral concentrations in plant foods that leaves tended to be better sources of minerals other plant foods (Milton, 1979; Janson & Chapman, 1999; Lambert, 2011). However, with more studies generating new information, such pattern may not necessarily be true. For example, emerging evidence suggests that there is high

variation in mineral concentrations among plant species, differences in minerals in same tree or plant species based on parts and position on the tree as well as mineral diversity across habitats (Yeager, & Dierenfeld, 2000; Cancelliere et al., 2014; Irwin et al., 2017). Given these findings it is clear that a lot is yet to be understood on how minerals influence the feeding behavior among wild primates.

Minerals are undoubtedly essential for individual health (Rode et al., 2006). Consequently, there are few studies that have focused on primate behavioral strategies that emphasize on the important role of minerals in primates. One proposed behavioral strategies is geophagy. The function of geophagy, which is a common behavior in colobines (Oates, 1978; Struhsaker et al., 1997; Fashing et al., 2007), implicates the dietary importance of minerals. Oates (1978) found that the guereza monkeys in western Uganda sought swamp clay rich in magnesium, while Fashing et al. (2007) observed that conspecifics in Kakamega forest in Kenya periodically traveled distances twice as much as their daily path to access sodium rich soils from an abandoned rest house.

Another primate behavior potentially associated with accessing essential and limited minerals is chewing tree bark or decaying wood. Again, Fashing and his colleagues reported that bark chewed by guereza monkeys contained as much as 49 times more sodium than the leaves that accounted for the highest levels of sodium in the normal diet. Among the colobines, sodium is essential for de-acidifying the fore-stomach to improve fermentation (Rode et al., 2003). While more research needs to be done to better understand the dietary role of minerals across different

taxa, these studies at least suggest that minerals are likely to impact on primate foraging strategies.

3.1.2.3 Juvenile-adult differences in nutritional intake

Juvenile survival has been argued to be single most challenging period in primate developmental stages (Altmann, 1998, Pereira & Fairbank, 2002; Chalk et al., 2016). Mortality rates in juveniles outstrip those of adults, including reproducing females, most of which derives from nutritional constraints due challenges in food acquisition (Ross & Jones, 1999; Janson & van Schaik, 2002; Pereira & Fairbanks, 2002). Complexity in primate foraging behavior, which may demand increased cognitive ability, social learning, and mastery of extractive foraging skills compared to other mammals, exacerbates the vulnerability of relatively inexperienced juveniles, compromising their proficiency to acquire adequate and balanced diet (Lonsdorf & Ross, 2012). Exploitation of opportunities to learn foraging competency as well as to overcome nutritional stress may partly explain the pronounced curiosity that generally characterizes juvenile primates (Pereira & Fairbank, 2002). Compared to adults, juveniles in vervet monkeys (*Chlorocebus pygerythrus*) display the shortest latencies to approach and explore unfamiliar objects, locations, animals, and humans (Fairbanks, 2002). These predilections potentially impose risks on juveniles through elevated exposure to danger or short-term reduction in foraging efficiency (e.g., investing in trying foods of low energetic returns or unfit for consumption). Social play, which dominates juvenile activity, is also potentially costly, regarding time, energy, risk of injury, and social interference (Nowell & Fletcher, 2008). These factors cumulatively place juveniles in a delicate situation

regarding the balancing social activities, learning skills, and food acquisition to meet daily nutritional needs mediating most of the juvenile-adult differences in nutrient intake.

Systematic comparisons of the juvenile-adult dietary differences in nutritional intake are limited, but numerous relevant observations have been made across species. For example, in mountain gorillas, energetic demands of reproduction, lactation, and infant transport in females, and of rapid growth in juveniles influenced protein and mineral intake compared to adult males (Rothman et al., 2008a): adult females and juveniles consumed more protein relative to body mass, and juveniles' diet selectivity focused on foods high in minerals, such as phosphorus, zinc, and iron, compared to both adult females and males. Protein and these three minerals play an essential role in growth, repair, and function of body tissues and organs, which are significant for lactating females and growing juveniles (Underwood & Suttle, 1999).

Feeding time in immature Japanese macaques (*Macaca fuscata*) is three times higher than in adults, and immatures also target a greater number of food types (Jaman & Huffman, 2010). High use of terminal branches for foraging in these young monkeys may have nutritional consequences since more easily digestible young leaves are likely to occur there than in other areas of the tree crown (Jaman & Huffman, 2010).

Differences in nutritional intake between juvenile and adult females to meet the increased demands of growth and lactation, respectively, have been found in

Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) (Liu et al., 2016). Compared to adults of both sexes, juveniles' food selection disproportionately emphasized high-quality foods (i.e., those rich in energy and protein, especially young leaves, fruits, seeds, and buds) over low-quality foods (such as bark and lichens). When food was limited both juveniles and adult females subsisted on fewer foods that were accessible. These results clearly demonstrate that both foraging in juveniles and lactating females is constrained by different nutritional needs, which underlie their divergent dietary strategies. Although the majority of Old World primates generally occupy habitats characterized by high seasonality in food availability (Estrada et al., 2017) their nutritional strategies to survive in such habitat are yet to be understood.

3.1.6 The Tana River mangabey as study subjects

Tana River mangabeys live in an environment in which food resources are unpredictable (Homewood, 1978). Consequently, individuals may have to go through periods of nutritional stress, necessitating reliance on tough and hard fallback foods. This problem may be less relevant for other mangabey species (e.g., *Cercocebus atys, Cercocebus torquatus, Lophocebus albigena, Cercocebus sanjei*), which occupy more productive habitats and experience reduced severity of seasonal food scarcity (Shah, 2003; Wieczkowski, 2009; McCabe et al., 2013; McGraw et al., 2014). Moreover, mangabeys are generally more adapted for exploitation of difficult-to-process foods compared to other papionin primates (Cooke & McGraw, 2010) suggesting they can better utilize tough but nutritionally rewarding fallback foods. Evidence from feeding studies indicates that Tana River mangabeys process

and ingest tough seeds and nuts, which other sympatric primates such as Sykes monkeys (*Cercopithecus mitis*), vervet monkeys, and yellow baboons avoid or eat at lower rates (Wahungu, 1998; Wieczkowski, 2009). Thus, its specialized dietary adaptations for exploiting difficult to process fallback foods, in highly seasonal habitats make the Tana River mangabey a suitable model for this study.

Unfortunately, there are few data on how juveniles meet their daily nutritional requirements to survive in such unpredictable environments. While previous studies have focused on the understanding of the food species distribution, general behavior, and feeding ecology (Homewood, 1978; Kinnaird, 1992; Wahungu, 1998; Wieczkowski, 2003), there has been no explicit effort to understand the species nutritional ecology as well as juvenile-adult feeding differences. Such information is fundamental to understanding how juveniles and adults cope with chemical problems of foods, which carries important implications for the evolution of dietary adaptations among primates.

3.1.6 Hypotheses tested

In this chapter, I aim to examine the nutritional properties of different plant foods consumed by the Tana River mangabeys, and how these food properties influence juvenile feeding strategies. In order to achieve this goal I compare feeding data of juveniles and lactating females to test the following two hypotheses (H) and associated predictions (P):

H1: *Juveniles' nutritional needs differ from those of lactating females because of their different physiological requirements, and foraging capabilities.* During periods

when fruit or food resources are abundant nutritional intake to promote growth and development in juveniles and lactation females is a priority. During lean periods when fruit availability or preferred foods are limited, the need to survive becomes a priority for both age classes necessitating switch to consumption of less preferred foods, which are poor in nutrients or difficult to extract and process, is expected. In contrast to this pattern, during the periods when fruit availability and preferred foods are unlimited, nutrients are readily accessible and primates easily meet their daily nutritional needs. I predict that: **(P1)** during periods (i.e., study months) when preferred foods are abundant, compared to lactating females, juveniles have higher relative intake (i.e., per metabolic body mass) of nitrogen (protein) to maximize growth and development. This is not the case during periods of low fruit or food abundance when nutrient intake is limited and it is potentially difficult to ingest enough protein: and **(P2)** juveniles will have higher intake of essential macro-minerals (calcium, phosphorus, potassium, magnesium & sodium) and micro-minerals (iron, zinc, copper, manganese & molybdenum) per unit of body mass than lactating females. While, juveniles are expected to ingest more protein and minerals than adults, in general, plant secondary compounds, which often occur in primate foods impair intake of such nutrients (Dearing et al., 2005). For instance, qualitative chemical compounds (those occur in small amounts of < 2% of dry weight e.g., cyanide) interrupt the metabolic process and are toxic, while quantitative secondary compounds (those occur large amounts e.g., tannins) reduce digestibility of foods (Chapman et al., 2012). Thus, primates' feeding strategies are potentially aimed at overcoming these chemical compounds to maximize the intake of protein and

minerals leading to my second hypothesis.

H2: *Because of the potential negative consequences of plant secondary metabolites (PSMs), the monkeys will organize foraging to minimize intake of these compounds.* The Tana River mangabeys primarily fruits and seeds from woody species, and particularly include unripe fruit and immature seeds (44%), which potentially suggests the dietary composition of mangabeys contain high concentrations of condensed tannins (CT) (Homewood, 1978; Bernays & Bilgener, 1989; Wieczkowski, 2003). The CT interferes with food digestion and nutrient uptake (Dearing et al., 2005). Thus, I predict that **(P3)** that mangabeys will forage selectively to avoid foods high in condensed tannins, and therefore, the dietary composition of the mangabeys will contain a higher percentage of foods that are free of CT than those have CT, and among only those comprising CT the mangabeys will target to consume foods that are qualitatively low in CT because of food selection to avoid or minimize intake of chemical problems.

Rationale of the predictions

Protein plays a significant role in maintenance of body tissues, growth, and supporting essential biochemical processes (NRC, 2003). Protein requirements are strongly predicted by animal life stages, reproduction, stress, and its quality and digestibility (Chapman et al., 2012). Generally, protein demands decrease with age suggesting that immature primates require more protein per unit of body mass than adults. It is true that in females, the need for protein increases with pregnancy and lactation. Nevertheless, daily protein requirements of primates are typically less

than three grams (g) per kilogram (kg) of metabolic body mass, but juvenile requirements usually exceed this limit (Oftedal et al., 1991). For instance, in white-fronted capuchins (*Cebus albifrons*), a juvenile weighing half the weight of an adult (Kg) requires more than double the amount of protein adequate for a mature conspecific (NRC, 2003).

It is also important to recognize that the quantity of food available at a given time is likely to influence the protein intake. This is particularly relevant because the majority of primate habitats are characterized by pronounced temporal variation in food availability (Kinnaird, 1992; Palombit, 1997; Hill & Dunbar, 2002; Vogel et al., 2017). Therefore, I expect juveniles to consume more of the environmentally available protein than females, and this is likely to vary with monthly food or fruit availability as the core food for mangabeys. I will compare how intake of available protein varies with age class and month and relate intake to food availability to address my P1.

Three hypotheses have been proposed for the role of minerals intake in different mammalian groups including primates: detoxification, anti-acidification, and nutritional function hypotheses (Voigt et al., 2008; Monaco et al., 2017). Detoxification hypothesis argue that primates and other mammals, which subsist on plant diet characterized by high concentration of secondary compounds ingest minerals to neutralize the negative effects of such compounds (Voigt et al., 2008). The anti-acidification hypothesis posits that primates consume mineral also to help in maintenance of appropriate pH for fermentation (Ohwaki et al., 1974; Mackie &

White, 2012). For instance, in the langurs monkeys (*Presbytis* sp.) and colobus monkeys (*Colobus* sp.) have to maintain a pH of 5.0 – 6.7 and 5.5 – 7.0 in the fore stomachs, which are ideal conditions for microbial fermentation (Mackie & White, 2012). Finally, the nutritional value hypothesis suggests that mineral intake is target as nutritional supplement (Felton et al., 2009; Chapman et al., 2012), which I emphasize on in this study.

Minerals play a critical role in growth as structural components of tissues and in bodily functions e.g., nerve impulses and pH maintenance (NRC, 2003; Irwin et al., 2017). Although required in small amounts, most studies have indicated that essential macro-minerals (e.g., calcium, magnesium, phosphorus, potassium, and sodium) and micro-minerals (e.g., iron, copper, zinc, manganese, and molybdenum) are generally limited in primate diets and habitats (Rode et al., 2003; Rothman et al., 2006; Fashing et al., 2007; Cancelliere et al., 2014; Francisco et al., 2016; Irwin et al., 2017). There is some evidence that deficiency of these elements is especially costly to juveniles, resulting in permanent and life threatening pathologies, such as retarded growth, weak bones, and impaired vision (Robbins, 2012; Chapman et al., 2012). Thus, I predict that these macro- and micro-minerals will be limited in the mangabey diets, and juveniles will strive to ingest more minerals than lactating females throughout the year. Because of the limited nature of minerals, I will use relative intake (i.e., intake per metabolic body mass) to test P2.

Tana River mangabey diets contain higher percentages of fruits and seeds compared to other types foods (Wieczkowski, 2003; Chapter 2). These plant parts

are believed contain chemical deterrents to consumers, particularly plant secondary metabolites (PSMs) with exceptions of ripe fruits (Milton, 1984; Lambert & Rothman, 2015). Such chemical compounds include condensed tannins (CT), which pose major costs to the foraging primates though their negative effects such as binding with protein making it unavailable, and reducing food digestibility (Dearing et al., 2005). Consequently, careful food selection or discarding of parts containing high levels of PSMs potentially to overcome these chemical challenges (Wrangham & Waterman, 1981; Milton, 1984; Waterman, 1984). Thus, the rationale of prediction (P3) is that CT concentration varies across foods, and because of the negative consequences of tannins I predict that Tana River mangabeys will target foods free or low in CT concentration.

This study will contribute to our understanding of primate feeding adaptations in two ways. First, the data will in enhance our knowledge on how nutritional properties of foods shape behavioral feeding strategies, especially diet selectivity, nutrient intake, and flexibility. Second, the data will clarify how nutritional food properties and physiological needs impact on relative nutrient intake and the ontogeny of juvenile foraging.

3.2 Materials and Methods

3.2.1 Study Area

I conducted this study in two ecologically contrasting locations, designated the Mchelelo and Kitere areas, within the Tana River National Primate Reserve (TRNPR), in Tana River County, Kenya (Fig 3.1). The reserve lies between 1°40' - 2°15' S and 40°07' - 40°10'E and is 20-40 m above sea level (Wieczkowski, 2009). Mean annual precipitation is 470 mm, and ranges from 122 mm to 1020 mm (Decker, 1994). Temperatures range from 17.5°C to 36.5°C with an annual mean minimum and maximum temperature of 21.4°C and 33°C, respectively (Wieczkowski, 2003). The lower Tana River floodplain forests are part of the East Africa Coastal Forests biodiversity hotspot (Myers et al., 2000). The forests support two of the globally threatened primate species: the Tana River red colobus (*Procolobus rufomitratus rufomitratus*), and the Tana River mangabeys (*Cercocebus galeritus*). These two species exclusively utilized the riverine forests (Wieczkowski, 2003; Kivai, 2013). The differences and similarities of the two study sites (Mchelelo & Kitere) are described in details in chapter 2.

The study sites offer ecological settings suitable for testing the role of nutritional properties of foods in primate diet selection. These is because the primate food resources in these forest fragments experience high seasonality and are dominated by important seeds and nut bearing fallback foods (Homewood, 1978; Kinnaird, 1992; Wieczkowski, 2009). The *Hyphaene compressa* and *Borassus aethiopum* are two palm-producing nuts, while *Vachellia robusta, Phoenix reclinata, Oncoba spinosa*, and *Diaspyros mesipiliformis* constitute some of the tree species

producing the hard fruits and/or seeds that are nutritionally valuable to the

mangabeys (Wieczkowski, 2003; Kivai 2013; Kivai et al., 2017).
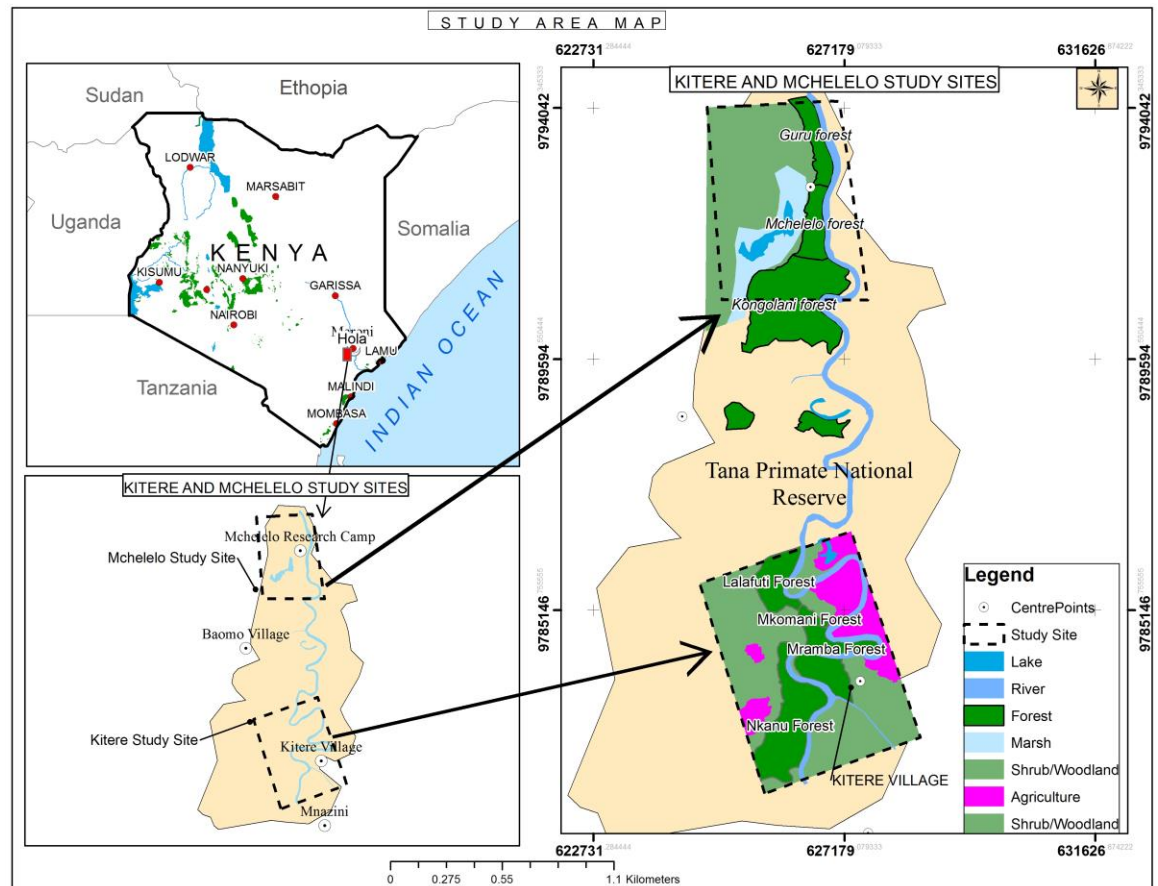
Figure 3.1. Map of the study area showing the locations of the Mchelelo and Kitere study sites (indicated by a rectangle with a broken line) within the Tana River Primate National Reserve, Kenya, in Tana River County, Coast Province, Kenya. Mchelelo study site is located in the north while Kitere study site is in the south of the reserve.

3.2.2 Study subjects & design

The study subjects were the juveniles and lactating females of the Tana River

mangabeys (*Cercocebus galeritus*) in one group in Mchelelo study site (N = 45) and

one group in Kitere study site (N = 49). I habituated both of these study groups,

positively identified all the individuals in seven months before I started data collection. I collected data on 12 lactating females, 10 juvenile males, and 9 juvenile females in Mchelelo group, and 11 lactating females, 12 juvenile males, and 9 juvenile females in the Kitere group. Overall, I had 63 study subjects from both study groups composed of 23 lactating females, and 40 juveniles. I will use the terms "study site" and "study group" interchangeably, and particularly the former when describing food and habitat attributes, and the latter when describing aspects directly relating to study subjects (the mangabeys).

I collected data on feeding behavior, nutrient intake, and food samples for nutritional analysis from October 2014 to December 2015. The nutritional analysis of the foods in the laboratory was performed later from March 2016 to February 2017 at the Primate Nutrition Ecology Laboratory at Hunter College, New York.

3.2.3 Data collection method

3.2.3.1 Feeding behavioral monitoring

I collected data for 3 – 5 days each week for approximately 21 days per month. I recorded behavioral data continuously in 10-minute focal animal sampling (Altmann, 1974). I scheduled these samples in a rotational manner whereby no individual was repeated before all other subjects were recorded. Rest intervals of approximately 5 minutes separated the focal sessions.

During the focal sampling, I recorded activity, which was one of these categories: feed, rest, move, social interactions, and other (see Appendix 3.3 for

operational definitions), and duration of the activity. When the focal was feeding, I recorded: the food species that was eaten, type of food selected, and transition times feeding on different food types. The foods eaten were categorized into "food type" (i.e., basic or general kind of food) and then into "food class" (i.e., subdivision of food into more specific food item based on state, nature, or stage of development) as follows: i). Fruit – ripe fruit, unripe fruits, fruit buds, pulp, husk, and exocarp; ii). Seed – dry seeds (old seed picked from the ground or extracted from dry fruits or pods), mature seeds (from ripe fruits or pods), and immature seeds (from unripe fruits or pods); iii). Leaf – mature leaves, young leaves, leaf buds, petioles, and grass blades; iv). Flower – open petal and sepal, closed buds; v). Nut fluid – water enclosed in palm nuts; vi). Stem – stem sap, pith, inner bark, and outer bark; and v). Deadwood – non-living dry decaying wood.

In order to obtain data needed to estimate intake rates for assessment of nutrients intake, I followed each 10-minute focal session with a 5-minute focal period in which I continuously recorded feeding rates. I focused more feeding events scored the number of food units consumed per feeding bout. I defined "food unit" as any discrete food item that the focal individual picked and put in the mouth. Typically, this was a discrete food, such as an entire fruit or leaf. In cases where monkeys fed on large items, the "food unit" was any portion of that item put in the mouth. Essentially, feeding rates reflected hand movements delivering food to the mouth. I defined "feeding bout" as a discrete unit of feeding time starting when the focal individual made its first physical contact with a food item until the time when

it terminated contact for at least 5 seconds or switched to another food item or activity.

3.2.3.2 Phenological monitoring and vegetation survey

To assess the temporal variation in food availability, I tagged 542 individual trees distributed across Kitere (N = 250) and Mchelelo (N = 292), and performed their phenological assessment once per month, starting from October 2014 to December 2015. A tree was selected for inclusion in the phenological sample in the following manner: I established line transects within the study groups home range, at an interval of 200 m apart. The transects ran from the river bank to the edge of the riverine forest and the length varied between 300 – 400m from the riverbank. I selected the trees to tag randomly along the transects, and using the riverbank as baseline, I tagged individual within 0 – 50 m, 100 – 150 m, and 250 to forest edge. These forests rely on underground water seepage from the river, and this was important to avoid potential phenological bias due to such effects. The trees selected were the 20 "Principal Plant Food Species" plus 16 other species, which I the mangabeys had frequently utilized during the habituation and pilot survey phases. I defined "Principal Plant Food Species" as species that accounted more than 1% of the overall annual diet of juvenile or adult female mangabeys. I tagged at least 10 individuals from each species, except where the species was rare, and I could not locate enough individuals. All the trees were tagged within the home range of the two study groups.

I scored the phenophase of the trees using a score of 0 to 4 based on the relative abundance of leaves, fruits, and flowers in the tree crown as described by

Morellato et al. (2010). I designated the phenological score based on the percentage of tree branches that were in any phenophase (i.e., 0 = 0%, 1 = 1 - 25%, 2 = 26 - 50%, 3 = 51 - 75%, and 4 = 76 - 100%), and in case of fruits I combined it with numerical estimates (i.e., where young leaves, mature leaves, flowers or fruits in each branch were counted in: tens = 1, hundreds = 2, thousands = 3, and in tens of thousands = 4). I categorized fruits into ripe or unripe and leaves into mature or young.

I conducted vegetation surveys in both sites to measure the relative abundance of the species. I used nested plots sampling method along line transects for the vegetation assessment (Kent & Coker, 1992; Ganzhorn et al., 2010). The plot size used was 20 x 20 m, which is recommended for forest habitats and was also ascertained to be ideal using species curve (i.e., relevé approach or minimum size area where majority if not all species were represented) (Kent & Coker, 1992). I measured vegetation in 170 plots in Mchelelo (N =76) and Kitere (N = 94) study sites along 13 lines transects in each study site (detailed sampling method described in chapter 2). The plots were placed along line transects 250 - 400 m long running from the riverbank to the forest edge in east to west direction. The line transects were placed at a distance of 200 m from each other, and along each transects the vegetation plots were laid at an interval of 50 m starting from the riverbank.

In each plot I recorded species of tree, its diameter at breast height (DBH) for trees with DBH > 5 cm; trees of each species; number of stems ranging from 1 to 14 for tall shrubs. I also measured cover of short shrubs and herbaceous species by using the Braun-Blanquet scale of 0 to 5 as described by Kent & Cocker (1992). Four

1 m x 1 m grids were randomly placed within each vegetation plot and the percentage of each herbaceous species in that area was scored as: 0 = < 1%, 1 = 1 – 5%, 2 = 6 - 25%, 3 = 26 - 50%, 4 = 51 – 75%, and 5 = 76- 100%. The mean score across the four samples was then assigned to each species in the vegetation plot.

In addition to measuring vegetation in the plots, I also estimated the abundance of insects using the same plots using 1 m x 5 m quadrant method (Kuno, 1991; Zaller et al., 2015). Within each quadrant, I scored all insects numerically and by order encountered and the total number (see chapter 2 for detailed methodology).

3.2.3.3 Nutritional Analyses of the food materials

I collected and processed food and fecal samples in the field and later performed the nutritional analyses in the laboratory following the standard procedures described by Rothman et al. (2012). I analyzed the food samples and calculated the macronutrients concentration (i.e., Neutral detergent fiber-NDF, Acid detergent fiber - ADF, Acid detergent lignin - ADL, Fat, Crude protein – CP, Available protein –AP, Acid detergent insoluble crude protein (ADICP), and Total non-structural carbohydrates – TNC) in the mangabeys foods as well as fiber digestibility in the same way and using similar equations as described in chapter 2. Thus, for detailed methodology on food sample collection, preparation, packaging, milling, and running of the laboratory assays see chapter 2.

Estimation of Nutrient Intake

I calculated the nutrient and mineral intake per minute by focal subjects following the equation used by Rothman et al. (2008a) and as modified from Altman, (1998), but I omitted snacking and daily intake components of the equation since I did not measure this in my study.

Equation 3.1*: Estimation of nutrient intake from the food by focal animals*

$$Np, x, j = [(\textstyle\sum Fi, xUiQi)/Mx]$$

Where, *Nix, j, k* = Intake of nutrient p by the focal individual x in age class j; *Fi, x* = number of food units of plant part I fed on by focal individual x; *Ui* = Average food unit mass (g) of the plant food eaten on dry matter basis; *Qi, j* = Proportion of the nutrients in the dry matter part of eaten plant part, *M, x* = Time (in minutes) the focal individual was engaged in feeding on food item or feeding bouts.

Minerals analysis

Minerals were determined by first burning the food sample in a muffle furnace at 500°C for 4 hours to obtain the ash residue, which contains the minerals. The ash remains were then suspended in 3 ml of 6N HCI and evaporated on 100 - 120°C hot plate then the minerals were extracted with an acid solution (1.5N HNO_3 + 0.5N HCI) using a Thermo Jarrel Ash IRIS Advantage HX Inductively Coupled Plasma Radial Spectrometer. Data were obtained in percent dry matter or as fed for macro-minerals (calcium, phosphorus, potassium, magnesium, and sodium) and parts per million (ppm) for micro-minerals (iron, zinc, copper, manganese, and molybdenum).

Estimation of relative intake of macronutrients and minerals (per metabolic body mass -MBM)

I obtained relative intake of both macronutrients and minerals on dry matter basis, by dividing their total intake obtained from ingesting each food item consumed during the feeding events (see operational definition in chapter 2) by the estimated metabolic body mass ($MBM^{0.75}$) of the focal individuals. To obtain basal MBM, I used the average adult female body mass of 5.30 kg reported by Gautier-Hion & Gautier (1976). Then I calculated and assigned juvenile body size (i.e., those < 2 years or >2 years of age) using the same quantitative criterion described in details in chapter 2.

Condensed tannins (CT) analysis

I analyzed the plant food samples for condensed tannins (CT) using the acid-butanol assay (butanol–HCl) followed by Porter et al. (1986) and Rothman et al. (2009). This method allowed me to qualitatively examine the presence or absence of CT in food items eaten by the Tana River mangabeys. To run the assay, I measured about 0.2g of the sample into a centrifuge tube and then added 70% acetone and capped the tube. I vortexed the tube to mix the sample and then sonicated it for 20 minutes in ice water. Using 2ml capped centrifuge tubes I added 600μl of acid butanol (5% HCL), 100μl of the sample extract, and 20 μl of iron reagent (2% $FeNH_4$ (SO_4) in 2N HCl). I repeated the same procedure to create three duplicates of sample mixture that I arranged in three rows of test tube holder and labeled row A, B, and C, whereby row C contained my control. In addition, I created a blank sample

that contained only 600µl of acid butanol, 100µl of acetone and 20µl of iron reagent, which I used to standardize the absorbance reading of the sample in the spectrophotometer. I capped all the tubes, vortexed the mixture and then heated only sample mixtures in row A and B in an oven at 90°C for about 50 minutes after which I removed and allowed the samples to cool before reading the absorbance using spectrophotometer at 550nm. The blank was first read before reading the absorbance score of all other in row A, B, and C. I recorded the absorbance score and indicated the presence or absence of CT by observing the color change of the sample.

The presence of tannin was indicated by a change of the sample color to pink while the absence of tannins was indicated by the lack of color change. In addition, I combined the used intensity or depth of color change and the absorbance score criteria (Rothman et al., 2006; Righini et al., 2017) of the sample to qualitatively describe the tannins in the foods, where absorbance value of < 0.1 indicates absence of tannins, 0.10 – 0.50 show low presence of tannins (+), 0.50 – 1.00 medium presence of tannins (++), and > 1.00 high presence of tannins (+++). Subjectively, the high presence of tannins (+++) was characterized by deep pink color change hard to see through the mixture in the test tube, while moderate (++) presence of CT (++) color change was deep but it was possible to see through the mixture in a test tube, and in case of low CT presence (+) the color change was light with a little pink coloration. The samples without CT remained colorless. Finally, to obtain the sample absorbance I averaged the sample values in row A and B and subtracted it from the values of control sample in row C to obtain the final absorbance value.

3.2.3.5 Data Analysis

To understand the influence of nutritional properties of foods on feeding aspects of the Tana River mangabeys, I first present data relating to food productivity and availability, which changes with environmental conditions and may also influence food properties and therefore, feeding strategies of the mangabeys (Hill & Dunbar, 2002). For weather, I obtained data on temperature and rainfall collected for the last six years at Hola airstrip weather station, which is located 49 km away from the Tana River Primate National Reserve, in Tana River County, in Coast Province, Kenya.

To understand temporal changes in food productivity and fruit availability, I used a total of 7,484 phenological observations, collected for 15 months from 542 tree individuals (250 and 292 individuals in Kitere and Mchelelo study sites, respectively), representing 36 tree species. I calculated mean percentages of the available young leaf, fruit, and flower from the phenological scores recorded every month. Because mangabeys eat mostly fruit and seeds, I calculated the monthly fruit availability index (FAI) for the 36 plant foods monitored throughout the study period (Fashing et al., 2001; Dasilva, 1994). I used the following equation:

Equation 3.2: *Calculation of fruit availability index (FAI)*

$Fruit\ Availability\ Index\ (FAI) = Average\ fruit\ score\ \times$

$Basal\ Area\ (BA)\ of\ species\ i$

The monthly FAI was calculated by averaging the FAI obtained from the phenological assessment of each of the 542-tagged trees individuals using equation

3.2. I calculated the Basal area (BA) as the product of tree diameter at breast height (DBH) in centimeters, a correction factor of 0.5, and pi, i.e., BA = $[0.5×DBH]^2$ ×π (Kool, 1989).

Moreover, to gain understanding on foods that are utilized by mangabeys during periods of low food resource availability to buffer effects of nutritional stress, I monitored year-round fruit productivity of the tagged mangabey plant foods to determine key fallback foods. I adopted the recommended operational definition of "fallback foods" those foods whose consumption by mangabeys was in inverse proportion to the availability of their preferred food resources (Marshall et al., 2009). Therefore, food species, which had fruits throughout the year or fruit availability and consumption coincided with period of low abundance of preferred foods were considered fallback foods.

To understand the nutritional chemistry of the dietary composition of the and mangabeys and test the predictions relating to food nutrition, I first calculated the average macronutrients content of the foods consumed by mangabeys, expressed as a percentage of dry matter of food ingested. Moreover, I expressed protein and other macronutrient intake in both absolute and per metabolic body mass in grams (g) of the dry matter of food consumed based on the total number of food units consumed. For minerals, I estimated the concentrations in foods as a percentage of total intake and parts per million (ppm) on dry matter basis for macro-minerals and micro-minerals, respectively. I expressed absolute and relative intake of mineral intake by focal individuals in the same manners as I did for

macronutrient intake.

For the macronutrients analysis, I used the nutritional data from the 394 food samples collected. I excluded samples of cultivated crops that were raided by the monkeys and samples with no feeding observations captured in focal feeding data. To perform all the analyses relating to nutrient intake, I matched the nutritional data from specific food samples obtained from the laboratory analysis with the corresponding field feeding data from the same month. In cases where nutritional data were missing for a particular focal feeding observation, I used the nutritional average across all the samples collected in the month (Conklin-Brittain et al., 2006; Rothman et al., 2006).

In order to test the prediction (P2) that juveniles ingest more essential minerals relative to body mass than females, for each food type (e.g., fruit, leaf, bark, etc.) and each food class (e.g., ripe, unripe) eaten, I randomly selected one sample from Mchelelo and one sample from Kitere to analyze, which came to a total of 217 samples. I first estimated total mineral intake on the basis of dry matter (g), and then matched the laboratory analyses with field focal data in a similar way as I did for estimation of macronutrients intake per feeding event.

To test my prediction (P3) that mangabeys will forage selectively to avoid foods high in condensed tannins and will consumed more foods free or lower in CT compared to those high concentration in CT, I qualitatively analyzed the presence or absence of condensed tannins in the dietary composition of the Tana River mangabeys. I used data from 163 unique samples (Mchelelo – 117, Kitere – 46) that

I analyzed. I compared the percentage of food samples that contained CT and those free of such compounds. For samples that tested positive for CT, I examined the percentage of those containing low (+), medium (++), and high (+++) levels of CT.

Statistical analysis

To test my predictions (P1 & P2) relating to the nutritional properties of foods and dietary intake, I used linear models (i.e., Generalized Linear Mixed Models - GLMMs, and Generalized Linear Models - GLM one-way analysis of variance (ANOVA), Kruskal-Wallis test, chi-square, and t-tests. I performed one-way ANOVA and student t-test to compare the mean percentages of fruit, leaves, and flowers productivity within and between sites as well as variation across months. To understand the effects of monthly variation in food availability I used GLM, where I examined how availability index (FAI) fruit as a response (dependent) variable changed in response to month and study site as fixed effects (independent variable).

To compare the variation in general macronutrient concentrations of the overall mangabey dietary composition different and in general food types eaten, I used Kruskal-Wallis test and Dunn's correction for multiple comparisons. However, I utilized GLM to compare the macronutrient levels in various food classes in each food type (i.e., food developmental stage or state e.g., ripe fruits, unripe fruits, dry fruit, immature seeds, mature seeds, young leaves, mature leaves, outer bark, inner bark, mushroom caps, among others). I fitted a model with percent macronutrient concentrations as the response variable, and food class as a fixed effect.

To test my predictions that compared to lactating females, juveniles: have higher relative intake of protein (P1), and essential macro-minerals (P2), I constructed different GLMMs. The response, fixed, and random variables were selected based on the test variables of the prediction test and possible influential factors to be controlled.

Before fitting and running any statistical test or model, I checked the data to ensure they met the required assumptions for each particular test used and especially normal distribution of the data. I used quantile-quantile (q-q) plots to test data normality where the Shapiro–Wilk test could not be used due to sample size limitations. Where data were not normally distributed, I performed either log or inverse log transformations. I used nonparametric tests where a normal distribution of data was not possible with transformation.

For all the statistical tests performed in the analyses, alpha was set at 0.05. I performed all the statistical analysis using R statistical software version 3.3.2 (R Core team (2013). First, I selected the best variable and model to test my prediction test by constructing a full model, which included all variables that were likely to have some effect on the test outcome. Second, I fitted reduce models that eliminated effects of a single variable at a time. I then compared all the models using analysis of variance (anova) in R, and finally selected the significant model that had the lowest Akaike information criterion (AIC) value as the best model fit for my analysis.

I fitted and ran the following models for each prediction: **P1** - I fitted a GLMM whereby I assessed how both absolute and relative intake of available protein (as

response factor) varied with response to age class and season (as fixed effects) while controlling for focal ID and study group (as a random effect). Season referred to either period or study months of low fruit availability (FAI < 50% percentile i.e., 43.83) or high fruit availability (FAI > 50% percentile). I did this in two steps: first with only age class as fixed effect controlling for season, and second, including season as fixed effect. Even though I did not have a prediction on other macronutrients (i.e., neutral detergent fiber, Fat, and total non-structural carbohydrates), I as well examined their intake between juveniles and adults in similar way as the available protein intake.

P2 - I fitted a similar GLMM as I used to test P1, but instead I used macro-minerals and micro-minerals intake as response factor, and included season as fixed variables since I was not testing for the monthly variation in mineral intake.

Finally, to test my prediction **(P3)** that in general mangabey dietary composition constitutes more foods free or low in condensed tannins (CT), I used the Chi –square goodness of fit. I compared the percentage of mangabey foods that were free versus those contained CT. In similar manner, I further assessed the percentages of foods that qualitatively contained high (+++), medium (++), and low (+) levels of tannins.

3.3 Results

Before testing my predictions relating to nutritional properties of foods and juvenile foraging, I first present weather data illustrating the rainfall and temperature patterns of my study site. This is fundamental because the two environmental variables either operating independently or interactively with other factors potentially influence the quantity, quality, and seasonal dynamics of food resources. Second, I present descriptive data on monthly phenological patterns as an indication of seasonal food availability.

3.3.1 Rainfall and temperature patterns of the study

The weather data for six years (2010 – 2015) obtained from Hola airstrip weather station showed that the area received a bimodal rainfall pattern (Fig. 3.2). The wet seasons occurred between October to December and March to May. The wettest months in each of these two rain seasons were November (mean $\pm$ SEM = 124.20 $\pm$ 16.35 mm) and March (102.60 $\pm$ 73.44 mm). The short dry period occurs between January and February while the extended dry period occurred between June and September.
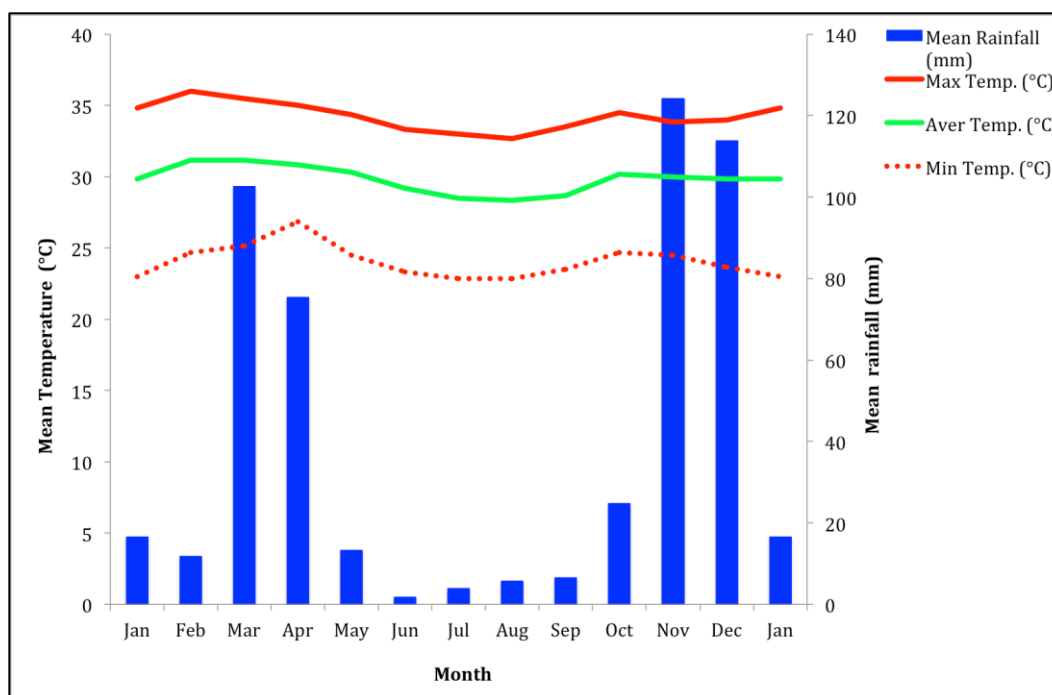
Figure 3.2. Mean monthly rainfall and temperature (mean, maximum & minimum) for six consecutive years (2010 to 2015). Data obtained at Hola airstrip weather station, in Tana River County.

During the short dry period, February was the hottest month with an average temperature ($\pm$ SEM) of 31.17 $\pm$ 0.17°C, a monthly maximum of 36.00 $\pm$ 0.89°C and a monthly minimum of 24.67 $\pm$ 0.42°C. The same month was also the hottest of the year. During the long dry spell between June and September, the latter was the hottest month with average temperatures of 28.67 $\pm$ 0.52°C, and a maximum of 33.50 $\pm$ 0.43°C, and a minimum of 23.50 $\pm$ 0.34°C.

3.3.2 Phenological patterns of food productivity

3.3.2.1 Spatial and temporal phenological changes

The wet and dry seasons did not coincide with high or low peaks in food productivity (Fig. 3.3). Thus, I considered actual monthly phenological changes as more informative of seasonal variation in food productivity than the weather

delimited seasons. Consequently, henceforth I will use term month also to imply seasonal changes.

a) Overall phenological pattern as an indicator of food productivity

Combined phenological data for both Kitere and Mchelelo study sites revealed changing trends of young leaves, fruits, and flower productivity (Fig 3.3). Young leaves in general were relatively higher compared to fruits and flowers, except in August 2015, when fruits slightly overshot. Typically, flowers maintained lower percentage levels than leaves and fruits over the entire period of my study. November 2014 (26.42% ± 4.2%), August 2015 (20.84% ± 4.87%), and March 2015 (7.67% ± 1.97%) were characterized by the highest percentage of young leaves, fruits, and flowers, respectively. December 2015 exhibited the lowest levels of young leaves (8.31% ± 1.11%), fruits (7.81% ± 2.13%), and flowers (0.58% ± 0.26%) (Fig. 3.3).
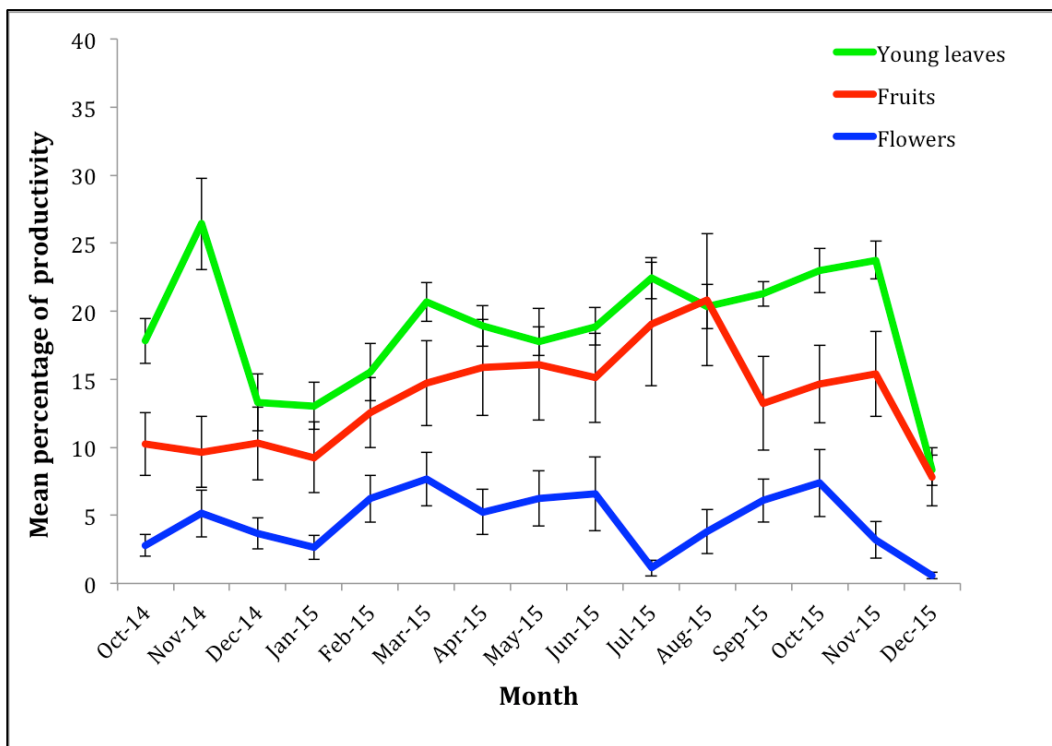
Figure 3.3. Productivity of young leaves, fruits, and flowers of the Principal Plant Food Species and other plant species commonly consumed by the mangabeys. Mean percentage of productivity (y axis) is the phenophase score (0 -100%) recorded every month for 15 months. Data pooled for the two study sites (N = 542 trees representing 36 species and 7484 observation records, error bars indicate the standard error)

Generally, November 2014 and the period from March to November 2015 were characterized by high young leaves abundance, but a shortfall of young leaves was experienced between December 2015 to February 2015 and December 2015. July and August exhibited the highest fruit productivity while the period of fruit scarcity was from October 2014 to January 2015, and December 2015. Flowers increased between February and June 2015 as well as September to October 2015, but declined in October 2014, January, July and December 2015 (Fig 3.3). Statistically, only the young leaves showed overall significant difference across the

months (F = 9.25, df = 14, p < 0.0001, N = 15) but not fruits (F = 2.15, df = 14, p = 0.0831) and flowers (F = 1.98, df = 14, p = 0.0751). December 2014, December 2015, and January 2015 experienced lower productivity of young leaves compare to the peak months (November 2014, March 2015, July 2015 and November 2015) in leave abundance (p < 0.05).

b) Spatial variation in productivity of young leaves, fruits and flowers in Kitere and Mchelelo study sites

Mchelelo and Kitere study sites experienced great variation in food productivity (Fig 3.4). The annual productivity of young leaves in Mchelelo (mean ± SEM = 20.21% ± 1.55%) exceeded that in Kitere (14.08% ± 2.19%). Compared to Kitere (7.91% ± 2.26%), fruit abundance was more than double in Mchelelo (16.08% ± 3.80%). This was also true for flowers in Mchelelo (5.69% ± 2.02%), which were twice as much as the annual percentage in Kitere (2.37% ± 0.89%). Fruit productivity in Mchelelo was significantly higher than Kitere (t = 2.87, df = 14, p = 0.0122, N = 15 months) as well as flowers (t = 2.30, df = 14, p = 0.0382, N = 15 months), but there were no difference in young leaves between the two sites (t = 1.87, df = 14, p = 0.0826, N = 15 months).

c) Temporal variation in young leaves, fruits and Flowers in Kitere and Mchelelo

The abundance of young leaves, fruits and flowers also varied within each study site over time (Fig. 3.4). At the Kitere study site, the monthly average (± SEM) of young leaves ranged from 6.67% ± 1.06% (April 2015) to 32.82% ± 4.34% (November 2014), while the average fruit productivity was between 2.92% ± 0.93%

(June 2015) and 13.37% (February 2015). Among the three food categories in Kitere, flowers were the most scarce, recording 0.18% ± 0.12% and 9.67% ± 3.00% for the lowest and highest average scores, respectively. Young leaves showed in Kitere displayed four peaks November 2014 (32.8%), February 2015 (17.3%), July - 2015 (12.4%), and October 2015 (14.4%), while fruits three peaks (December 2014 (12.7%), February 2015 (13.4%), and October 2015 (11.8%). Flowers as well peaked in November 2014 (6.7%), February 2015 (9.7%), and slightly in September 2015 (2.8%).

Mchelelo study site experienced a different pattern of food productivity (Fig. 3.4). Young leaves averaged (± SEM) between 5.18% ± 0.94% (December 2015) and 28.39% ± 094% (September 2015) demonstrating almost similar range as fruit, which varied between 4.3% ± 1.63% (December 2015) and 28.51% ± 6.25% (August 2015). Compared to young leaves and fruits, flowers were more than twice as rare, and displayed a narrower range of 0.61% ± 0.35% and 12.30% ± 4.14% in December 2015 and October 2015, respectively. Young leaves abundance increased sharply in November 2014, reaching 18.9%, before falling to as low as 8.8% in February 2015, after which they rose and remained relatively higher (above 20%) from March to November 2015. The percentage of fruits remained lower than leaves throughout the study period, except in August when fruits overshot the young leaves (Fig. 3.4). Fruits in Mchelelo exhibited one major peak in August 2015 (28.5%), but there were minor peaks in April 2015 (22.5%) and November 2015 (21.3%). The percentage of the flower yield in Mchelelo remained lower than fruits

and young leaves in across all the study months (Fig 3.4). However, three peaks were evident in March 2015 (11.5%), June 2015 (9.4%), and October 2015 (12.3%).
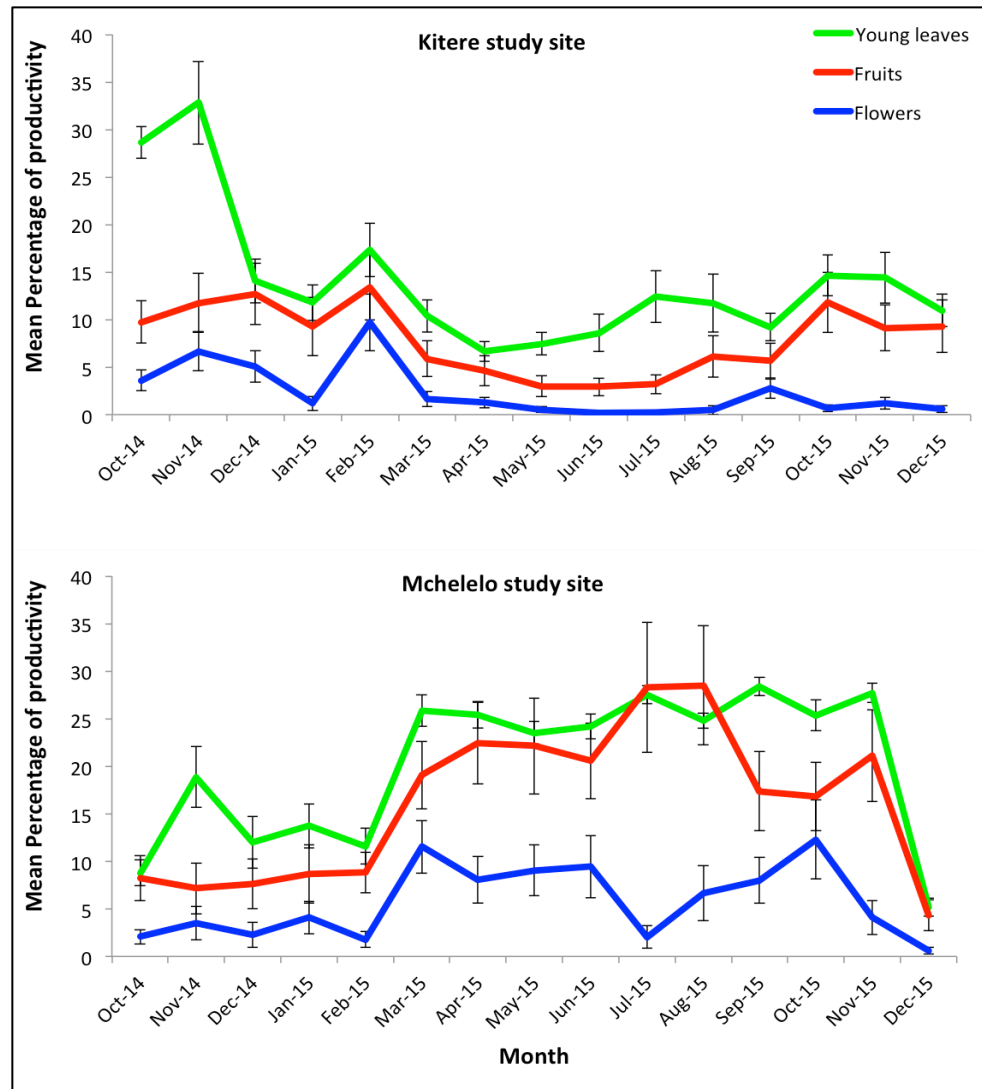
Figure 3.4. Productivity of young leaves, fruits, and flowers of the Principal Plant Food Species and other plant species commonly consumed by the mangabeys in Kitere (top) and Mchelelo (bottom) study sites. Mean percentage of productivity (y axis) is the phenophase score (0 -100%) recorded every month for 15 months (N = 542 trees representing 36 species and 7484 observation records, error bars indicate the standard error).

3.3.2.2 Fruit productivity of common fallback foods

The eight species, which constituted key mangabeys' fallback foods based on monthly fruit productivity, availability and inclusion in the annual diet, were: *Diaspyros mesipiliformis*, *Ficus sycomorus*, *Hyphaene compressa*, *Oncoba spinosa*, *Synsepalum msolo*, *Phoenix reclinata*, *Sorindeia madagascariensis*, and *Vachellia robusta*. Among these species, *Ficus sycomorus, Oncoba spinosa, Hyphaene compressa*, and *Diaspyros mesipiliformis* had fruits throughout the year. These four species contributed more than 10% to the fruit diet in any given month except for latter, which had no fruits between October and December (Fig. 3.5). *Ficus sycomorus* produced more fruits than other trees in all the months except in October – November 2014 and August 2015 when *Vachellia robusta* and *Diaspyros mesipiliformis* fruiting peaked, respectively. The fruit peak of *Ficus sycomorus* was observed in July 2015 (56.5%) while the lowest was in the October 2014 (10.4%). *Phoenix reclinata,* which was the highest-ranking annual diets of mangabeys, had fruits for about 8 months (October 2014 – August 2015) peaking in February (26.6%). The fruiting peak of *Vachellia robusta* was in November 2014 (63.5%), and the dropped seeds persist in the forest floor year-round and were consumed continuously. Overall, three food species (*Ficus sycomorus*, *Synsepalum msolo,* and *Vachellia robusta*) had positive electivity index (see chapter 2) suggesting they were more sought compared the other fallback foods.
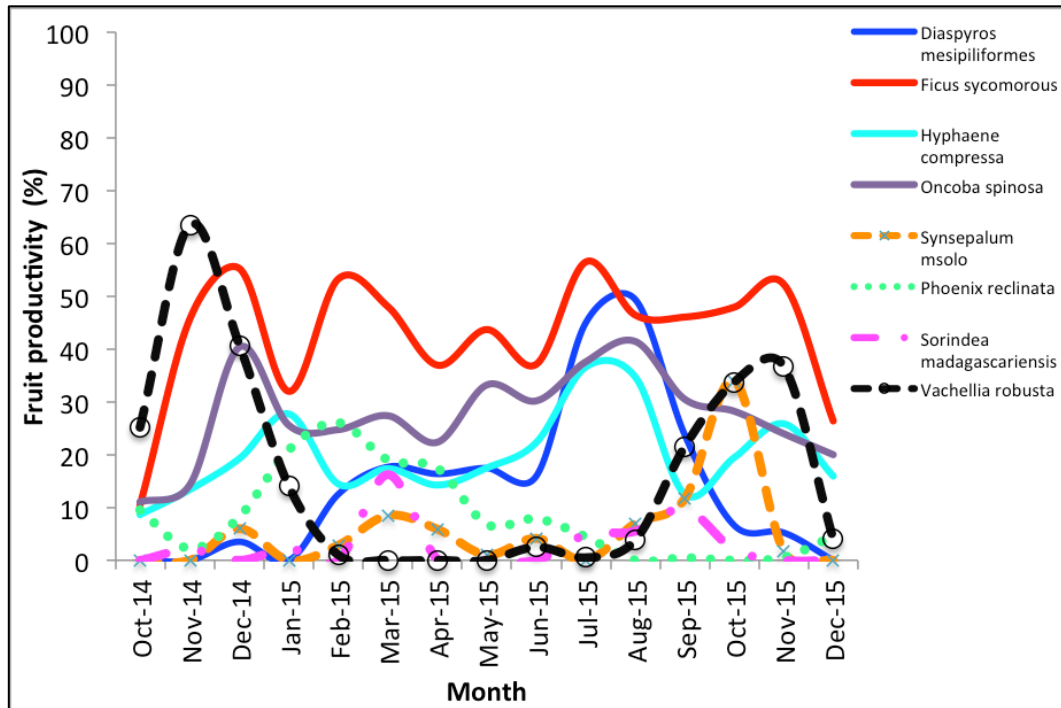
Figure 3.5. Monthly fruit productivity among the eight fallback food species consumed by juveniles and lactating females in both Kitere and Mchelelo study sites (N = 1,200 observations, 80 trees individuals from 8 species).

3.3.2.3 Fruit availability

a) Fruit availability index (FAI) between study sites

The two study sites experienced variable levels of fruiting (Fig. 3.6). The fruit availability index (FAI) in Mchelelo (mean ± SEM = 123.30 ± 32.07) was more than four times greater than that in Kitere study site (29.62 ± 0.76). The same was true for basal area (BA), and Mchelelo (mean ± SEM = 712.33 ± 77.36 cm²/ha) recorded three times more the basal area registered in Kitere (244.55 ± 17.48 cm²/ha). Both the mean FAI (t = -3.30, df = 1021, p = 0.0002, N = 540) and the BA (t = -3.839, df = 1042, p = 0.0001, N = 36 tree species were significantly higher in Mchelelo compared to Kitere study site.
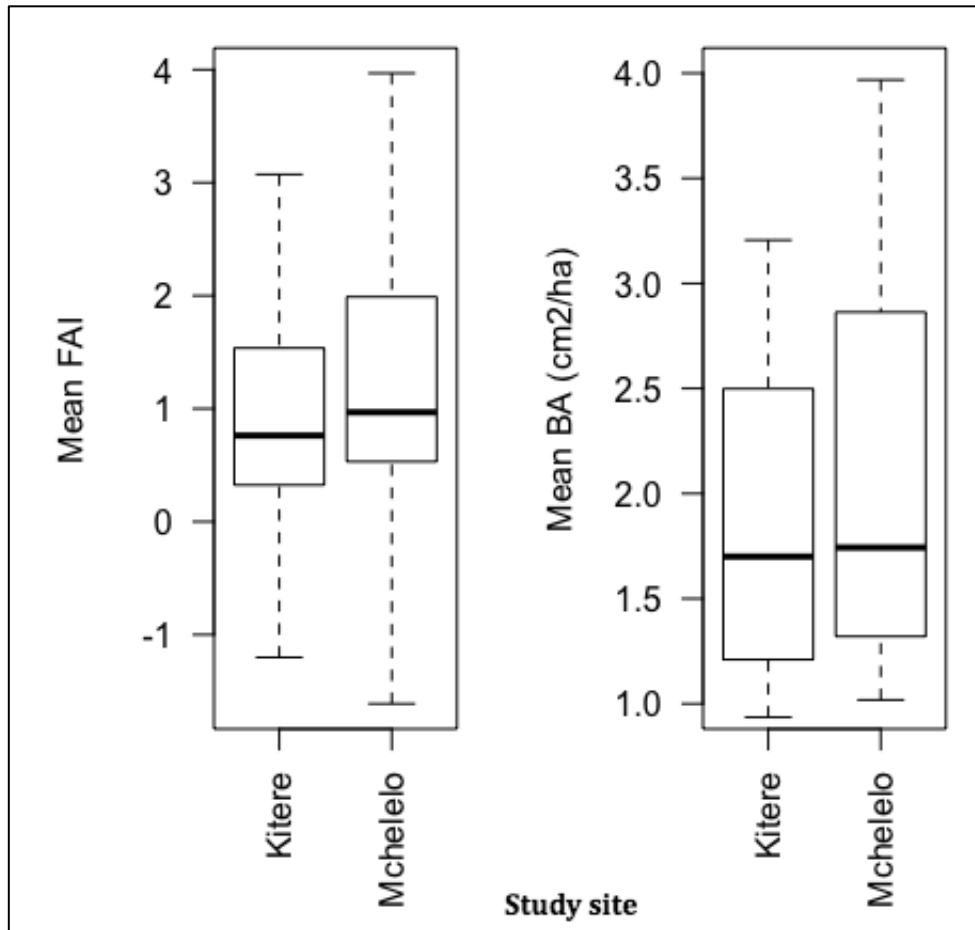
Figure 3.6. Fruit Availability Index (FAI) and Basal Area (BA) of plant foods consumed by Tana River mangabeys in Kitere and Mchelelo study sites. Data are log transformed and error bars indicate standard deviation.

b) Seasonal variation in fruit availability

The low and high seasons of fruit availability were designated based on fruit availability index (FAI). Study months or period characterized by fruit availability index lower than 50% percentile (i.e., FAI < 43.83) were considered as season of low fruit availability while those with FAI more than 50% percentile as season of high fruit availability. This criterion was based on the examination of overall pattern of

annual fruit availability and picking the median of the FAI data set as the boundary between the two seasons (Fig. 3.7).
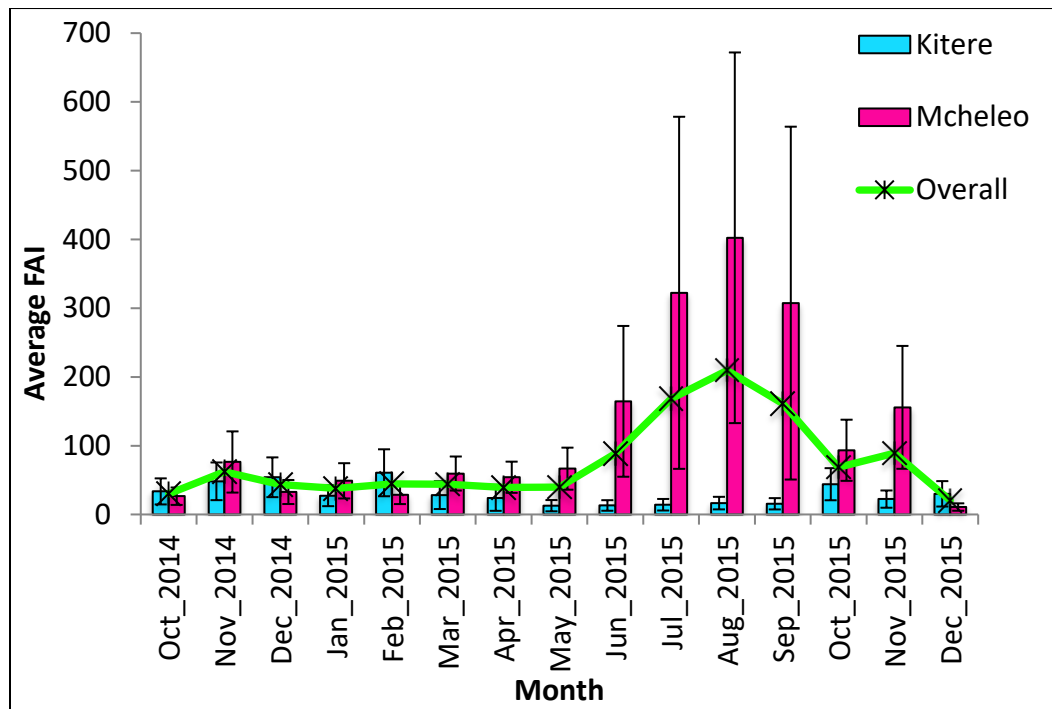
Figure 3.7. Mean monthly variation in Fruit Availability Index (FAI) in Kitere, Mchelelo, and both sites (overall) from data recorded in Kitere and Mchelelo (N = 15 months, 36 species, 540 individual trees, error bars indicate standard error). The green line indicates the monthly average FAI for the two study sites.

Fruit availability index fluctuated across seasons (i.e., study months) in the two study sites (Fig 3.7). In Mchelelo, the highest FAI was recorded in November 2015 (mean ± SEM = 402.40 ± 269.54) while the lowest was in December 2015 (10.77 ± 5.39; Fig. 3.7). This marked the peak of fruit availability during the season of high fruit availability and the highest decline in fruit availability during season of low fruit availability, respectively. Kitere recorded the highest FAI in August 2015 (60.63 ± 34.13) while the lowest was in May 2015 (12.75 ± 8.19) indicating the peak in fruit abundance over the season of high fruit availability and period of fruit

scarcity during the period of low fruit availability. Overall, FAI was significantly higher in Mchelelo compared to the Kitere study site (t = -2.89, df = 564, p = 0.004, N = 15).

c) Species variation in Basal Area (BA) and Fruit Availability Index (FAI)

The three plant food species that recorded the highest FAIs were Sterculia appendiculata (mean ± SEM = 1,150.17 ± 502.23), Borassus aethiopum (527.19 ± 49.47), and Ficus sycomorus (344.95 ± 36.02) (Table 3.1). Alternatively, Sterculia appendiculata (4,808.76 ± 833.44), Ficus bussei (3,145.88 ± 577.78), and Tamarindus indica (1,423.87 ± 54.41) had the highest BA (cm^2/ha). Pavetta sphaerobotrys had the lowest FAI as well as BA (FAI = 2.88 ± 0.85, BA = 11.72 ± 0.05).

The plant FAI in overall varied significant across species (F = 29.47, df = 35, p < 0.0001, N = 36 species). *Sterculia appendiculata, Borassus aethiopum,* and *Ficus sycomorus* differed significantly from all other species in FAI (p = 0.0001) when I performed post hoc analysis. Basal area also varied significantly across species (F = 144.20, df = 35, p < 0.0001, N = 36 species). Sterculia appendiculata, Ficus bussei, and Tamarindus indica had significantly higher BA compared to all other species (p < 0.0001).

Table 3.1. The twenty species with the highest average Fruit Availability Index (FAI) and their corresponding Basal area (BA), standard error of the mean (SEM), standard deviation (SD), and maximum (Max.) values.

Species	Fruit Availability Index				Basal Area cm2/ha			
	Mean	SEM	SD	Max.	BA	SEM	SD	Max.
Sterculia appendiculata	1150.17	520.23	2849.44	9296.95	4808.76	833.44	4564.92	9296.95
Borassus aethiopum	527.19	49.47	270.95	1183.36	1256.1	52.54	287.8	1539.06
Ficus sycomorus	334.95	36.02	197.31	758.17	628.23	29.24	160.14	785.67
Ficus bussei	258.11	150.81	826.02	3128.65	3145.88	577.78	3164.61	6257.31
Vachellia robusta	135.21	35.2	192.81	552.69	597.56	27.73	151.86	746.87
Hyphaene compressa	93.86	16.58	90.81	390.49	372.03	7.98	43.72	415.02
Tamarindus indica	45.4	12.79	70.04	251.93	1423.87	45.41	248.7	1668.39
Ficus natalensis	41.27	9.15	50.13	158.84	314.4	20.91	114.51	426.99
Diospyros mespiliformis	32.86	11.36	62.21	254.34	145.98	19.35	105.97	250.17
Ficus bubu	30.62	12.08	66.16	273.93	481.13	13.04	71.45	551.38
Synsepalum msolo	30.43	17.76	97.26	473.8	443.05	72.42	396.67	833.05
Majidea zanguebarica	10.73	3.89	21.28	83.89	65.1	10.49	57.45	121.58
Garcinia livingstonei	10.71	3.36	18.39	79	96.77	5.32	29.12	125.4
Phoenix reclinata	5.56	1.12	6.16	17.97	60.73	0.56	3.05	63.73
Mimusops fruticosa	5.16	2.5	13.68	68.39	139.84	10.69	58.56	197.42
Oncoba spinosa	4.2	0.41	2.23	9.62	13.62	0.37	2.05	15.64
Polysphaeria multiflora	3.56	0.89	4.88	17.61	17.97	0.07	0.38	18.35
Saba comorensis	3.42	0.71	3.9	15.81	30.77	0.97	5.31	35.99
Pavetta sphaerobotrys	2.88	0.85	4.66	12.62	11.72	0.05	0.3	12.02

3.3.3 Nutritional analysis of mangabey foods

3.3.3.1 Macronutrient variation

a) *Overall nutrient concentration*

Macronutrient concentrations differed across the plant foods consumed by the Tana River mangabeys (Fig. 3.8, Appendix 3.2). Overall, the foods contained on average (± SEM) 40.04% ± 0.95% Neutral Detergent Fiber (NDF), 35.75% ± 0.83% Acid Detergent Fiber (ADF), 15.49% ± 0.53% Acid Detergent Lignin (ADL), 4.50% ± 0.22% Fat, 9.68% ± 0.42% Available Protein (AP), and 28.30% ± 0.90% Total Non-structural Carbohydrates (TNC) (Fig. 3.8).
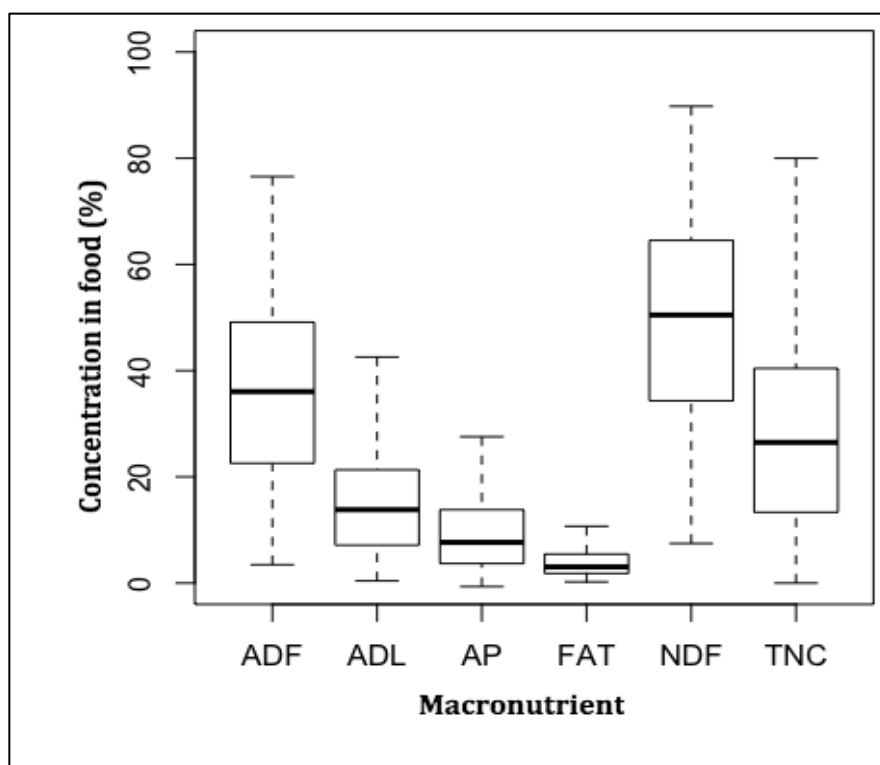
Figure 3.8. Average concentration of macronutrients (Acid Detergent Fiber – ADF, Acid Detergent Lignin – ADL, Available protein – AP, Fat – FAT, Neutral Detergent fiber – NDF, Total Non-structural carbohydrates – TNC) in the mangabey foods (N = 394 food samples, representing 75 species, error bars indicate standard deviation).

These macronutrient concentrations varied significantly in the foods eaten by the mangabeys (H = 1414, p < 0.001, N = 6 macronutrients, 394 food samples). Post hoc Dunn's multiple comparison test indicated that the percentage content of fiber in the foods, particularly NDF and ADF, exceeded the content of fat, AP, TNC, and ADL (p < 0.0001) The foods contained significantly lower percentages of fat compared to NDF, ADF, AP and TNC (p < 0.0001), while the TNC content surpassed AP concentration in the foods (p < 0.0001). Overall, the foods were high in fiber (NDF, ADF) and TNC, but low in fat and AP.

b) *Variation in macronutrients across food types*

The food types (basic or general kind of food e.g., fruit, leaves) utilized by the Tana River mangabeys differed in nutrient concentrations (Fig. 3.9). Deadwood had the highest amount of NDF (mean ± SEM = 89.78% ± 0.00%) and ADF (76.55% ± 0.00%), which was about twice the average NDF and ADF content in other foods (Fig. 3.9). Mushrooms and gum recorded the lowest NDF (35.73% ± 2.27%) and ADF (14.33% ± 1.33%), respectively. The average percentage of ADL ranged from 6.78% ± 1.30% in mushrooms to 20.81% ± 2.05% in bark. Mushrooms in general had the lowest percentage of fiber content among all the food types.

Fat concentration also varied greatly among mangabey foods with seeds having the highest concentration of fat (mean ± SEM = 5.50% ± 0.61%) compared to the other plant foods. Insects, however, contained almost twice as much fat as in seeds (9.03% ± 1.75%). Deadwood and pith were the most deficient in fat containing as little as 0.33% ± 0.00% and 1.64% ± 0.27%, respectively. Non-plant foods, specifically insect (50.31% ± 3.83%) and mushroom (26.91% ± 5.11%), were

the richest in protein content among all the foods consumed. Protein concentration was five times and three times higher in insects and mushrooms, respectively, compared to all other foods (Fig. 3.9). Subterranean structures (42.00% ± 0.00%) and gum (35.18% ± 16.78%) exhibited the highest concentration of TNC compared to other foods, while pith (14.40% ± 3.98%) and insects (12.44% ± 4.57%) had the lowest percentages.

Food types consumed by the mangabeys differed in fiber (NDF, ADF, ADL), fat, AP, and TNC (Fig. 3.9). The NDF was statistically significant across the food types (H = 28.14, df = 10, $p < 0.0017$, N = 387 samples) as well as ADF (46.90, df = 11, $p < 0.0001$, N = 394), and ADL (H = 33.61, df = 10, $p = 0.0002$, N = 387). Dunn's multiple comparison tests indicate that, compared to mushroom, bark had significantly higher NDF, ADF, and ADL ($p < 0.05$). Stem also contained higher NDF and NDF than mushrooms and insect, respectively ($p < 0.05$). However, seeds exhibited lower ADL compared to leaves, fruits, and bark ($p < 0.05$). Other food types did not show any significant difference in NDF, ADF, and ADL content.

Fat concentration in mangabey foods was the lowest among all the macronutrients (Fig. 3.9). The concentration of fat in various food types varied significantly (H = 60.14, df = 11, $p < 0.0001$, N = 394 samples). The post hoc analysis confirmed that the concentration of fat in insects was significantly higher compared to that found in stem, leaves, and bark ($p < 0.05$). Similarly, seeds and fruits had significantly higher fat content than leaves and stem, while the concentration in mushrooms exceeded that found in stem ($p < 0.05$).

Concentration of available protein (AP) among the food types was remarkably high in insects and mushrooms compared to other foods (Fig. 3.9). The percentage of AP concentration across the food types varied significantly ($H = 94.02$, $df = 11$, $p < 0.001$, $N = 394$ samples). The post hoc analysis revealed that, AP content in insects and mushroom significantly surpassed the content in bark, seed and fruit as well as stem for the former ($p < 0.05$). The AP content in leaves also exceeded the concentrations in seed and fruit ($p < 0.05$).

Different food types ingested by mangabeys exhibited variable concentrations in total non-structural carbohydrates (Fig. 3.9). The discrepancies in TNC percentage in foods were statistically significant ($H = 25.63$, $df =$, $p = 0.0047$, $N = 394$ samples). However, Dunn's multiple comparison test failed to detect significant differences across the foods ($p > 0.05$).
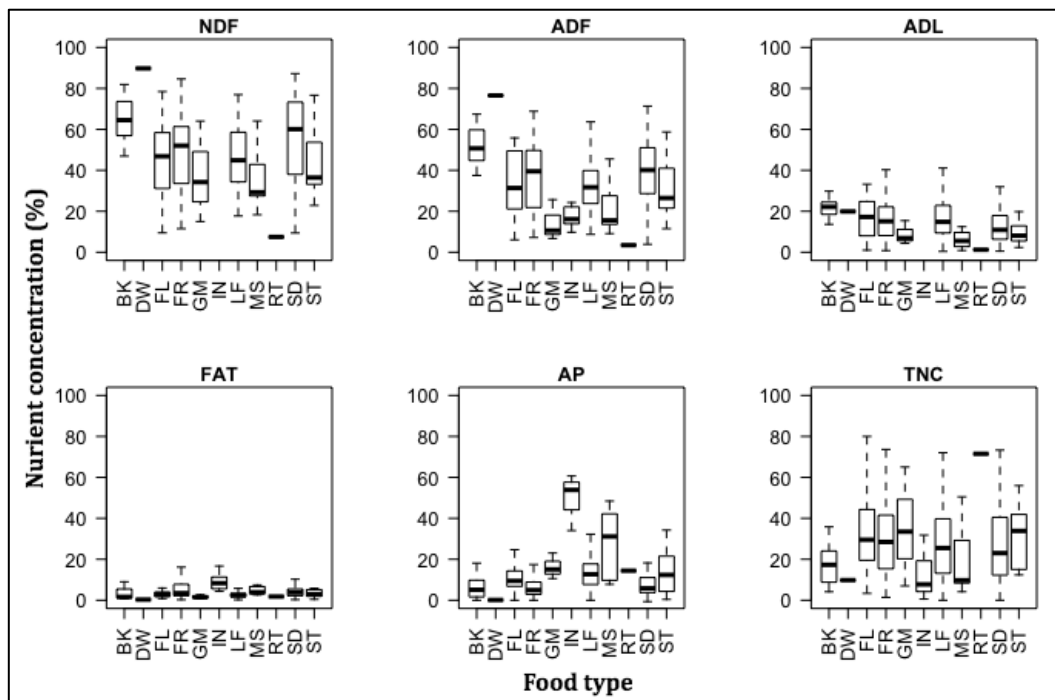
Figure 3.9. Mean percentage of fibers (neutral detergent fiber - NDF, acid detergent fiber – ADF &, acid detergent Lignin - ADL), fat, available protein (AP) and total non-structural carbohydrates in bark (BK), deadwood (DW), flowers (FL), fruits (FR), gum (GM), insects (IN), leaves (LF), mushrooms (MS), subterranean structures (RT), seeds (SD, and stems (ST) for the 397 food samples eaten by juveniles and lactating females (error bars are mean standard deviation)

c) Nutrient concentration in different classes of food

The various food classes (more specific subdivision of food type e.g., ripe fruit, unripe fruit, inner bark, outer bark) consumed by the mangabeys varied in concentration of NDF, ADF, fat, AP, and TNC (Table 3.2). Excluding deadwood tissue, outer bark had the highest fiber content (mean $\pm$ SEM = NDF - 74.44% $\pm$ 5.18%; ADF (61.10% $\pm$ 5.36%). This was more than twice the amount of NDF found in mushrooms cap & stem (33.89% $\pm$ 5.47%) and more than four times the ADF in mushrooms' cap alone (16.83% $\pm$ 3.80%). Dry seeds (6.99% $\pm$ 1.97%) contained the highest fat content among the food classes and contained slightly less the fat content in insect skeletal tissues (9.03% $\pm$ 1.75%). Among the plant food classes, mature leaves (15.60% $\pm$ 2.96%) and immature seeds (15.60% $\pm$ 1.32%) had the highest AP. However, the AP content was about three times less than that found in insect exo-skeletons (50.31% $\pm$ 3.83%) and about twice less in mushrooms' cap (39.13% $\pm$ 4.10%). Subterranean structures had the highest TNC content (38.25% $\pm$ 16.76%) and exceeded the concentration in mushrooms' cap (7.63% $\pm$ 1.75%) by more than five times (Table 3.2).

The statistical analysis (i.e., GLMs) indicated that the food classes differed from in other in macro nutrient concentrations (Table 3.2). Relative to the intercept

(i.e., inner bark), the discrepancies in NDF concentrations (Intercept = 89.78% ± 18.11%, t = 4.96, df = 19, p = 0.0001, N = 21 food classes) as well as ADF (Intercept = 76.00% ± 15.30%, t = 5.003, df, p < 0.0001, N = 21 food classes) in various classes of foods were significant (Table 3.2). The NDF in mature leaves, mushrooms (stems & caps), ripe fruits, mature seeds, subterranean structures, unripe fruits, and young leaves was significantly lower than the intercept (p < 0.05). However, the ADF was significantly lower in: insect skeletal tissues, mature leaves, gum, and mushroom caps (p < 0.0001); unripe fruits, seeds & husks, shoot, and subterranean structures (p < 0.001); and mature seeds, young leaves, ripe fruits, mushroom caps & stems, flowers, and dry seeds (p < 0.01). The ADL content in the food classes did not differ significantly (p > 0.05).

The various food classes also demonstrated significant differences in both fat (intercept = 0.33% ± 4.08%, t = 0.08, p = 0.0469, N = 21 food classes) and AP levels (intercept = 0.13% ± 7.23%, t = 0.018, p = 0.98, N = 21 food classes). Compared to inner bark fat and AP content, insect skeletal tissues showed higher content of fat (p = 0.0473), but all other food classes did not indicate any significant variation (p > 0.05). For AP the insect skeletal tissues, mushroom caps/caps & stems, and mature leaves contained more AP than inner bark.

Table 3.2. Percentage of macronutrients concentration in different classes of food consumed by mangabeys in the Tana River forests patches (± SEM; (n) = the number of samples analyzed; N/A – implies a single sample was analyzed or test was not performed). The food classes are: Deadwood tissue - DT, Dry fruits - DF, Dry seeds - DS, Flowers - FL, Gum - GM, Inner bark - IB, Mature leaves - ML, Mushroom caps - MC, Mushroom caps & stems - C&S, Outer bark - OB, Petiole - PL, Pith - PT, Ripe & unripe fruits - R&UF, Ripe fruits - FR, Mature seeds - RS, Subterranean structures (S. structures) - RT, Young stem - ST, Unripe fruits - UF, Immature seeds - US, and Young leaves - YL, Exo- & endoskeleton - EES.

Food Type	Food Class	NDF	±	ADF	±	ADL	±	FAT	±	AP	±	TNC	±
Bark	IB (11)	62.41	5.05	50.59	4.69	19.78	2.39	2.00	0.95	5.92	4.92	19.28	3.26
	OB (3)	74.44	5.18	61.10	5.36	24.85	3.63	1.55	0.62	4.72	2.62	13.07	4.50
Stem	ST (7)	54.24	6.98	41.02	5.81	12.44	2.37	2.22	0.47	9.61	4.34	24.12	6.85
	PT (7)	67.06	5.33	53.07	4.82	15.89	1.56	1.58	0.28	7.15	3.32	15.25	2.78
Fruit	DF (6)	54.81	5.30	45.88	6.00	33.79	8.36	4.71	0.97	5.74	0.77	25.95	5.91
	R&UF (8)	59.30	3.05	43.07	1.79	15.66	0.55	6.05	1.13	7.84	1.49	20.38	3.02
	RF (91)	47.40	1.93	35.74	1.66	16.12	1.14	5.76	0.54	5.72	0.52	32.31	1.90
	UF (40)	50.71	3.09	37.92	2.97	15.75	1.58	4.56	0.56	7.75	0.79	29.48	2.81
Leaf	ML (8)	34.42	6.09	19.94	2.81	7.32	1.21	4.91	1.14	15.60	2.96	32.88	6.19
	PL (1)	45.07	NA	25.22	NA	0.41	NA	6.31	NA	15.30	NA	23.95	NA
	YL (83)	55.84	7.21	37.96	6.73	16.61	3.73	2.93	0.47	11.08	2.02	20.81	5.97
Mushroom	C (3)	37.55	5.02	16.83	3.80	4.75	1.11	3.32	0.17	39.13	4.10	7.63	1.75
	C&S (8)	33.89	5.47	23.34	4.83	8.95	3.19	6.13	1.28	22.33	6.20	23.51	5.93
Seed	DS (18)	41.94	6.02	28.98	4.67	10.07	2.06	6.99	1.97	10.88	1.67	35.52	5.26
	RS (32)	55.32	5.85	36.03	4.18	12.47	1.80	5.01	1.23	10.65	1.28	20.08	4.20
	US (32)	50.65	3.81	38.84	3.45	16.6	1.99	4.91	0.55	15.6	1.32	25.99	3.37
Deadwood	DT (1)	89.78	NA	76.55	NA	19.93	NA	0.33	NA	0.13	NA	9.82	NA
Flower	FL (24)	44.2	3.72	33.16	3.06	16.93	2.11	3.65	0.64	10.77	1.21	32.44	3.80
Gum	GM (3)	37.76	14.27	14.33	5.78	8.89	3.35	1.67	0.56	16.23	3.64	35.18	16.78
Insect	EES (7)	NA	NA	17.47	2.10	NA	NA	9.03	1.75	50.31	3.83	12.44	4.57
S. structures	RT (4)	46.86	16.81	35.71	12.42	13.61	4.40	3.35	2.45	5.17	0.93	38.25	16.76

d) Macronutrient concentration of Principal Plant Food Species

The Principal Plant Food Species (i.e., those contributing > 1% of the annual diets of both juveniles and lactating females) had varying levels of the macronutrients (Table 3.3). Phoenix reclinata contained the highest concentration of both NDF and ADF (67.83% ± 2.49% & 48.00% ± 2.29%, respectively). The fat concentration was highest in Synsepalum msolo (11.04% ± 4.96%) and Oncoba spinosa (10.98% ± 0.92%), which was more than six times the levels in Hyphaene compressa, and the least in fat content (1.65% ± 0.17%). Vachellia robusta whose young leaves, green seeds and dry seeds were utilized by the mangabeys contained the highest AP (20.38% ± 2.64%), which was less than half the AP content in insects (Table 3.3). Mango (Mangifera indica) contained the highest level of TNC (54.96% ± 5.01%), which was almost double the average percentage of TNC in all foods. Mangabeys consumed utilized flowers, young leaves, ripe and unripe fruits, and dry seeds from this species.

Table 3.3. Mean percentage of neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), fat, available protein (AP) and total nonstructural carbohydrates (TNC) of the important food plants eaten by the juveniles and lactating females (± is standard error of mean - SEM).

Food Species	% Nutrient concentration (± SEM)											
	NDF	±	ADF	±	ADL	±	FAT	±	AP	±	TNC	±
Phoenix reclinata	67.83	2.49	48.00	2.29	15.36	2.25	3.46	0.32	5.39	0.66	18.81	2.52
Ficus sycomorus	55.09	1.66	44.99	1.88	25.04	2.60	5.65	0.41	4.24	1.21	25.66	2.11
Vachellia robusta	36.35	3.76	20.70	2.41	7.73	1.15	2.88	0.41	20.38	2.64	34.08	4.23
Synsepalum msolo	38.58	7.97	32.03	8.48	13.42	3.80	11.04	4.96	15.87	7.42	28.61	8.42
Hyphaene compressa	49.55	5.29	31.20	3.97	13.22	2.41	1.65	0.17	2.77	0.41	34.44	6.03
Agaricus sp.	35.73	2.27	22.71	2.03	6.78	1.30	4.59	0.54	28.81	2.81	14.94	2.60
Oncoba spinosa	26.43	2.66	18.89	2.25	8.29	1.01	10.98	0.92	6.21	0.47	43.46	2.61
Sorindeia madagascariensis	40.61	6.10	25.70	3.89	9.91	1.56	2.75	0.41	11.96	1.50	37.75	6.84
Diospyros mespiliformis	65.82	4.74	44.47	2.84	12.52	2.41	2.75	0.53	5.24	1.54	19.26	3.71
Grewia densa	63.32	4.21	46.90	4.28	19.68	2.69	3.08	0.79	9.43	1.23	16.31	2.99
Polysphaeria multiflora	61.26	2.51	49.31	2.44	28.37	2.63	2.96	0.31	5.84	0.90	22.73	2.34
Brachiaria subquadripara	67.67	1.89	36.84	2.26	10.15	2.52	2.80	0.55	14.51	1.30	3.63	1.26
Mimusops fruticosa	54.50	3.53	40.03	3.62	18.11	3.43	6.86	1.62	12.37	4.02	17.06	4.47
Pavetta sphaerobotrys	54.25	3.58	35.85	2.27	15.19	0.96	3.27	0.29	10.86	0.29	22.33	3.44
Alangium salviifolium	43.13	6.53	31.06	5.73	15.44	2.57	1.92	0.24	20.01	2.61	26.79	6.31
Mangifera indica	29.64	4.35	23.15	4.32	11.94	2.92	4.27	0.88	6.99	2.00	54.96	5.01
Garcinia livingstonei	36.31	9.51	24.72	6.92	10.04	2.69	5.52	1.81	7.77	2.54	43.82	12.01
Cissus rotundifolia	50.33	5.35	42.17	5.16	21.63	1.90	2.01	0.27	5.74	0.72	28.08	4.57
Drypetes natalensis	49.54	7.18	38.75	7.05	16.27	3.08	7.24	3.20	10.62	3.36	23.23	4.36
Lecaniodiscus flaxinifolius	29.39	2.38	20.53	2.10	12.80	1.51	6.02	1.48	9.79	1.73	50.07	3.98
Insect	0.00	0.00	17.47	2.10	0.00	0.00	9.03	1.75	50.31	3.83	12.44	4.57

3.3.4 Protein and other nutrient intake: Juveniles versus lactating females

To test my prediction (**P1**) that juveniles have a higher intake of protein than the lactating females, I examined the variation in protein intake between age classes and with fruit availability. I compare both absolute intake and relative intake of AP per minute.

3.3.4.1 Protein Intake between juveniles and lactating females

a) Overall age class variation in protein intake

Juveniles and lactating females diverged more in their relative intake of AP and slightly in the absolute intake (Fig. 3.10). Absolute mean in grams ($\pm$ SEM) protein intake per minute on dry matter basis by the juveniles was 0.60 ± 0.01, while for the lactating females it was 0.61 ± 0.02. Relative AP intake (i.e., per MBM) by juveniles was on average of 0.18 ± 0.004 while the lactating females ingested 0.12 ± 0.004 (Fig. 3.10). Absolute intake of AP did not vary with age class (F = 0.28, df = 1, p =0.6015, N = 63) but relative AP intake varied significantly (F = 23.77, df = 1, p < 0.0001, N = 63), controlling for focal ID. The per minute analysis of absolute AP intake showed that juveniles consumed similar amounts of AP than lactating females (t = 0.53, df = 62, p = 0.6010, N = 63), but for relative intake of AP, juveniles consumed significantly more AP per unit body mass than (t = -8.52, df = 67, p < 0.0001, N = 63). This result was consistent with my prediction (P1) that juvenile AP intake per metabolic body mass between will be higher than that of lactating females.
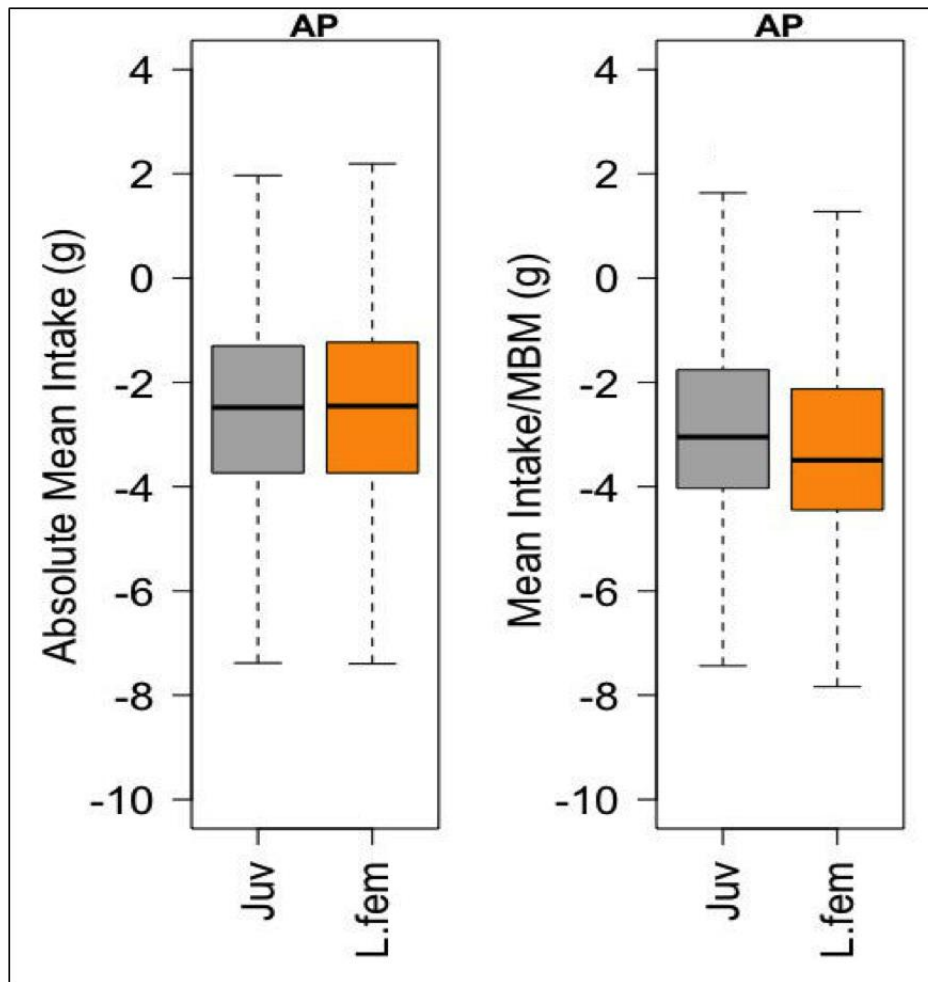
Figure 3.10. Absolute mean intake (left) and mean intake per metabolic body mass (MBM) (right) of the available protein (AP) expressed as total intake in grams (g) of dry matter between juveniles and lactating females. Data combined for Kitere and Mchelelo study groups and transformed using inverse log, error bars are mean standard deviation, N = 63 focal individuals, 20,486 feeding events).

ii) Protein intake variation with age class and season of fruit availability

Available protein (AP) intake by juveniles and lactating females varied considerably over seasons of both high and low fruit availability (Fig. 3.11). The per minute analysis indicated that the absolute mean AP was similar between age class

(F = 0.40, df = 1, p = 0.5297) but differed significantly in response to season of fruit availability (F = 6.15, df = 1, p = 0.0131) controlling only for focal ID. Lactating female consumed the same amount of absolute protein compared to juveniles (t = 0.63, df = 1, p = 0.5297) but absolute intake of AP was significantly higher during periods of high fruit availability compare to low fruit availability (t = 2.48, df = 1, p = 0.013) (Fig. 3.11).

The per minute analysis of AP per MBM varied significantly in response to age class (F = 22.46, df = 1, p < 0.0001) and season of fruit availability (F = 6.73, df = 1, p < 0.0095). Juveniles exhibited a higher relative AP intake than the lactating females over the study period (t = -4.74, df = 1, p < 0.0001) while relative intake of AP was significantly higher during the season of high fruit availability compared to when fruits were limited (t = 2.59, df =1, p < 0.0095) (Fig. 3.11). The findings on available protein per metabolic body mass supported the prediction that juveniles will ingest more protein compared to lactating females, per unit of body mass, the two age classes will maximize intake of protein during the season of high fruit abundance.
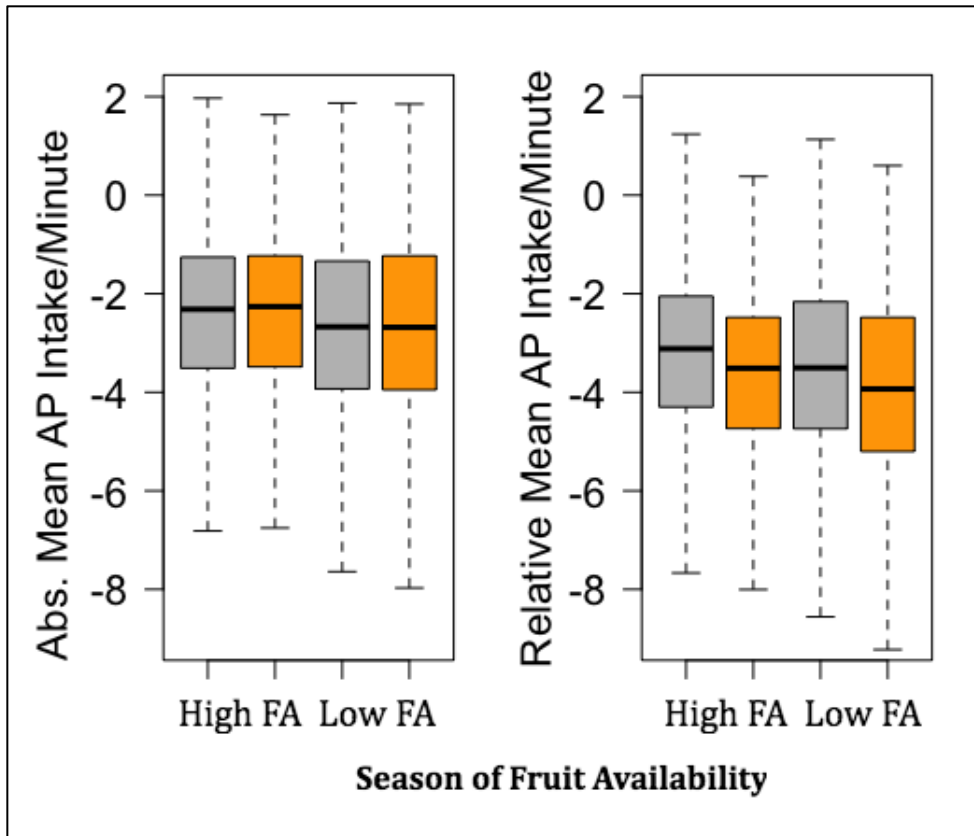
Figure 3.11. Seasonal variation (i.e., period of high versus low fruit availability-FA) in absolute (Abs.) mean total available protein (AP) intake per minute and per metabolic body mass (MBM) expressed in grams of dry matter between juveniles and lactating females (N = 63 individuals, error bars represent mean standard deviation).

b) Non-protein nutrient intake

i) Age classes variation in available non-protein intake

While I did not have any prediction on non-protein macronutrient intake, I appreciate that such nutrients are as well important and influence juveniles feeding. Even though protein intake is necessary for growth and lactation and may be more limited in primate foods, other macronutrients are essential as key sources of energy and maintenance. Thus, I felt necessary to examine how intake of non-

protein nutrients (NDF, Fat, and TNC) varied with age class both in absolute and relative intake per minute. In addition, I assessed the seasonal variation of non-protein macronutrients intake on basis of fruit availability as I did for protein. These data are important and may be relate to protein intake.

Absolute intake of non-protein nutrients: Consumption of non-protein nutrients on absolute basis exhibited some variation between juveniles and lactating females (Fig. 3.12). Absolute intake of the three macronutrients did not vary in response to age class, and compared to lactating females, juveniles ingested similar amounts of NDF (F =0.02, df =62, p = 0.8820; t = 15, df = 1, p = 0.8820), fat (F = 0.18, df = 62, p = 0.6700; t = 0.43, df = 1, p =0.6700), and TNC (F = 0.06, df = 1, p = 0.8040; t = 0.25, df = 62, p = 0.8040) controlling for focal ID.

Relative intake of non-protein nutrients: Juveniles and lactating females differed considerably in the per minute relative intake of NDF, fat and TNC (Fig. 3.12). Intake per metabolic body mass (MBM) of non-protein nutrients varied significantly with response to age class, particularly in the intake of NDF (F = 18.00, df = 1, p < 0.0001), fat (F = 8.87, df = 1, p = 0.0044), and TNC (F = -3.34, df = 1, p = 0.0015). Juveniles exceeded that of lactating females in the intake of NDF (t = -4.24, df = 1, p < 0.0001, N =63), fat (t = -2.96, df = 1, p < 0.0044, N =63) and TNC (t = -3.34, df =1 p < 0.0015) (Fig. 3.12).

ii) Non-protein nutrient intake variation with season or fruit availability

Absolute Intake of non-protein macronutrients

Absolute consumption of non-protein nutrients exhibited great variation in between age classes and across season of fruit availability (Fig. 3.13). Statistically,

there were no age class differences in absolute intake of non-protein nutrients intake and compared to lactating females, juveniles ingested similar amount of NDF (F =0.6, df =1, p = 0.8008; t = 0.25, df = 1, p = 0.8008), fat (F = 0.25, df = 1, p = 0.6215; t = 0.50, df = 1, p = 0.6215), and TNC (F = 0.12, df =1, p = 0.7353; t = 0.34, df = 1, p = 0.7353) controlling for focal ID.

Absolute intake of non-protein macronutrients also differed significantly in response to fruit availability and intake during the periods of high fruit availability exceeded that exhibited during low fruit availability for both juveniles and lactating females (Fig. 3.13). This was true for NDF (F = 9.88, df = 1, p = 0.0017; t = 3.14, df = 1, p = 0.0017), fat (F = 5.13, df = 1, p = 0.0236; t = 2.26, df = 1, p = 0.0236), and TNC (F = 8.96, df =1, p = 0.0028; t = 2.99, df = 1, p =0.0028) (Fig. 3.13).

Relative intake of non-protein macronutrients

Relative (per metabolic body mass - MBM) intake of non-protein macronutrients showed major differences between age classes and across season of fruit availability (Fig. 3.13). The ingestion of NDF per metabolic body mass, varied significantly with age class (F = 16.90, df = 1, p < 0.0001, N = 63). This was also consistent for fat (F = 5.28, df = 1, p < 0.0216, N = 63) and TNC (F = 10.46, df = 1, p = 0.0020, N = 63). Juveniles exceeded lactating females in their relative intake of NDF (t = -4.11, df = 1, p < 0.0001), fat (t = -2.40, df =1, p = 0.0001), fat (t = -2.88, df = 1, p = 0.0054), and TNC (t = -3.23, df = 1, p < 0.0020) (Fig. 3.12).
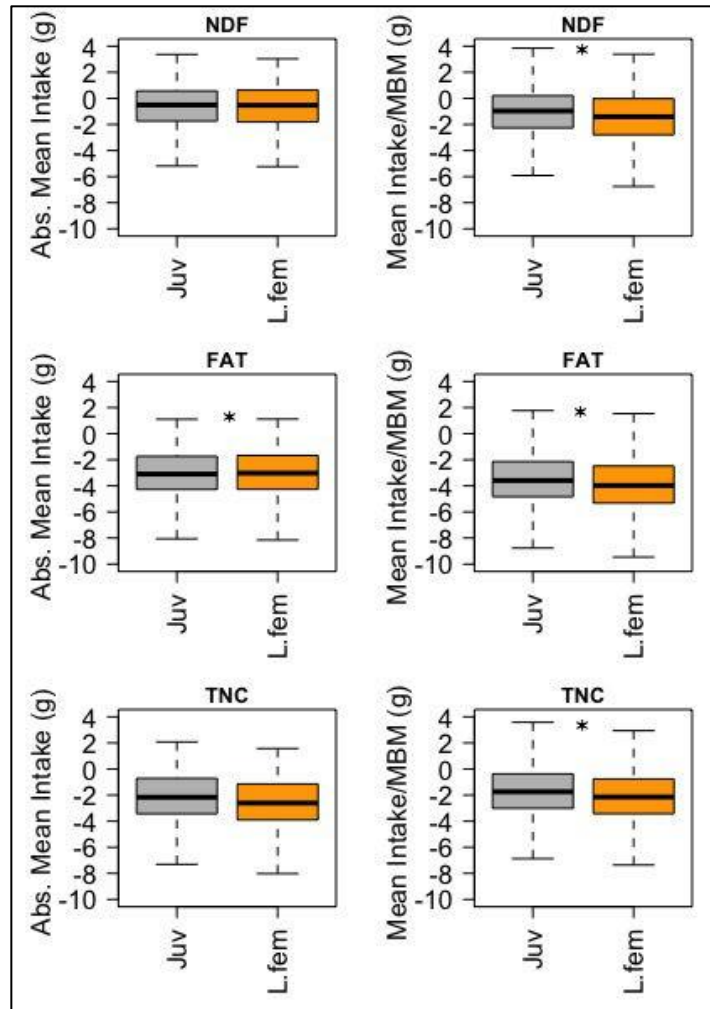
Figure 3.12. Absolute (Abs.) mean intake (left) and mean intake per metabolic body mass (MBM) (right) of non-protein nutrients (NDF, Fat, TNC) expressed in grams (g) of dry matter intake per minute between juveniles (Juv) and lactating females (L.Fem). Data inverse log (ln) transformed data, error bar is standard deviation, asterisk (*) indicates significant difference $p < 0.05$, N = 63 focal individuals, 20,486 feeding events.

Over the study period, significantly differences were evident in the relative

intake of NDF (F = 10.35, df = 14, p = < 0.0001, N = 2 seasons of fruit availability), fat

(F = 5.28, df =1, p < 0.0216), and TNC (F = 3.05, df = 14, p = 0.0023) with response

to season of fruit availability. Compared to the season of high fruit availability,

during the period of low fruit availability period both juveniles and lactating females

exhibited a higher intake of NDF (t = 3.22, df = 1, p = 0.0013), fat (t = 2.30, df = 1, p = 0.0216), and TNC (t = 3.05, df = 1, p = 0.0023) (Fig. 3.13).
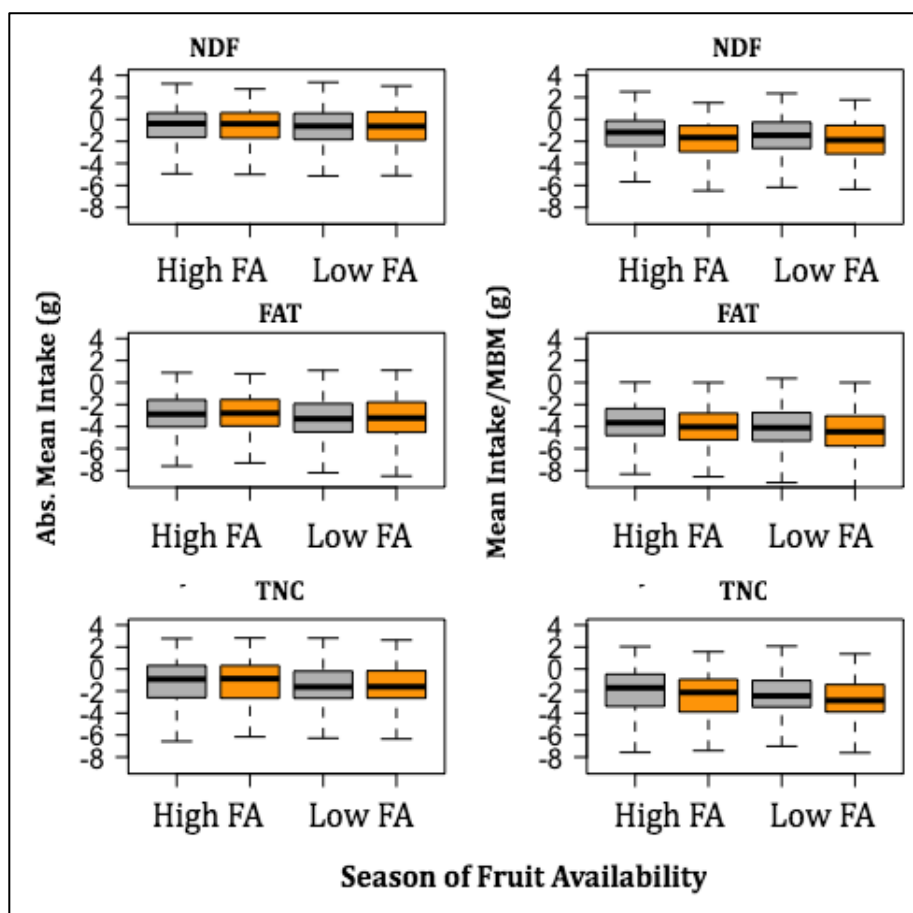
Figure 3.13. Seasonal variation (i.e., period of high versus low fruit availability-FA) in the per minute absolute (Abs.) mean intake and per metabolic body mass (MBM) of Neutral detergent fiber (NDF), Fat, and Total non-structural carbohydrates (TNC) expressed in grams of dry matter between juveniles and lactating females (N = 63 individuals, error bars represent mean standard deviation).

3.3.5 Mineral content of the mangabeys dietary composition

3. 3.5.1 Description of mineral profiles in mangabey dietary composition

a) *Macro-mineral variation in foods*

Foods consumed by the mangabeys were higher in potassium (K) and calcium (Ca) than in phosphorus (P), magnesium (Mg), and sodium (Na) (Fig. 3.14). Overall, the mangabey foods had a low percentage of macro-minerals content. Calcium was highest in bark and leaves (mean ± SEM = 2.11% ± 0.34% & 1.07% ± 0.15%, respectively) and lowest in dry seeds (0.14% ± 0.00%) and mushrooms (0.01% ± 0.02%). Phosphorus was highest in mushrooms (1.36 ± 0.21%) and lowest in gum (0.05% ± 0.01%). Mushrooms contained more than three and half times the percentage of phosphorus content in stems (0.38% ± 0.05%) the second ranking food item in phosphorus content. Leaves had the highest concentration of magnesium (0.35% ± 0.03%) while deadwood had the least amount (0.12% ± 0.00%). Mushrooms contained the highest percentage of potassium (4.71% ± 0.66%), and the concentration was more than one and half times as much as that found in stems (2.78% ± 0.52%). Overall, sodium had the lowest concentrations in all the food items compared to other macro-mineral, and it was found in high percentage in gum (0.26% ± 0.00%) (Fig. 3.14).

b) *Micro-mineral variation in foods*

The micro-minerals (trace elements) contained in different food types also varied (Fig. 3.15). Mushrooms had the highest amount of copper (Cu) (mean ± SEM = 60.83 ± 21.59 ppm), which was almost five times more abundant than in flowers (12.38 ± 1.26 ppm). Deadwood and stems had the least content in copper (3.00 ± 0.00 ppm & 3.40 ± 0.98 ppm, respectively). Gum (1223.50 ± 406.50 ppm) contained the highest concentration of iron (Fe) followed by mushrooms (513.70 ± 166.70

ppm). Deadwood and dry seeds contained the least amount of iron (113.00 $\pm$ 0.00 & 124.00 $\pm$ 29.00 ppm, respectively). Leaves and stems ranked highest in manganese (Mn) concentration (47.43 $\pm$ 5.23 ppm & 42.60 $\pm$ 13.22 ppm, respectively). Molybdenum (Mo) was the most limited micro-mineral and was highest in dry seeds (1.70 $\pm$ 1.20 ppm) and bark (1.38 $\pm$ 0.13 ppm). Fruits (0.37 $\pm$ 0.03 ppm) and flowers (0.39 $\pm$ 0.28 ppm) were the most deficient in molybdenum. Zinc (Zn) was abundant in mushrooms (109.17 $\pm$ 10.52 ppm), which was almost three times as much the amount found in stems (35.40 $\pm$ 7.08 ppm). Zinc was, however, most limited in gum (5.500 $\pm$ 1.05 ppm) and deadwood (9.00 $\pm$ 0.00 ppm).

Statistical comparison of mineral concentration in foods

Statistically, the foods consumed by mangabeys differed significantly in macro-minerals concentrations (H = 717.90, df = 4, p < 0.0001, N = 5 macro-minerals, 217 food samples) (Fig. 3.14). Potassium was statistically higher in the foods compared to the concentration of phosphorus, magnesium, and sodium (p < 0.0001). Calcium levels in the mangabeys' diet were also significantly higher compared to magnesium and sodium (p < 0.0001).
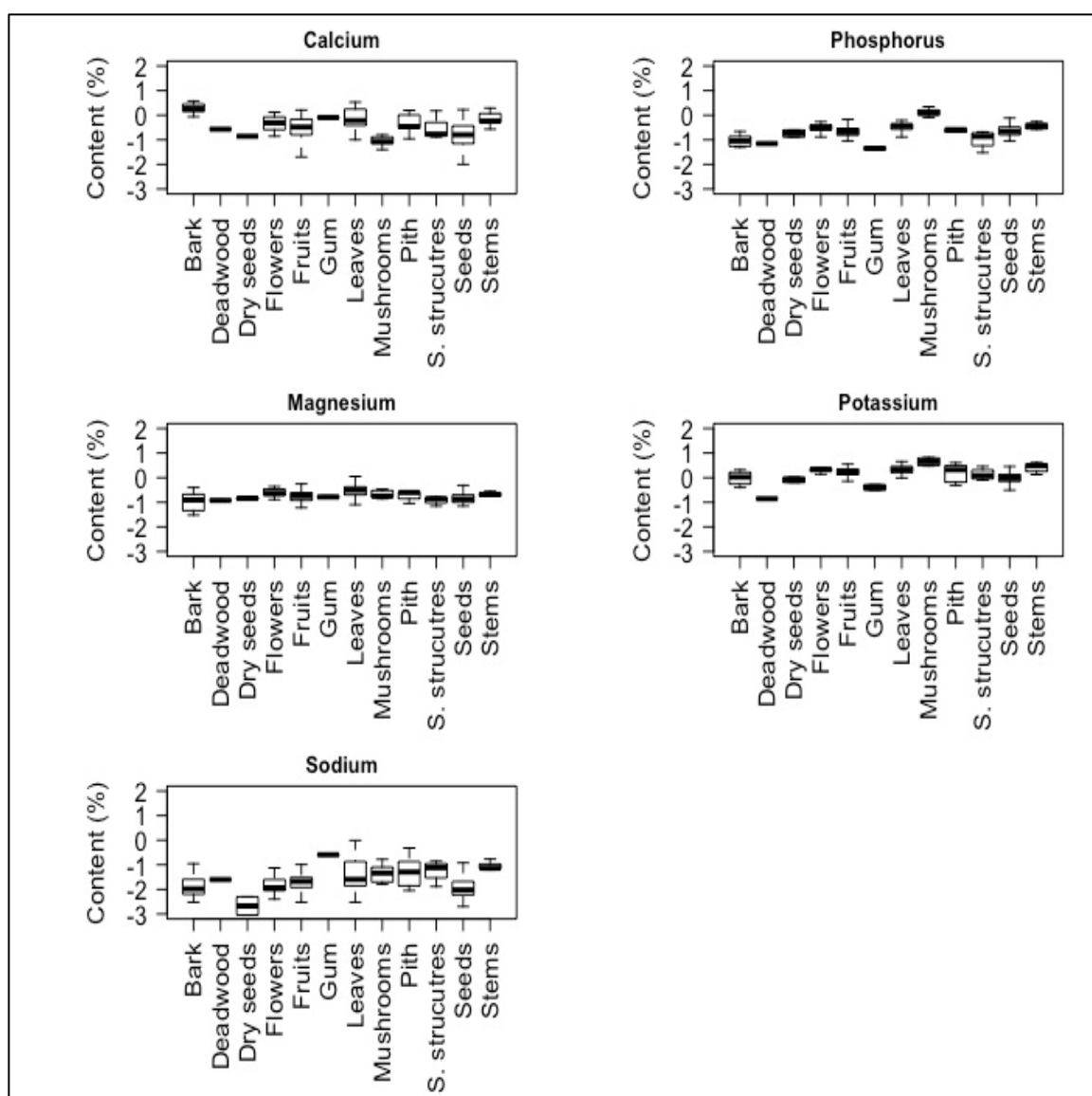
Figure 3.14. Mean percentages of macro-minerals content on the dry matter basis of the 217 foods consumed by juveniles and lactating females (data log transformed, and error bars indicate the standard deviation, S. structures = Subterranean structures**.**

The micro-minerals concentrations in the mangabeys' foods as well varied significantly as well (H = 868.40, p < 0.0001, N = 5 micro-minerals, 217 food samples) (Fig. 3.15). Based on Dunn's multiple comparison analysis, iron concentration in the foods was significantly higher than that of zinc, manganese,

copper, and molybdenum ($p < 0.0001$). Zinc and manganese occurred in almost equal concentrations, but they were significantly higher than copper and molybdenum ($p = 0.0001$). Molybdenum was the most limited and was statistically lower than the other four micro-minerals (Fig 3.15).
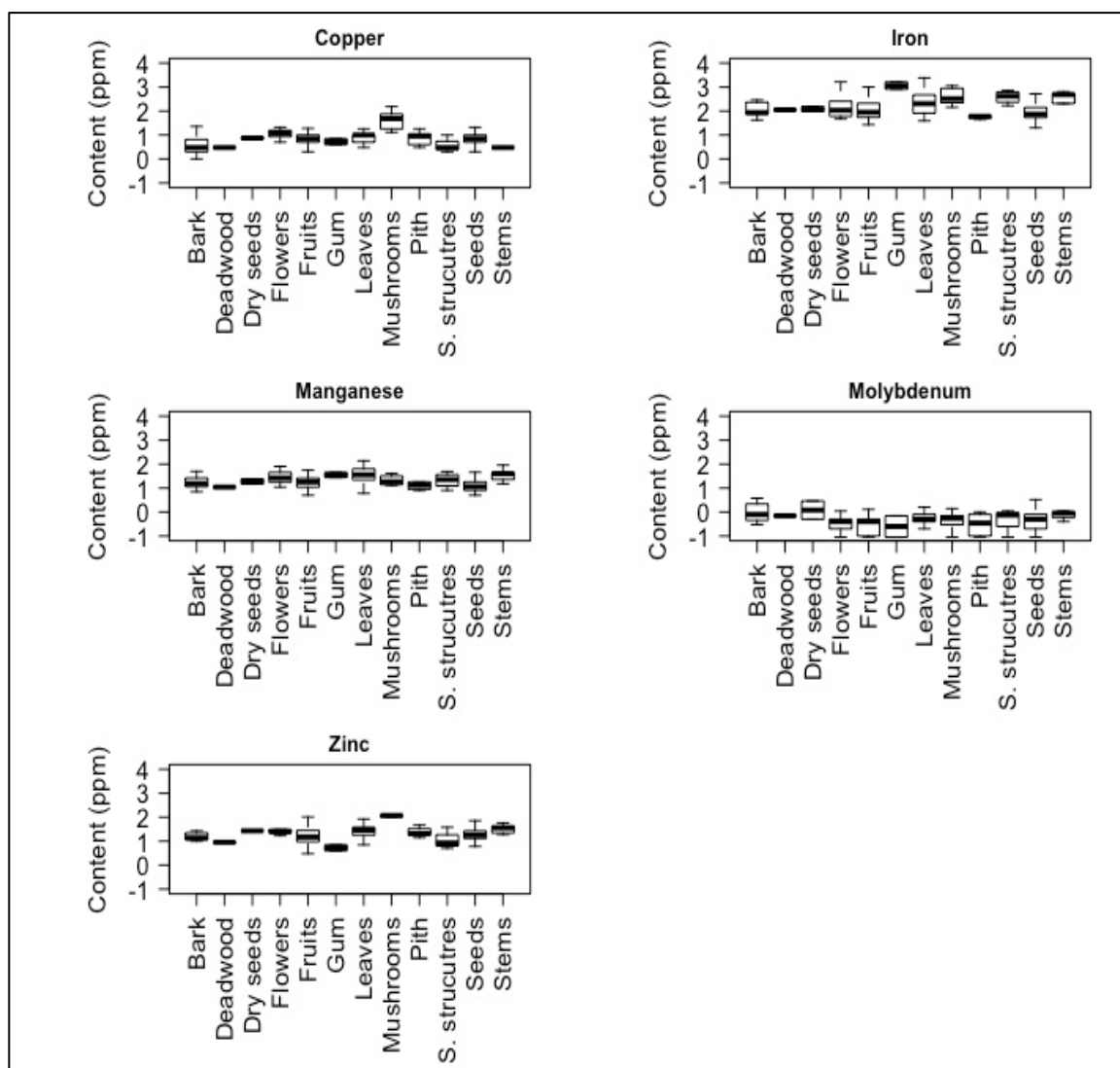
Figure 3.15. Mean micro-minerals concentrations expressed in parts per million (ppm) of dry matter of the 217 plant foods consumed by juveniles and lactating females (data log transformed, and error bars indicated the standard deviation of the mean, S. structures = Subterranean structures).

c) Mineral content in the Principal Plant Food Species

The majority of the foods consumed by the mangabeys were poor in both macro- and micro-minerals (Table 3.4, Appendix 3.1). Oncoba spinosa (2.69%) and Cissus rotundifolia (47%) had the highest amounts of calcium and magnesium, respectively, among the important plant foods. Agaricus sp. contained the highest levels of phosphorus (1.36%), potassium (4.71%), and Zinc (109.17 ppm). Brachiaria subquadripara (0.22%) and Hyphaene compress (0.14%) were important sources of sodium among the important foods. Cissus rotundifolia contained high levels of iron (659.25 ppm) and manganese (64.75 ppm). Mangifera indica (48.40 ppm), which is cultivated crop in the study site, was also rich in manganese (Table 3.4). Vachellia robusta (2.06 ppm) had the highest concentration of molybdenum among the wild foods. However, cultivated crops raided by the mangabeys, particularly Vigna radiate and Vigna unguiculata, had relatively high amounts of Molybdenum (Appendix 3.1). Overall, the majority of the food plants that offered good sources of minerals were not among the important or most consumed foods (Appendix 3.1).

Table 3.4. Mineral content of the Principal Plant Food Species (> 1% in the annual diet) consumed by juveniles and lactating females. The macro-minerals (calcium – Ca, magnesium – Mg, potassium – K, phosphorus – P, and sodium – Na) are expressed as a percentage while the micro-minerals (copper – Cu, iron - Fe, Manganese – Mn, Molybdenum – Mo, & zinc – Zn) as concentration in parts per million (ppm) of the dry matter content of the foods.

Species	% in Diet		Macro-mineral content (%)					Micro-mineral content (PPM)				
	Juv	L.fem	Ca	Mg	K	P	Na	Cu	Fe	Mn	Mo	Zn
Phoenix reclinata	21.06	21.22	0.67	0.12	1.30	0.20	0.02	9.50	182.20	22.40	0.49	14.00
Ficus sycomorus	17.62	17.82	0.40	0.21	2.20	0.23	0.03	8.18	176.82	22.00	0.30	23.55
Vachellia robusta	9.13	8.68	0.27	0.23	0.83	0.24	0.09	6.14	424.43	22.29	2.06	20.71
Synsepalum msolo	4.61	4.94	0.10	0.23	1.09	0.11	0.01	12.67	92.00	25.00	0.67	17.67
Hyphaene compressa	4.40	4.95	0.51	0.19	3.64	0.27	0.14	7.00	275.00	20.33	0.19	73.00
Agaricus sp.	4.12	4.51	0.14	0.22	4.71	1.36	0.06	60.83	513.67	22.83	0.60	109.17
Grewia densa	2.71	2.49	0.39	0.31	1.82	0.29	0.02	10.50	220.33	27.33	0.52	22.17
Oncoba spinosa	2.69	3.41	1.55	0.15	2.08	0.22	0.01	9.20	198.60	13.40	0.48	33.40
Sorindeia madagascariensis	2.68	2.77	0.92	0.14	1.41	0.27	0.01	8.00	105.25	14.38	0.26	17.00
Diospyros mespiliformis	2.61	2.78	0.28	0.13	0.96	0.22	0.01	6.86	321.43	10.29	0.28	18.86
Polysphaeria multiflora	2.49	1.82	1.08	0.24	1.63	0.19	0.02	5.00	145.20	32.00	0.40	11.20
Brachiaria subquadripara	2.17	2.32	0.44	0.32	2.33	0.34	0.22	7.33	269.67	45.67	1.47	31.33
Mimusops fruticosa	1.92	1.80	0.15	0.17	1.29	0.10	0.08	2.63	125.00	30.00	0.36	9.67
Pavetta sphaerobotrys	1.60	1.30	0.46	0.31	2.43	0.20	0.03	8.00	95.33	12.00	0.47	24.67
Alangium salviifolium	1.39	1.51	0.09	0.23	1.55	0.26	0.02	7.83	125.67	25.83	0.68	25.17
Mangifera indica	1.31	1.10	1.00	0.19	1.43	0.28	0.01	8.40	372.40	48.40	0.40	20.80
Cissus rotundifolia	1.21	1.12	0.37	0.47	2.62	0.30	0.14	6.25	659.25	64.75	0.30	20.25
Garcinia livingstonei	1.19	1.38	0.14	0.10	1.13	0.11	0.01	7.00	245.33	12.33	0.20	15.00
Drypetes natalensis	1.00	0.90	0.70	0.26	1.88	0.25	0.02	11.67	88.00	35.00	0.20	24.67
Lecaniodiscus fraxinifolia	1.00	0.82	0.14	0.12	1.79	0.34	0.01	12.00	327.60	18.00	0.52	42.20

3.3.5.2 Mineral intake variation between juveniles and lactating females

To test my prediction (**P2**) that juveniles have a higher intake of essential macro- and micro-minerals per metabolic body mass than the lactating females, I examined the macro- and micro-minerals relative intake in the per minute intake analysis, while controlling for focal ID and study group, and fruit availability. Relative to body mass, both juveniles and lactating females exhibited different levels of macro-minerals intake (Fig 3.16). The intake per MBM of the macro-minerals varied significantly with response to age class and intake by juveniles exceeded that of the females (Fig 3.16). This was true for calcium ($F = 85.13$, $df = 1$, 67.91, $p < 0.0001$; $t = -9.23$, $p < 0.0001$, $N = 63$) phosphorus ($F = 85.52$, $df = 1$, 65.27, $p < 0.0001$; $t = -9.25$, $p < 0.0001$, $N = 63$), magnesium ($F = 97.53$, $df = 1$, 67.33, $p < 0.0001$; $t = -9.87$, $p < 0.0001$, $N = 63$), potassium ($F = 83.35$, $df = 1$, 67.39, $p < 0.0001$; $t = -9.13$, $p < 0.0001$), and sodium ($F = 50.07$, $df = 67.81$, $p < 0.0001$; $t = -7.08$, $df = 1$, $p < 0.0001$, $N = 63$). The results of the relative intake of the five macro-minerals were consistent with my prediction (P2).
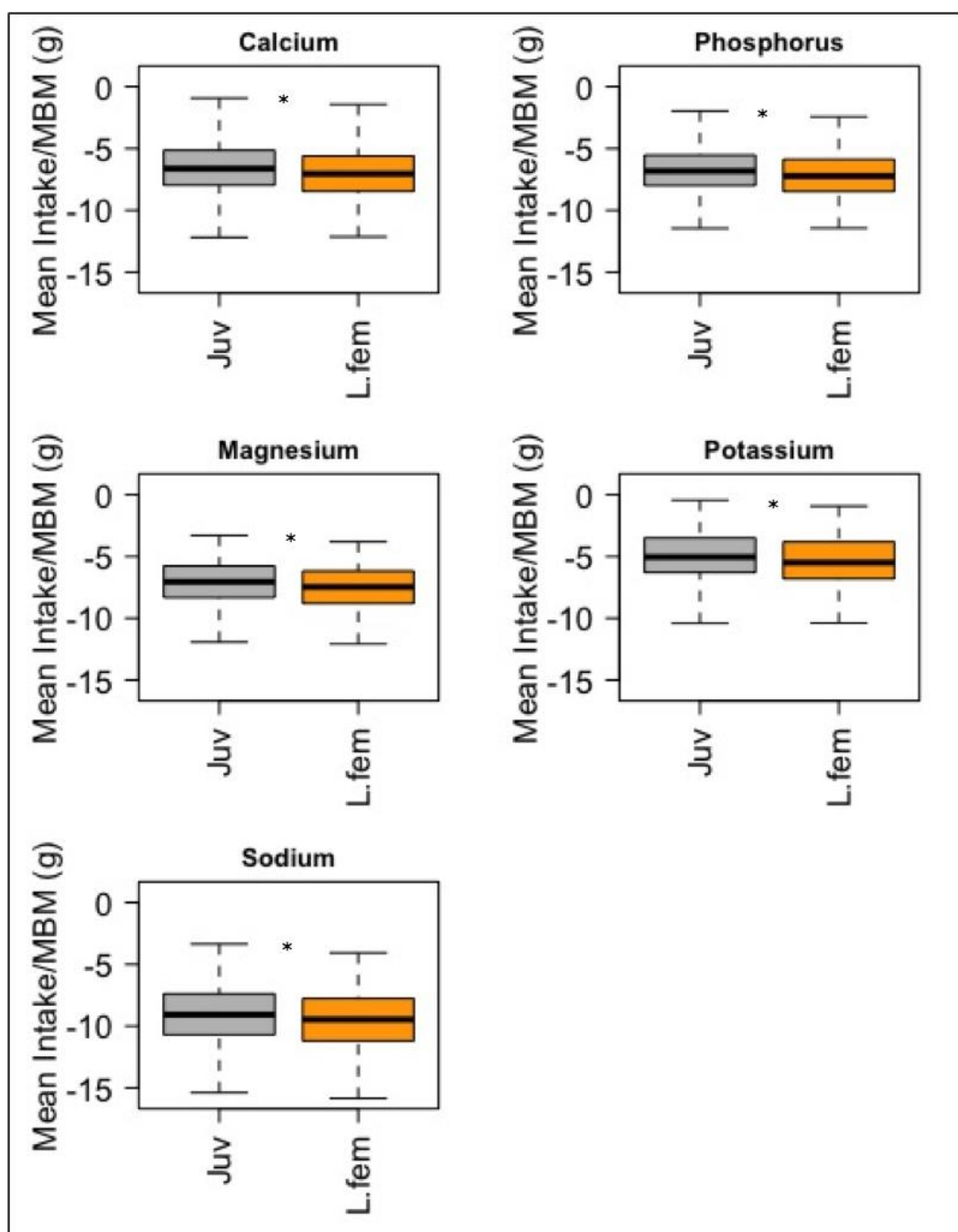
Figure 3.16. Mineral intake per minute on dry matter (g) basis expressed as mean intake per metabolic body mass (MBM) of macro-minerals (calcium - Ca, phosphorus - P, magnesium - Mg, potassium - K, sodium - Na) between juveniles (Juv) and lactating females (L. fem). Data are inverse log transformed, N = 63 individuals, and error bars indicate standard deviation, asterisk (*) indicate significant difference, $p < 0.05$).

As I predicted the per minute relative ingestion of micro-minerals as well expressed great variability between the age classes (Fig. 3.17). Age class predicted the intake of micro-minerals and overall juveniles consumed more micro-minerals per MBM than the lactating females. This was reflected in utilization iron (F = 53.14, df = 1, 68.33, p < 0.0001; t = -7.29, p < 0.0001), zinc (F = 64.45, df = 1, 65.80, p < 0.0001; t = -8.03, p < 0.0001), copper (F = 85.17, df = 1, 65.89, p < 0.0001; t = -9.23, p < 0.0001), manganese (F = 71.44, df = 1, 69.06, p < 0.0001; t = -8.45, p < 0.0001), and molybdenum (F = 103.66, df = 1, 69.83, p < 0.001; t = -10.18, p < 0.0001). Like the macro-mineral intake, the intake of micro-minerals supported P2.
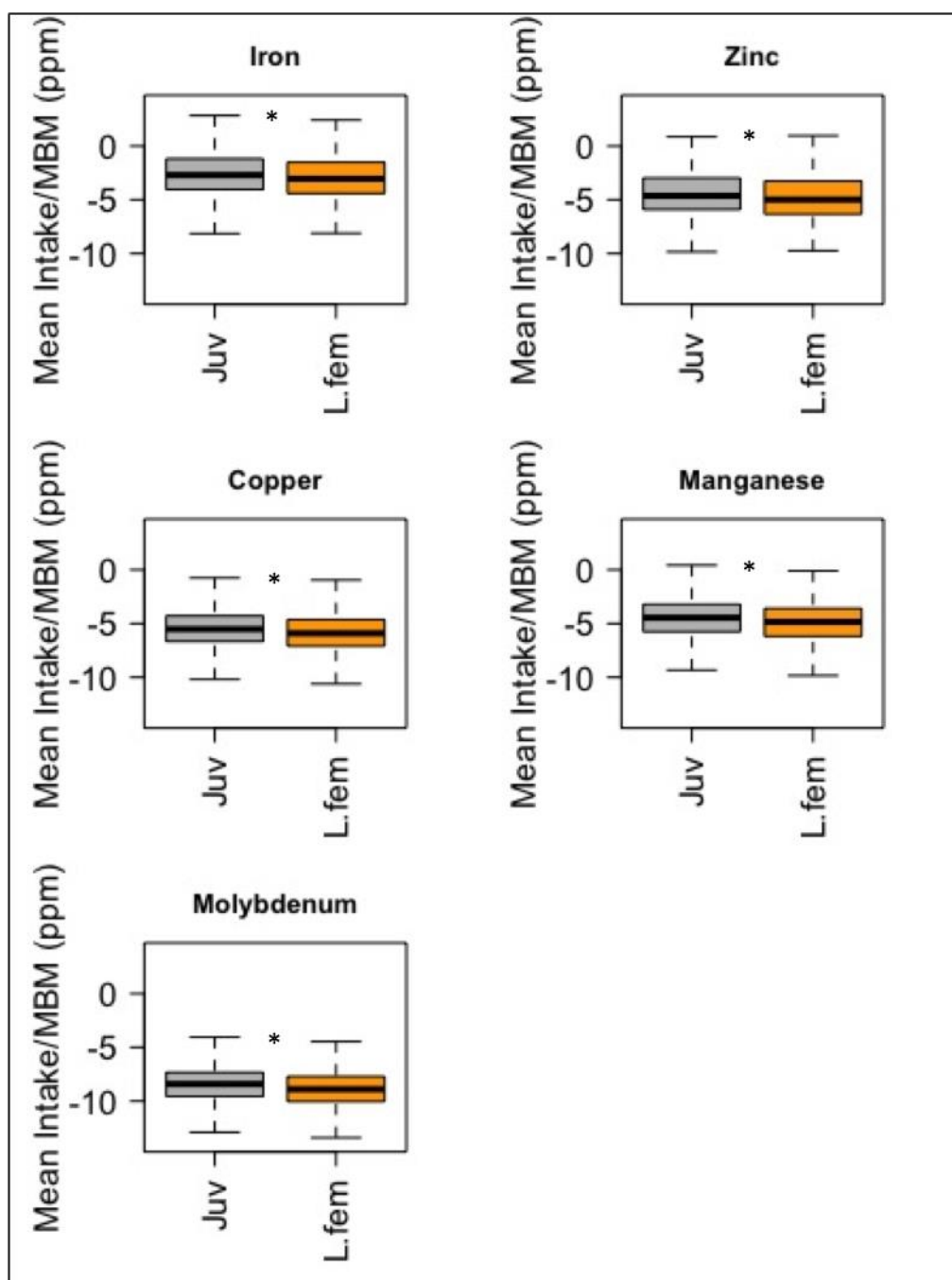
Figure 3.17. Mean intake per metabolic body mass (MBM) of micro-minerals (iron - Fe, zinc - Zn, copper - Cu, manganese - Mn, molybdenum - Mo) expressed in parts per million (ppm) of dry matter intake between juveniles (Juv) and lactating females (L. fem). Data are inverse log transformed, N = 63 individuals, error bars indicate standard deviation, asterisk (*) indicate significant difference, $p < 0.05$.

3.3.6 Condensed tannins in Tana River mangabey foods

3.3.6.1 Condensed tannins in different food types

Among the all food types (i.e., bark, deadwood, flowers, fruits, gum, leaves, mushrooms, roots, seeds, and stems) fruits, leaves, and seeds were highly represented than other food samples in the condensed tannins (CT) analysis (Fig. 3.18). For all the foods combined, 73.6% of the foods consumed by the mangabeys contained CT, while 26.4% were free of CT. Except deadwood all other food types contained CT.

Fruits (39%), seeds (19%), and leaves (18%) samples were highest in CT (Fig. 3.18). Mushrooms and roots (2% each) samples had the least percentage of samples containing CT. Similarly, fruits (34%), leave (25%), and stem (14%) had the highest number of samples testing negative for CT (Fig. 3.18). Overall, more bark, flowers, fruits, gum, and seeds samples contained CT compared to those free of CT. However, the overall proportions of foods that contained CT exceeded those were free of CT significantly (χ^2 = 18.27, df = 7, p = 0.0322). The findings did not support prediction (P3) that mangabeys ingest more foods free of CT than those containing CT.
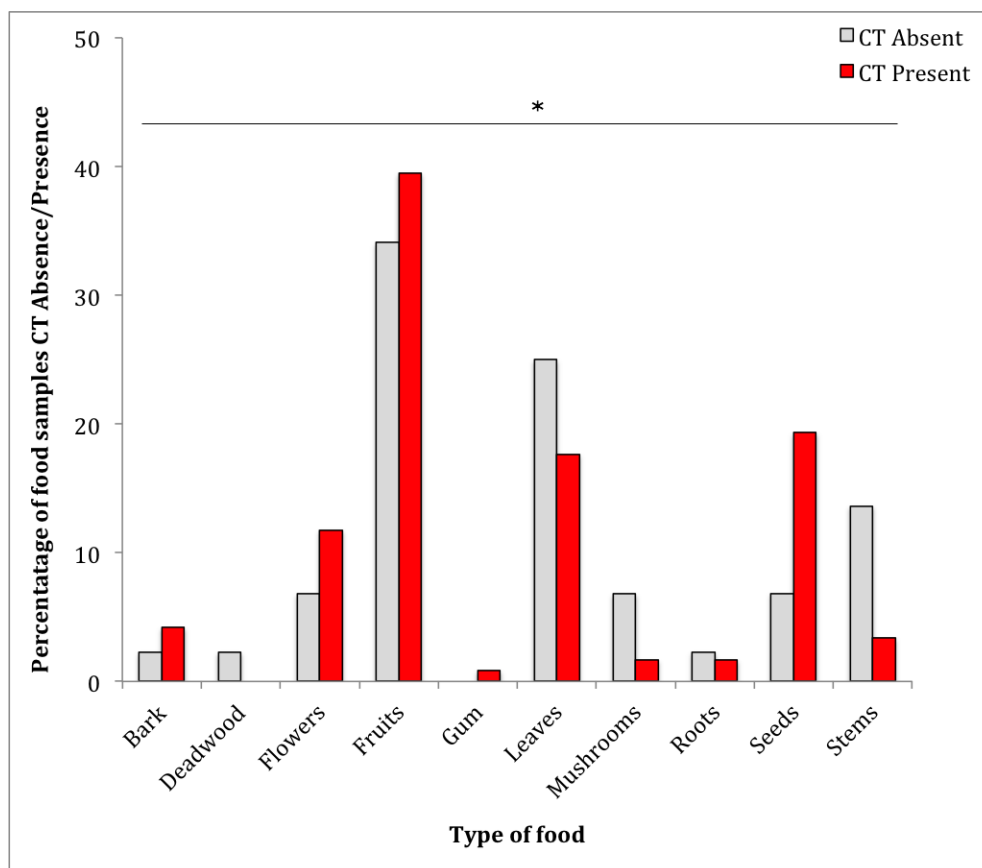
Figure 3.18. Absence (absorbance value < 0.10) and presence (absorbance value > 0.10) of condensed tannins (CT) in different food types eaten by the mangabeys which included: bark (6), deadwood (1), flowers (17), fruits (62), gum (1), leaves (32), mushrooms (5), roots (3), seeds (26), and stems (10), whereby N = 163 food samples, number in brackets indicates samples analyzed per food type while * Indicates significant differences $p < 0.05$.

3.3.6.2 Qualitative description of CT levels in food types

Different types of foods varied in CT concentrations based on qualitative description of whether the foods contained high, medium or low CT. Overall, 46.7%, 44.2%, and 9.2% of the foods, which tested positive for CT contained medium, low, and high CT, respectively (Fig. 3.19). Flowers (27%), stems (25%), and bark (20%) had highest percentages of foods with presence of high levels of CT (Fig. 3.19). A few fruits (6%) and seeds (9%) samples were characterized by present of high CT

presence (Fig. 3.19). A high percentage of roots, bark, and leaves indicated presence of medium CT (100%, 60%, & 57%, respectively), while mushrooms (100%), gum (100%), and stems (75%) constituted the majority of food samples that contained low concentration of CT. The percentages of the foods containing low (+) and medium (++) levels of CT were significantly more than those containing high (+++) levels of CT (χ^2 = 101.81 df = 4, p < 0.0001). These findings partly supported my P3 that mangabey foods containing CT constituted more foods low in CT and fewer with high (+++) CT concentration.

In summary, overall the majority of flower, stem and bark contained high levels of CT while roots, bark, leaves, seeds and fruits contained medium or low levels of CT (Fig. 3.19). Gum and mushroom contained the lowest levels of CT among all the foods.
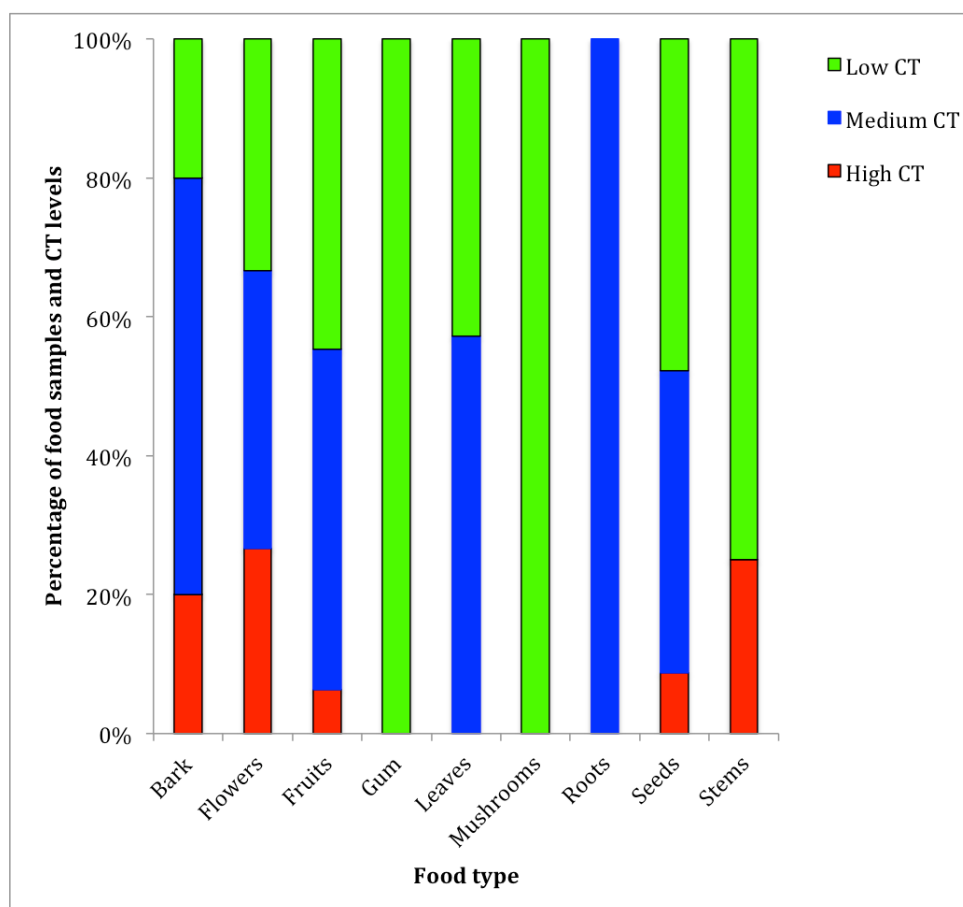
Figure 3.19. The percentage of food types that contained low (absorbance 0.10 - 0.50), medium (absorbance 0.50 - 1.00), and high (absorbance > 1.00) levels of Condensed tannins (CT), whereby N = 120, and number of samples for each food were: bark - 5, flower - 15, fruit - 47, gum - 1, leaf - 21, Mushroom - 2, roots – 2, seed - 23, stem.

3.4 Discussion

Phenological patterns and food availability

Findings of this study suggest young leaves were more abundant than fruit and flowers throughout the year except in August when there was a peak in fruiting. However, leaves constitute less than 8% of annual diet of Tana River mangabeys, compared to fruit, which account more than 50%. Phenological data indicate that the two study sites were characterized by lack of fruiting synchronization (Fig. 3.3 & 3.4). Fruiting of trees occurred year-round, although quantity of available fruits varied across the months showing peak and declines.

Temporal variation in rainfall did not clearly match the food availability season. Some spikes in fruit availability seemed to occur after the peak rainy season, however, especially in Kitere, suggesting potential influence on fruiting of some tree species. Based on the fruit availability index, the period from October 2014 to May 2015 with exception of November 2014, and February 2015 as well as December 2015 experienced low fruit availability (i.e., FAI < 50% percentile) while June to November 2015 was characterized by high fruit abundance (i.e., FAI > 50% percentile). However, the period from June to November 2015 experienced the highest fruit availability with the maximum occurring in August. The results are consistence with earlier findings of Kinnaird (1992) and Wieczkowski & Kinnaird (2008) that fruiting as well as flowering schedule is highly variable in the lower Tana riverine forests leading to period of low and high fruit availability. Similar to

my study, Kinnaird (1992) reported one major fruiting peak (between January and March) during a 13 months study, but the timing varied with my study, which occurred between June and September during my 15 months study. However, some tree species fruited outside the fruiting peak period. Kinnaird attributed this phenological pattern to the underground water supply from the river, which maintains these forests. While I agree with such observation generally my results suggest that the Mchelelo forest depended more on this mechanism than the Kitere forests, which are influenced more by weather conditions than the effects of underground water seepage. The variation in main fruiting peak timing may be attributed to fluctuating river flow regimes and unpredictable shifts in local weather patterns, which have also been implicated in changing composition of mangabey foods (Wieczkowski & Kinnaird, 2008).

Moreover, some important fallback foods (*Hyphaene compressa, Diaspyros mesipiliformis, Oncoba spinosa* and *Ficus sycomorus* produce fruits in most parts of the year (Fig. 3.5). Other important species, such as *Vachellia robusta*, experience fruiting peak between October and November, but produce abundant seeds, which drop upon drying and remain on the forest floor throughout the year constituting a significant fallback food when preferred foods diminished. This is true for *Synsepalum msolo* and *Sorindeia madagascariensis,* although seeds do not persist throughout the year.

Fruit productivity and availability fluctuated throughout the year and differed between the two study sites (Fig. 3.3, 3.4). Analysis of the phenological score gave a higher estimate of fruit availability compared to calculation of Fruit

Availability Index (FAI), which considers phenology in the context of basal area. Fruit Availability Index scores were generally higher in Mchelelo than in Kitere. The period of fruit availability peak in Kitere was from October 2015 to November 2014, with an additional peak in October 2015, while in Mchelelo the maximum peak was in August 2015 with lower peaks in November 2014 and November 2015. Compared to weather data, the overall period of high fruit availability fell within the long dry season coming right after the long rains. Consequently, plant species that rely on rainfall for fruiting, as well as those depending on flooding of the river, are likely to fruit at around the same time. Thus, combined effects of flooding and precipitation on tree phenology may explain the increase in fruit availability during this period.

The observed site variation in phenological patterns and food availability can be attributed to both anthropogenic and non-anthropogenic influences on the habitat. Kinnaird (1992) reported that apart from the river water levels, the phenology in the lower Tana River was influenced by the local environmental conditions. While the same explanation is consistent with my observations, the distinct differences between my study sites also suggest that anthropogenic effects potentially influenced the phenological patterns and food availability. In Kitere, farming along the riverbanks separated the river channel and the forest edge with a distance of more than 200m, whereas in Mchelelo the forest cover extends to the riverbanks. The cleared riverbanks may decrease the influence of the river water level on plant reproduction and growth, exaggerating the effects of other environmental factors, such as precipitation.

The indiscriminate poaching of trees for local use and forest clearance for agriculture as noted during this study and earlier (Moinde-Fockler et al., 2007) may as well explain the lower basal area and FAI of the majority of food species in Kitere. Moreover, effects of habitat modification due to the increasing population of resident herds of African elephants (*Loxodonta africana*) in the two study sites may also contribute to the low fruit availability. I observed that elephants toppled mature fruiting trees utilized by the Tana River mangabeys, potentially reducing their density and creating forest gaps that are quickly taken up by invasive species. All these compounding factors on food availability potentially modify the nutritional quality of the mangabeys' dietary species and the habitat at large.

Nutritional composition and variation in mangabey foods

Fiber levels were mostly high in deadwood, pith, stems, and subterranean structures potentially suggesting presence of more indigestible plants components compared to mushrooms, which were low in fibers. These plant food parts as well as seeds and fruit external parts such as exocarps are potentially reinforced with fiber for structural support and physical defense of the plant (Garber, 1987; Lucas et al., 2012). Consequently, these food types are expected to be rich in fiber.

Generally, the plant foods had low fat concentrations, but overall, fruits and seeds had the highest fat content. This is typical of the diets of many wild primates (Oftedal, 1991). Excluding insect and mushrooms, the average protein percentage in plant foods was about 9.13% slightly higher than the recommended 6 – 8% content of dry matter of primate foods (Chapman et al., 2012). This emphasizes on the

nutritional significance of arthropods and mycophagy in primates (Hanson et al., 2003; Rothman et al., 2014).

Apparently, it appears that the mangabeys are able to meet their protein needs in their normal diet. However, the inclusion of insects and mushrooms in the diet cushions the Tana River mangabeys from negative effects of inadequate daily protein intake. This is necessary because ingestion of adequate protein may be compromised by unpredictable food resources fluctuations and though available in plant foods may be bound by fiber or its digestion and uptake is impaired by plant secondary metabolites in foods (NRC, 2003). These results support recent studies suggesting that insects constitute an important and often overlooked source of lipids, protein, and minerals for large primates (Finke, 2007; Rode et al., 2006; Deblauwe & Janssens, 2008; Rothman et al., 2014; Bryer et al., 2015). For instance, Rothman et al. (2014) found that lipid content in insects ranged from a low of 7.0%, in immature bugs in order Hemiptera, to a high of 58.5%, in immature dragonflies (order Odonata) while protein was between 37.3%, in immature beetles (order Coleoptera), and 76.2%, in adult dragonflies. Bryer et al. (2015) reported similar values for insects consumed by red-tailed monkeys, a frugivorous species comparable to the Tana River mangabeys. Bryer and colleagues found that the insect component of monkeys' diets in Kibale forest, Uganda, contained 56.7% protein, 16.7% fat, and 7.9% ADF on average (chitin). These values are close to the values I obtained for the same macronutrients for the Tana River mangabeys. The marginal differences may be explained by geographical variation in insect diversity and abundance.

The majority of primate studies report that mushrooms provide a trivial part of primates' diet (Hanson et al., 2003). Findings from this study instead suggest that mushrooms are a significant source of protein and fat, which are often the most limited macronutrients in primate foods (Milton, 1984), thus making them a valuable food resource. Mushrooms are taxonomically poorly understood, however, and may be limited in their availability year-round since they only thrive under moist canopy cover or during the wet seasons. This perhaps explains why they are mistakenly considered insignificant food source.

Finally, the concentration of total non-structural carbohydrates (TNC) was significantly higher in flowers, fruits, gum, and seeds compared to the other of food types (i.e., deadwood, mushrooms, bark, insects, leaves, pith roots, and stems). These findings are biologically meaningful given that these are reproductive parts and are likely to be rich in energy reserves (Garber, 1987; Lambert, 2010).

Available Protein Intake

Findings on protein intake supported my prediction (P1), that juveniles consume more protein per metabolic body mass than the lactating females and protein intake varied with fruit availability. Thus, as I predicted, both juveniles and lactating females may be maximizing protein intake for growth and lactation during period of high food availability and altering this pattern during period of low food availability when survival is the priority.

The patterns of protein intake between age classes in mangabeys may be explained partly by the high nutritional demands especially for growth in juveniles

and also the energetic need to maintain smaller bodies, compared to lactating females (Pereira & Fairbanks, 2002). Additionally, spatial and temporal differences in food availability as well as the efficiency of foraging strategies employed by juveniles may as well explain the seasonal patterns of protein intake (Gunst et al., 2010). For instance, both juveniles and lactating females ingested more available protein during the season of high fruit availability than when fruit availability was low. This may suggest that, during period of low food availability protein is limited, while during periods of high fruit availability mangabeys are likely to meet most of their protein requirement mainly through fruit consumption feeding partly influencing protein ingestion rates. However, when fruit is limited they may require flexibility in diet selection and altering usual feeding strategies and supplementing fruit with leaves or insects to enhance their protein acquisition as an essential macronutrient. Altogether, fruit is argued to be low in protein content and thus the mangabeys potentially achieve their protein intake via increased fruit consumption when fruit is abundant. This result agreed with observations by Felton et al. (2009) that primates may compensate for low protein content in their diets by consuming large amounts of food to stabilize their protein intake. This may require prolonging the feeding time. However, the need to consume mechanically challenging foods or fallback fruits during the season of low fruit availability, which require more handling time, may especially hinder juveniles' nutrient acquisition due to low foraging efficiency (see chapter 4). The findings are also supported by data on interaction of food properties on diet selection (chapter 4), which suggests that during period of low fruit availability mangabeys target available protein more

compared to when fruits are abundant. This partly explains the low protein intake when fruits are limited.

Typically, diets containing 6 - 8% protein of dry matter is deemed adequate for primate daily requirements, but primates may require values up to 14% due to increased demands for growth, maintenance, and reproduction (Waterman & Kool, 1994). However, protein is often limited in primate plant foods, and where it is abundant, its quality and seasonality may limit it (Oftedal et al., 1991; Felton et al., 2009). These observations partly explain why protein intake per MBM was higher in juveniles than in lactating females. Altmann (1991, 1998) reported similar findings in yellow baboons, where he found that protein intake during the juvenile stages determined the rate of growth and lifetime fitness, but was ability to meet protein needs was constrained by unpredictability.

In addition, mangabeys like other primates should have maximum protein threshold requirement and consequently adjust the feeding behaviors to balance protein intake not to exceed the limit or have deficiency in intake (Felton, et al 2009). Similarly, among humans protein starvation is observed when protein concentration in foods exceed 30% since there exists a physiological necessity of maintaining critical ratio of protein to fat dictating the liver limit in handling protein (Cachel, 1997). Although little is known in liver limits in handling protein, it is likely such limits exists and may partially explain the seasonal differences in protein intake.

Mineral concentrations in foods and variation in intake

The required concentrations (%) of macro-minerals for nonhuman primates' foods to meet their daily requirements according to NRC (2003) are: calcium 0.54%, phosphorus 0.43%, magnesium 0.16%, sodium 0.71%, and potassium 1.44%. The suggested micro-mineral requirements in ppm are: iron 196, zinc 106 - 505, manganese 31 -176, and copper 14 - 22. This clearly shows that primates require small quantities of these minerals in their diet.

Macro- and micro-minerals occurred in small concentrations in mangabey foods. Among the macro-minerals: calcium (0.64%), magnesium (0.24%), and potassium (1.79%) occurred in sufficient concentrations, while phosphorus (0.30%) and sodium (0.07%) were below the recommended concentrations (NRC, 2011) on basis of percent content in food and not daily intake requirements. Minimum concentrations of at least 0.25 - 0.65% of sodium are appropriate for maintenance roles in primates at all stages of development (NRC, 2003). However, the concentration of sodium in the diet of the Tana River mangabeys was less than one-third the minimum requirement. Similarly, low levels of sodium have also been reported in the diets of black and white colobus monkeys, (Rode et al., 2003) and mountain gorillas (*Gorilla beringei beringei*), (Cancelliere et al., 2014). In contrast to low sodium content in foods eaten by Tana River mangabeys, however, diets of Western lowland gorillas (*Gorilla gorilla gorilla*) (Magliocca & Gautier-Hion, 2002) and diademed sifakas (*Propithecus diadema*) have been found to contain sodium above the required levels (Irwin et al., 2017). While the majority of sodium-limited primate species engage in geophagy to access it (Krishnamani & Mahaney, 2000).

This behavior was not observed among the wild Tana River mangabeys, and it remains unclear how they cope with this deficiency.

Phosphorus was found in insufficient concentration in Tana River mangabey foods (NRC, 2011). The average concentration of phosphorus in foods eaten by the mangabeys was 0.30% compared to the primate requirements of 0.43 - 0.92% (Oftedal, 1991; NRC, 2003). Similar deficiencies have been observed in diademed sifakas (Irwin et al., 2017). Edaphic and habitat modifications may explain the differences in phosphorus as well as other mineral content in the diets of the wild primate (Maglocca & Gautier-Hion, 2002).

Among the micro-minerals, only iron occurred in concentrations (237 ppm) exceeding primate requirements (196ppm) (NRC, 2003). Although there are very few data for comparison from other mangabey species, Irwin et al. (2017) found that the sifaka's diet had insufficient levels of iron, zinc, and copper. Similarly, Rode et al. (2003) reported insufficient iron and zinc concentrations in black and white colobus monkey foods. Discrepancies in micro-mineral deficiencies found in Tana River mangabey foods with what is reported in sifakas and guereza colobus monkeys, potentially suggest that, the micro-mineral content of primate diets vary considerably with geographical location. Although it is clear that the mangabeys experience mineral deficits in their diet the coping mechanisms to alleviate such dietary challenges are yet to be established, and further studies are required. However, one possibility may be that the water sources they utilize supply some of these minerals, which can be tested by sampling their water for the relevant minerals in it. The mangabeys mainly drink water from the river except during the

rain season when water collects on tree holes or natural ditches on the ground, which are short-lived water sources.

Variation in mineral content of food items

Rode et al. (2003) reported that leaves both mature and young leaves supply considerable amounts of calcium, potassium, magnesium, iron, and manganese while petiole in addition is a good source of zinc for black and white colobus. Flowers were reliable source of copper while bark and stem supplied sodium and some calcium. The Tana River mangabey also ingested similar food type, potentially to ingest same minerals even though they consume more of fruits and seeds than leaf diet. Findings in my study indicated that calcium, potassium, phosphorus occurred in high amounts in bark, seeds, mushrooms, and stems. Mature and young leaves were good sources of magnesium, calcium potassium, manganese and zinc. Interestingly, mushrooms demonstrated high concentrations of zinc, iron, copper, phosphorus, and potassium, partly explaining their high preference by the mangabeys. Research on dietary ecology of patas monkeys (Erythrocebus patas) found that gum was a significant source of sodium, iron and manganese (Isbell et al., 2013). My results support these finding and gum eaten by mangabeys showed high concentration the same macro- and micro-minerals. Surprisingly, molybdenum was the most limited micro-mineral and rarely occurred in concentration more than 2 ppm while, iron was found in higher amounts than the recommended for primates (NRC, 2003). Similar findings have been found in mountain gorillas (Cancelliere et al., 2014). Ingestion of minerals and other nutrients in excess may have some

negative health consequences (Oftedal et al., 1991), however, such effects in wild primates are subject to further investigations.

Most of both the fallback foods were deficient in the essential minerals but levels were higher in particular in certain foods. These included: *Brachiaria subquadripara* (magnesium, sodium, and molybdenum), *Ficus sycomorus* (calcium), *Hyphaene compressa* (potassium, zinc, and sodium), *Vachellia robusta* (molybdenum and iron), *Cissus rotundfolia* (iron and manganese), *Synsepalum msolo* (copper), and *Lecaniodiscus flaxinifolia* (zinc and copper). Importantly, the raided agricultural crops (especially *Vigna radiata* and *Vigna unguiculta*) were strikingly high in molybdenum, which was the rarest trace element. These results reinforce previous findings that the nutritional content of primate foods varies significantly across species and plant parts (Magliocca & Gautier-Hion, 2002; Irwin et al., 2017). Herbaceous species and species in secondary forests contain more minerals (sodium, calcium & potassium), as observed in gorilla studies (Magliocca & Gautier-Hion, 2002; Rothman et al., 2008a; Cancellier et al., 2014). Although majority of the mineral food sources for the mangabeys are trees and tall shrubs, one herbaceous grass (*Brachiaria subquadripara*) was rich in sodium, magnesium, & molybdenum, partly supporting the idea that herbaceous species may be rich in minerals.

Age class differences in mineral intake

True to my prediction (P2), I found that juveniles consumed more of the essential macro- and micro-minerals than the lactating females. Juveniles ingested more calcium, phosphorus, sodium, potassium, magnesium, iron, zinc, and

molybdenum per unit of MBM. According to the NRC (2003), all these minerals play crucial roles in growth, maintenance, and health. Consequently, juveniles are especially likely to have a high intake of such minerals relative to body mass because of their need to grow and build strong immunity. Primate studies on juvenile-adult differences in mineral intake are still scanty. However, Rothman et al. (2008a) reported that juvenile gorillas ingested more minerals per unit body mass compared to adults. Evidence of primate feeding targeting essential minerals has been provided by studies of chimpanzees and gorillas (Deblauwe & Jannesen, 2006), black and white colobus monkeys, (Rode et al., 2003), patas monkey, (*Erythrocebus patas*), and vervet monkeys (*Chlorocebus pygerythrus*) (Isbell et al., 2013).

Condensed tannins in foods & behavioral counter strategies

I found that proportionally more (74%) mangabey foods contained some condensed tannins than were free of these secondary compounds, contrary to my prediction. Qualitatively, high levels of CT, however, characterize only small subset of foods as I predicted: only 9% had high levels of tannins, while 46% and 44% had medium and low levels of CT, respectively. Bark and flower were characterized by the highest presence of CT, while mushroom and gum had the lowest levels of CT. This suggests that mangabeys may be regulating intake of CT and/or perhaps have better physiological mechanism to handle digestibility-reducing compounds, given they ingested some foods high in CT. Plants invest in chemical defenses that deter foragers who damage or consume seeds or fruits prior to maturity (Freeland & Janzen, 1974; Rothman et al., 2009). Tana River mangabeys are known to include

mostly fruits and seeds in their diet (Homewood, 1978; Wieczkowski, 2003), which include high proportion of unripe fruits and immature seeds, potentially explain the high proportion of the foods containing CT. Mangabeys may deal with such chemical barriers (Dearing et al., 2005; Hanya et al., 2007) by ingesting only few plant foods with high levels of CT, and otherwise focusing majority on foods with low-medium concentration of CT. This pattern suggests that mangabeys exercise controlled intake of PSMs, possibly through dietary choice and food processing to discard chemically challenging parts (Glander, 1982; Dearing et al., 2005). Primates may have other strategies to deal with the PSMs, however, such use of gut microbes or enzymatic neutralization (Shimada et al., 2006). The Tana River mangabeys are likely to be utilizing these strategies given the food cheek pouching and eructation behaviors as well as ingestion of some foods high in PSMs.

Importantly, evidence from gorilla and chimpanzee studies suggest that PSMs may also provide some parasitological, pharmacological, and health benefits (Huffman, 1997). Thus, their consumption is not always entirely disadvantageous. The observed ingestion of plant parts with possibly high levels of CT, such as bark, may be attributed to health benefits. According to Medley (1993), some of the tree species that Tana River mangabeys exploit for bark or roots are known to be of medicinal value to local people. These trees included Albizia gummifera, which is known to have good anti-helminthes properties and is used by the locals. Other plants in the mangabey diets that are used by people to cure other ailments include the Ficus sycomorus and Harrisonia abyssinica, which people use the bark and the roots, respectively. Although it is not clear if consumption of these plant species

serve the same medicinal purpose in mangabeys, such benefit cannot be overlooked. Moreover, studies on ingestion of PSMs (particularly cyanine intake) by bamboo lemurs (*Hapalemur* sp. and *Prolemur* sp.) have indicated that these species target plants with high concentration of PSMs to enhance their intake in protein and sulfur-containing amino acids, which play crucial in detoxification (Eppley et al., 2017). Given that Tana River mangabeys ingest small proportion of foods containing high level of CT, it is likely that mangabeys ingest food high in PSMs for similar reasons as seen in lemurs, but it remains to be investigated.

In conclusion, I found support of my predictions (P1 & P2) that juveniles consume more protein and more macro- and micro-minerals per unit body mass compared to lactating females. Such differences are attributed to the metabolic consequences of body size and the nutritional demands for growth in the young individuals. The observed variation in protein intake across months suggests that food availability potentially influences the protein budgets among the mangabeys. Tana River mangabey foods were generally characterized by low mineral content, and the majority fell below the required concentrations, except iron and zinc.

Although more mangabey foods contained some CT than were free of CT, my prediction (P3) was supported by the observation that mangabeys included a very small percentage (9%) of the foods high in CT but more foods low (44%) or medium (47%) in CT. The pattern suggests controlled intake of CT, possibly through food selection. These findings contribute significantly in understanding of the nutritional properties of the Tana River mangabey foods and the different feeding and nutritional challenges faced by juveniles and lactating females.

Appendices

Appendix 3.1. Macro-minerals (expressed as a percentage) and micro-minerals (parts per million-ppm) content plant food species consumed by the Tana River mangabeys and the annual percentage diet in the diet of juveniles (Juv) and lactating females (L.Fem). * - Indicates foods cultivated and occasionally raided by the mangabeys and no percent score in the annual diet.

Species	% In Diet		Macro-mineral content (%)					Micro-mineral content (ppm)				
	Juv	L.Fem	Ca	Mg	K	P	Na	Cu	Fe	Mn	Mo	Zn
Phoenix reclinata	21.06	21.22	0.15	0.12	1.30	0.20	0.02	9.50	182.20	22.40	0.49	14.00
Ficus sycomorus	17.62	17.82	1.08	0.21	2.20	0.23	0.03	8.18	176.82	22.00	0.30	23.55
Vachellia robusta	9.13	8.68	0.67	0.23	0.83	0.24	0.09	6.14	424.43	22.29	2.06	20.71
Hyphaene compressa	4.40	4.95	0.14	0.19	3.64	0.27	0.14	7.00	275.00	20.33	0.19	73.00
Synsepalum msolo	4.61	4.94	0.92	0.23	1.09	0.11	0.01	12.67	92.00	25.00	0.67	17.67
Agaricus sp.	4.12	4.51	0.10	0.22	4.71	1.36	0.06	60.83	513.67	22.83	0.60	109.17
Oncoba spinosa	2.69	3.41	0.28	0.15	2.08	0.22	0.01	9.20	198.60	13.40	0.48	33.40
Diospyros mespiliformis	2.61	2.78	0.37	0.13	0.96	0.22	0.01	6.86	321.43	10.29	0.28	18.86
Sorindeia madagascariensis	2.68	2.77	0.27	0.14	1.41	0.27	0.01	8.00	105.25	14.38	0.26	17.00
Grewia densa	2.71	2.49	1.00	0.31	1.82	0.29	0.02	10.50	220.33	27.33	0.52	22.17
Brachiaria subquadripara	2.17	2.32	0.39	0.32	2.33	0.34	0.22	7.33	269.67	45.67	1.47	31.33
Polysphaeria multiflora	2.49	1.82	0.40	0.24	1.63	0.19	0.02	5.00	145.20	32.00	0.40	11.20
Mimusops fruticosa	1.92	1.80	0.46	0.17	1.29	0.10	0.08	2.63	125.00	30.00	0.36	9.67
Alangium salviifolium	1.39	1.51	0.70	0.23	1.55	0.26	0.02	7.83	125.67	25.83	0.68	25.17
Garcinia livingstonei	1.19	1.38	0.09	0.10	1.13	0.11	0.01	7.00	245.33	12.33	0.20	15.00
Pavetta sphaerobotrys	1.60	1.30	0.44	0.31	2.43	0.20	0.03	8.00	95.33	12.00	0.47	24.67
Cissus rotundifolia	1.21	1.12	1.55	0.47	2.62	0.30	0.14	6.25	659.25	64.75	0.30	20.25
Mangifera indica	1.31	1.10	0.14	0.19	1.43	0.28	0.01	8.40	372.40	48.40	0.40	20.80
Drypetes natalensis	1.00	0.90	0.51	0.26	1.88	0.25	0.02	11.67	88.00	35.00	0.20	24.67
Species	**Juv**	**L.Fem**	**Ca**	**Mg**	**K**	**P**	**Na**	**Cu**	**Fe**	**Mn**	**Mo**	**Zn**
Lecaniodiscus fraxinifolia	1.00	0.82	0.14	0.12	1.79	0.34	0.01	12.00	327.60	18.00	0.52	42.20

Species	Juv	L.Fem	Ca	Mg	K	P	Na	Cu	Fe	Mn	Mo	Zn
Mormodica trifoliata	0.58	0.78	0.58	0.32	2.81	0.49	0.10	5.50	580.50	29.50	0.70	57.50
Antidesma venosum	0.65	0.59	0.43	0.22	1.48	0.25	0.02	5.20	136.20	39.40	0.36	31.20
Ficus natalensis	0.49	0.54	0.76	0.27	1.88	0.14	0.02	5.00	182.50	21.00	0.65	25.50
Borassus aethiopum	0.58	0.52	0.12	0.13	1.72	0.16	0.02	8.00	212.80	21.80	0.15	18.40
Harrisonia abyssinica	0.64	0.50	1.46	0.17	1.29	0.17	0.05	5.00	131.50	22.00	0.80	10.00
Saba comorensis	0.78	0.47	0.17	0.15	1.50	0.17	0.02	6.75	118.00	23.50	0.17	23.00
Chytranthus obliquinervis	0.20	0.27	0.15	0.20	1.67	0.34	0.01	8.67	67.33	32.67	0.30	23.67
Thespesia Danish	0.38	0.23	0.40	0.23	1.65	0.52	0.06	14.00	249.00	26.00	0.80	28.00
Cordia sinensis	0.36	0.21	1.96	0.14	2.04	0.35	0.33	5.50	83.50	16.00	0.60	15.00
Flagellaria guineensis	0.28	0.21	0.72	0.33	3.03	0.20	0.11	6.67	450.67	42.67	0.83	31.33
Cassia abbreviate	0.31	0.18	0.23	0.16	1.05	0.18	0.05	2.45	89.50	16.50	0.85	17.00
Cordia goetzei	0.38	0.18	1.37	0.23	1.64	0.20	0.07	7.33	108.67	12.33	1.53	16.67
Albizia gummifera	0.15	0.14	1.05	0.08	0.68	0.12	0.00	3.33	156.00	22.67	2.03	13.67
Commelina forskaolii	0.03	0.14	1.10	0.35	4.54	0.42	0.58	10.00	558.00	138.00	1.20	47.00
Tamarindus indica	0.29	0.12	0.28	0.15	1.57	0.37	0.00	10.00	69.00	11.50	0.50	18.00
Ficus bubu	0.20	0.11	0.51	0.27	1.29	0.15	0.01	5.00	56.00	10.00	0.50	17.00
Commelina africana	0.01	0.09	1.95	0.28	4.14	0.28	0.07	1.00	527.00	91.00	0.40	19.00
Flueggea virosa	0.06	0.09	0.31	0.13	1.31	0.25	0.02	4.50	136.50	11.00	0.40	31.50
Keetia zanzibarica	0.18	0.09	0.62	0.19	1.96	0.15	0.07	6.00	41.00	8.00	0.40	14.50
Hunteria zeylanica	0.18	0.07	0.24	0.12	1.10	0.19	0.03	7.50	143.50	11.50	0.65	17.00
Paullinia pinnata	0.06	0.07	0.71	0.22	1.26	0.35	0.01	11.00	290.33	18.67	0.73	31.67
Justicia flava	0.05	0.05	2.95	0.74	3.39	0.47	0.11	7.67	250.33	45.33	0.70	39.67
Setaria verticillata	0.07	0.05	0.24	0.25	1.05	0.26	0.04	10.00	107.00	69.00	1.40	25.00
Ziziphus pubescens	0.05	0.05	0.42	0.17	2.00	0.14	0.04	3.50	54.50	20.00	0.70	13.00
Baragtonia racemosa	0.01	0.04	0.14	0.20	1.72	0.24	0.01	14.00	58.00	15.00	0.09	31.00
Rauvolfia mombasiana	0.07	0.04	0.49	0.20	2.30	0.17	0.01	8.00	77.50	26.00	0.15	11.00
Species	**Juv**	**L.Fem**	**Ca**	**Mg**	**K**	**P**	**Na**	**Cu**	**Fe**	**Mn**	**Mo**	**Zn**
Ruellia patula	0.08	0.04	1.68	0.63	2.37	0.27	0.15	10.00	99.00	36.50	0.55	20.50

Species	Juv	L.Fem	Ca	Mg	K	P	Na	Cu	Fe	Mn	Mo	Zn
Antidesma vogelianum	0.01	0.02	0.30	0.19	1.47	0.23	0.02	7.50	27.50	18.00	0.20	12.00
Cissus petiolata	0.03	0.02	0.47	0.20	2.41	0.43	0.25	5.67	414.33	44.33	0.97	35.00
Ficus bussei	0.03	0.02	0.64	0.26	1.80	0.18	0.05	11.00	83.00	9.00	0.09	15.00
Hibiscus macranthus	0.03	0.02	0.71	0.45	1.74	0.65	0.02	8.50	364.00	47.50	0.50	46.50
Indigofera schimperi	0.01	0.02	2.61	0.38	1.57	0.30	0.04	9.00	282.50	36.00	1.35	25.00
Kigelia Africana	0.03	0.02	0.36	0.24	2.05	0.40	0.01	14.00	271.00	14.67	0.50	38.33
Lawsonia inermis	0.00	0.02	0.63	0.13	0.66	0.15	0.03	8.67	76.00	12.00	0.26	14.00
Ocimum americanum	0.01	0.02	0.86	0.33	2.36	0.37	0.04	11.50	901.00	42.50	0.65	41.00
Phyllanthus ovalifolius	0.01	0.02	1.95	0.31	0.98	0.14	0.98	4.00	51.00	88.00	0.70	16.00
Sterculia appendiculata	0.08	0.02	0.15	0.30	1.38	0.57	0.01	17.00	118.50	10.50	0.25	33.00
Abutilon mauritianum	0.02	0.00	0.80	0.35	1.94	0.48	0.03	12.00	160.50	31.00	0.55	50.50
Afzelia quanzensis	0.02	0.00	0.34	0.15	1.81	0.32	0.12	9.50	63.50	7.50	0.60	26.00
Aporrhiza paniculata	0.03	0.00	0.56	0.35	1.96	0.47	0.02	10.00	134.00	37.00	0.30	35.00
Cassia afrofistula	0.03	0.00	0.37	0.40	1.42	0.69	0.01	6.00	904.00	32.00	2.10	43.00
Citrus limon	0.01	0.00	0.47	0.13	2.19	0.19	0.04	4.00	144.00	7.00	0.10	6.00
Clerodendrum acerbianum	0.01	0.00	0.37	0.12	1.97	0.21	0.04	10.00	310.00	33.00	0.50	17.00
Combretum botryiosum	0.01	0.00	0.11	0.14	1.61	0.24	0.01	18.00	51.00	8.00	0.40	33.00
Croton menyhartii	0.01	0.00	0.65	0.26	1.35	0.27	0.04	9.00	69.00	22.00	0.09	22.00
Grewia stulhmanii	0.01	0.00	1.11	0.22	1.44	0.15	0.02	3.00	50.00	33.00	0.60	13.00
Ixora narcissodora	0.00	0.00	2.13	0.13	1.62	0.10	0.11	1.00	258.00	21.00	0.40	10.00
Majidea zanguebarica	0.02	0.00	0.11	0.14	1.23	0.20	0.01	10.00	105.00	12.00	0.40	19.00
Panicum trichocladum	0.03	0.00	0.27	0.24	3.56	0.37	0.07	3.00	205.00	40.00	1.10	58.00
Sida ovate	0.01	0.00	1.69	0.49	1.43	0.66	0.01	10.00	394.00	46.00	0.70	52.00
Stenotaphrum dimidiatum	0.01	0.00	0.65	0.22	1.29	0.30	0.68	4.00	1830.0	76.00	0.60	38.00
Cajanus cajan	*	*	0.06	0.11	1.64	0.48	0.01	12.00	184.00	13.00	8.40	35.00
Carica papaya	*	*	0.45	0.18	3.01	0.30	0.10	5.00	277.00	14.00	0.50	9.00
Manihot esculenta	*	*	0.13	0.07	0.81	0.17	0.01	2.00	329.00	8.00	0.09	9.00

Musa acuminate	*	*	0.02	0.11	1.15	0.10	0.01	3.00	94.00	10.00	0.30	7.00
Oryza sativa	*	*	0.04	0.11	0.36	0.27	0.01	5.00	159.00	71.00	0.90	20.00
Phaseolus vulgaris	*	*	0.10	0.16	1.35	0.42	0.02	7.00	141.00	18.00	3.20	28.00
Sorghum bicolor	*	*	0.02	0.12	0.32	0.27	0.01	2.00	54.00	15.00	0.70	15.00
Vigna radiate	*	*	0.78	0.33	1.65	0.42	0.01	10.00	323.00	35.00	11.7	24.00
Vigna unguiculata	*	*	0.90	0.34	2.17	0.59	0.02	8.00	333.50	64.50	9.20	39.50
Zea mays	*	*	0.01	0.13	0.44	0.41	0.00	2.00	47.00	7.00	0.40	37.00

Appendix 3.2. The average percentage of macronutrient concentration in dry matter basis of Tana River mangabeys foods.

Food Species	% Nutrient concentration (± SEM)												% Diet
	NDF	±	ADF	±	ADL	±	FAT	±	AP	±	TNC	±	
Abutilon mauritianum	58.33	10.37	42.34	8.22	15.29	2.70	5.02	3.30	15.39	4.20	12.62	5.07	0.01
Afzelia quanzensis	29.24	4.14	17.92	5.84	7.62	3.33	16.36	3.24	13.45	1.19	36.23	3.10	0.01
Agaricus sp.	35.73	2.27	22.71	2.03	6.78	1.30	4.59	0.54	28.81	2.81	14.94	2.60	4.22
Alangium salviifolium	43.13	6.53	31.06	5.73	15.44	2.57	1.92	0.24	20.01	2.61	26.79	6.31	1.42
Albizia gummifera	67.67	3.01	51.21	4.16	23.00	4.77	1.38	0.12	13.02	3.51	10.77	3.45	0.15
Antidesma venosum	57.52	4.53	46.67	3.90	17.61	1.20	4.72	1.04	6.98	1.23	23.43	3.49	0.63
Antidesma vogelianum	57.70	1.97	48.61	3.30	19.43	2.77	5.57	2.03	3.66	0.87	26.59	0.34	0.01
Aporrhiza paniculata	52.23	2.69	38.40	3.35	19.03	1.95	1.52	1.00	8.79	6.27	29.38	8.13	0.02
Borassus aethiopum	36.41	5.20	26.62	4.07	8.88	4.16	1.82	0.23	3.55	0.57	54.25	6.37	0.56
Brachiaria subquadripara	67.67	1.89	36.84	2.26	10.15	2.52	2.80	0.55	14.51	1.30	3.63	1.26	2.22
Cassia abbreviata	35.09	2.20	11.65	1.89	1.20	0.24	5.35	0.30	16.99	1.52	36.81	3.61	0.27
Chytranthus obliquinervis	32.76	5.42	20.52	4.06	9.82	1.43	1.62	0.21	13.51	1.64	45.22	5.95	0.22
Cissus petiolata	71.55	3.80	51.69	5.83	14.27	3.10	1.58	0.65	5.70	3.99	10.19	4.29	0.02
Cissus rotundifolia	50.33	5.35	42.17	5.16	21.63	1.90	2.01	0.27	5.74	0.72	28.08	4.57	1.19
Citrus limon	29.30	0.00	20.36	0.00	2.35	0.00	4.68	0.00	9.89	0.00	48.53	0.00	0.01
Clerodendrum acerbianum	80.01	0.00	63.51	0.00	30.88	0.00	2.44	0.00	0.00	0.00	12.44	0.00	0.00
Combretum botyriosum	64.50	0.00	52.31	0.00	14.27	0.00	1.68	0.00	11.60	0.00	17.17	0.00	0.00
Commelina Africana	47.66	7.98	28.13	5.59	9.99	3.73	2.61	0.75	17.65	0.45	11.93	9.24	0.03
Commelina bangalensis	55.20	5.16	41.05	4.81	13.29	1.17	2.31	0.25	13.80	5.56	9.51	2.44	0.01
Cordia goetzei	68.68	4.35	58.46	3.70	32.11	5.54	1.88	0.51	5.62	2.05	13.44	1.04	0.32
Cordia sinensis	57.92	8.68	47.10	7.66	23.51	4.93	1.26	0.49	7.21	2.54	23.86	5.55	0.32
Croton menyhartii	74.80	0.00	52.91	0.00	16.47	0.00	4.15	0.00	0.00	0.00	17.46	0.00	0.00
Diospyros mespiliformis	65.82	4.74	44.47	2.84	12.52	2.41	2.75	0.53	5.24	1.54	19.26	3.71	2.66
Drypetes natalensis	49.54	7.18	38.75	7.05	16.27	3.08	7.24	3.20	10.62	3.36	23.23	4.36	0.97

Food Species	NDF	±	ADF	±	ADL	±	FAT	±	AP	±	TNC	±	% Diet
Ficus bubu	41.92	2.38	31.47	2.60	15.53	1.71	12.14	0.64	4.39	0.90	36.83	0.17	0.18
Ficus bussei	69.45	0.00	61.48	0.00	36.78	0.00	7.15	0.00	2.13	0.00	13.82	0.00	0.02
Ficus natalensis	57.02	1.82	49.83	1.57	26.57	1.28	4.13	0.70	3.05	0.56	28.20	2.26	0.51
Ficus sycomorus	55.09	1.66	44.99	1.88	25.04	2.60	5.65	0.41	4.24	1.21	25.66	2.11	17.66
Flagellaria guineensis	29.53	5.67	19.81	4.16	6.29	2.44	7.51	2.02	17.20	8.06	37.12	10.70	0.26
Flueggea virosa	47.61	12.59	34.09	12.32	13.77	4.82	7.94	3.07	5.28	1.80	33.56	11.61	0.07
Garcinia livingstonei	36.31	9.51	24.72	6.92	10.04	2.69	5.52	1.81	7.77	2.54	43.82	12.01	1.24
Grewia densa	63.32	4.21	46.90	4.28	19.68	2.69	3.08	0.79	9.43	1.23	16.31	2.99	2.65
Grewia stulhmanii	51.57	0.00	32.40	0.00	11.32	0.00	1.45	0.00	2.66	0.00	29.07	0.00	0.00
Harrisonia abyssinica	33.89	0.00	27.68	0.00	18.72	0.00	1.54	0.00	17.43	0.00	28.47	0.00	0.60
Hibiscus macranthus	45.16	0.00	28.62	0.00	14.64	0.00	2.21	0.00	17.85	0.00	20.93	0.00	0.03
Hunteria zeylanica	30.72	10.40	19.75	10.87	9.04	6.54	5.19	1.81	9.63	4.37	46.60	7.37	0.15
Hyphaene compressa	49.55	5.29	31.20	3.97	13.22	2.41	1.65	0.17	2.77	0.41	34.44	6.03	4.55
Indigofera schimperi	38.04	5.78	28.67	3.63	15.08	0.78	1.72	0.28	19.94	1.82	22.63	6.14	0.01
Insect	0.00	0.00	17.47	2.10	0.00	0.00	9.03	1.75	50.31	3.83	12.44	4.57	5.40
Ixora narcissodora	76.89	0.00	65.45	0.00	29.82	0.00	2.76	0.00	0.00	0.00	18.56	0.00	0.00
Justicia flava	40.64	3.33	30.66	2.79	12.44	3.83	2.63	0.14	9.66	6.77	36.80	12.03	0.05
Keetia zanzibarica	61.68	5.75	48.50	4.40	15.56	2.98	1.61	0.81	8.43	2.35	20.48	4.10	0.15
Kigelia africana	51.27	10.25	35.52	10.56	17.99	4.98	5.17	1.78	9.70	2.74	25.68	8.92	0.03
Lannea schweinfurthii	29.93	0.00	12.99	0.00	8.08	0.00	6.52	0.00	7.30	0.00	55.74	0.00	0.11
Lawsonia inermis	64.09	9.99	51.79	8.99	34.01	3.83	4.02	0.90	7.86	1.94	18.59	7.93	0.00
Lecaniodiscus flaxinifolius	29.39	2.38	20.53	2.10	12.80	1.51	6.02	1.48	9.79	1.73	50.07	3.98	0.95
Majidea zanguebarica	43.92	3.11	36.09	4.06	18.44	0.08	6.05	4.50	4.73	1.01	37.03	4.58	0.01
Mangifera indica	29.64	4.35	23.15	4.32	11.94	2.92	4.27	0.88	6.99	2.00	54.96	5.01	1.25
Mimusops fruticosa	54.50	3.53	40.03	3.62	18.11	3.43	6.86	1.62	12.37	4.02	17.06	4.47	1.89
Mormodica trifoliata	50.77	2.65	36.67	2.65	11.55	1.45	5.27	1.56	14.04	1.60	12.56	3.95	0.63
Ocimum americanum	41.89	22.50	33.55	19.07	14.37	8.54	8.05	0.19	5.96	1.70	32.18	19.54	0.01

Food Species	NDF	±	ADF	±	ADL	±	FAT	±	AP	±	TNC	±	% Diet
Oncoba spinosa	26.43	2.66	18.89	2.25	8.29	1.01	10.98	0.92	6.21	0.47	43.46	2.61	2.89
Panicum trichocladum	31.75	0.00	26.17	0.00	19.82	0.00	2.29	0.00	16.74	0.00	44.28	0.00	0.02
Paullinia pinnata	63.91	5.71	46.95	3.40	13.98	6.04	3.59	0.32	4.87	0.98	17.53	8.42	0.06
Pavetta sphaerobotrys	54.25	3.58	35.85	2.27	15.19	0.96	3.27	0.29	10.86	0.29	22.33	3.44	1.52
Phoenix reclinata	67.83	2.49	48.00	2.29	15.36	2.25	3.46	0.32	5.39	0.66	18.81	2.52	21.11
Phyllanthus ovalifolius	30.91	4.37	15.24	2.63	4.49	0.91	5.10	0.63	14.96	0.82	34.96	3.49	0.01
Polysphaeria multiflora	61.26	2.51	49.31	2.44	28.37	2.63	2.96	0.31	5.84	0.90	22.73	2.34	2.31
Rauvolfia mombasiana	54.24	3.02	44.21	4.12	17.07	0.60	18.70	0.24	10.14	1.00	7.34	0.36	0.06
Ruellia patula	35.71	0.64	27.73	3.92	14.75	3.95	2.48	1.03	12.71	8.51	35.42	15.05	0.07
Saba comorensis	50.49	5.55	37.66	5.82	16.73	7.62	4.07	0.87	7.60	1.20	32.23	4.65	0.70
Setaria verticillata	58.62	0.00	35.79	0.00	17.00	0.00	3.73	0.00	11.08	0.00	10.50	0.00	0.01
Sida ovate	18.37	0.00	5.29	0.00	2.01	0.00	4.49	0.00	6.55	0.00	68.14	0.00	0.00
Sorindeia madagascariensis	40.61	6.10	25.70	3.89	9.91	1.56	2.75	0.41	11.96	1.50	37.75	6.84	2.70
Stenotaphrum dimidiatum	38.64	0.00	32.21	0.00	22.22	0.00	1.85	0.00	16.41	0.00	38.58	0.00	0.01
Sterculia appendiculata	24.61	13.01	16.83	12.54	9.86	8.14	12.11	9.06	17.43	9.06	42.74	7.12	0.06
Synsepalum msolo	38.58	7.97	32.03	8.48	13.42	3.80	11.04	4.96	15.87	7.42	28.61	8.42	4.70
Tamarindus indica	34.95	0.27	30.68	0.03	23.07	0.70	1.22	0.41	16.28	0.81	40.75	1.23	0.24
Thespesia danish	57.34	0.00	39.52	0.00	14.66	0.00	9.31	0.00	7.94	0.00	19.42	0.00	0.34
Vachellia robusta	36.35	3.76	20.70	2.41	7.73	1.15	2.88	0.41	20.38	2.64	34.08	4.23	9.01
Ziziphus pubescens	61.45	8.41	47.34	8.04	14.28	0.91	6.12	4.79	10.28	4.56	16.20	1.02	0.05

Appendix 3.3. Ethogram of the general behaviors scored during focal sampling

Behavior	Operational definition
Feeding	Food procurement from the source into the mouth, including locating, picking, dextral manipulation, dental processing and finally swallowing it
Moving	Movement by walking on the ground or traveling within and between trees for at least five seconds or by making more than four steps without stopping
Resting	State in which an animal was in inactive position (sitting or lying down) for more than five seconds, and it is not engaged feeding, traveling or in any social activity
Social interaction	Other activities other than feeding, moving, and resting that involved manipulative, communicative, aggressive or friendly engagement behaviors between two individual or independently
Other	Any other behavior, which did not include feeding, moving, resting and social interaction and activities performed when focal individuals are out of sight.

3.4 References

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49(3), 227-267.

Altmann, S. A. (1991). Diets of yearling female primates (Papio cynocephalus) predict lifetime fitness. *Proceedings of the National Academy of Sciences*, *88*(2), 420-423.

Altmann, S. A. (2009). Fallback foods, eclectic omnivores, and the packaging problem. *American journal of physical anthropology*, *140*(4), 615-629.

Altmann, S.A., (1998). *Foraging for survival: yearling baboons in Africa*. Chicago: University of Chicago Press.

Amato, K. R., Leigh, S. R., Kent, A., Mackie, R. I., Yeoman, C. J., Stumpf, R. M., Wilson, B.A., Nelson, K.E., White, B.A. & Garber, P. A. (2014). The role of gut microbes in satisfying the nutritional demands of adult and juvenile wild, black howler monkeys (*Alouatta pigra*). *American journal of physical anthropology*, *155*(4), 652-664.

Bernays, E. A., Driver, G. C., & Bilgener, M. (1989). Herbivores and plant tannins. *Advances in ecological research*, *19*, 263-302.

Bryer, M. A., Chapman, C. A., Raubenheimer, D., Lambert, J. E., & Rothman, J. M. (2015). Macronutrient and energy contributions of insects to the diet of a frugivorous monkey (Cercopithecus ascanius). *International Journal of Primatology*, *36*(4), 839-854.

Cancelliere, E. C., DeAngelis, N., Nkurunungi, J. B., Raubenheimer, D., & Rothman, J. M. (2014). Minerals in the Foods Eaten by Mountain Gorillas (*Gorilla beringei*). *PloS one*, *9*(11), e112117.

Cachel S. (1974). Growth and allometry in primate masticatory muscles. *Archs oral Biol*. *29*(4) 287 – 293.

Cachel. S (1997). Dietary shifts and the European Upper Palaeolithic transition. *Current Anthropology 38*(4):579-603

Chalk, J., Wright, B. W., Lucas, P. W., Schuhmacher, K. D., Vogel, E. R., Fragaszy, D., Visalberghi, E., Izar, P. & Richmond, B. G. (2016). Age-related variation in the mechanical properties of foods processed by *Sapajus libidinosus. American journal of physical anthropology*, *159*(2), 199-209.

Chapman, C. A., Chapman, L. J., Naughton-Treves, L., Lawes, M. J., & Mcdowell, L. R. (2004). Predicting folivorous primate abundance: validation of a nutritional model. *American Journal of Primatology*, *62*(2), 55-69.

Chapman, C. A., Chapman, L. J., Struhsaker, T. T., Zanne, A. E., Clark, C. J., & Poulsen, J. R. (2005). A long-term evaluation of fruiting phenology: the importance of climate change. *Journal of Tropical Ecology*, *21*(01), 31-45.

Chapman, C., Rothman, J. M & Lambert E.J (2012). Surviving and growing up in difficult and dangerous world. In *The evolution of primate societies*. Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.). University of Chicago Press.

Conklin-Brittain, N. L., Knott, C. D., & Wrangham, R. W. (2006). Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. *Cambridge Studies in Biological and Evolutionary Anthropology*, *1*(48), 445-472.

Constantino, P. J., Lee, J. J. W., Gerbig, Y., Hartstone-Rose, A., Talebi, M., Lawn, B. R., & Lucas, P. W. (2012). The role of tooth enamel mechanical properties in primate dietary adaptation. *American journal of physical anthropology*, *148*(2), 171-177.

Cooke, C., & McGraw, W. S. (2010). Diet, food hardness, and tooth use in red-capped mangabeys (*Cercocebus torquatus*) from Sette cama, Gabon. *American Journal of primatology*, 72(1), 38.

Dasilva, G. L. (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*(5), 655-680.

Dearing, M. D., Foley, W. J., & McLean, S. (2005). The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annual review of ecology, evolution, and systematics*, *36 (11)*, 169-89.

Deblauwe, I., & Janssens, G. P. (2008). New insights in insect prey choice by chimpanzees and gorillas in southeast Cameroon: the role of nutritional value. *American Journal of Physical Anthropology*, *135*(1), 42-55.

Decker, B. S. (1994). Effects of habitat disturbance on the behavioral ecology and demographics of the Tana River red colobus (*Colobus badius rufomitratus*). *International Journal of Primatology*, *15*(5), 703.

Dew, J. L. (2005). Foraging, food choice, and food processing by sympatric ripe-fruit specialists: *Lagothrix lagotricha poeppigii* and *Ateles belzebuth belzebuth*. *International Journal of Primatology*, *26*(5), 1107-1135.

Di Fiore, A., Link, A. & Dew, J. L. (2008). Diets of wild spider monkeys. *Spider Monkeys: Behavior, Ecology, and Evolution of the Genus Ateles* (ed. C.J. Campbell), pp. 81–137. Cambridge University Press, Cambridge.Eppley, T. M., Tan, C. L., Arrigo-Nelson, S. J., Donati, G., Ballhorn, D. J., & Ganzhorn, J. U. (2017). High Energy or Protein Concentrations in Food as Possible Offsets for Cyanide Consumption by Specialized Bamboo Lemurs in Madagascar. *International Journal of Primatology*, *38*(5), 881-899.

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K.A.I., Nijman, V., Heymann, E.W., Lambert, J.E & Rovero, F. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, *3*(1), e1600946.

Fashing, P. J. (2001). Feeding ecology of guerezas in the Kakamega Forest, Kenya: the importance of Moraceae fruit in their diet. *International Journal of Primatology*, *22*(4), 579-609.

Fashing, P. J., Dierenfeld, E. S., & Mowry, C. B. (2007). Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of Colobus guereza in Kakamega Forest, Kenya. *International Journal of Primatology*, *28*(3), 673-703.

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

Felton, A. M., Felton, A., Wood, J. T., & Lindenmayer, D. B. (2008). Diet and feeding ecology of *Ateles chamek* in a Bolivian semi humid forest: the importance of Ficus as a staple food resource. *International Journal of Primatology*, *29*(2), 379-403.

Finke, M. D. (2007). Estimate of chitin in raw whole insects. *Zoo Biology*, *26*(2), 105-115.

Francisco, T. M., Lopes-Mattos, K. L. B., Picoli, E. A. D. T., Couto, D. R., Oliveira, J. A., Zanuncio, J. C., Serrão, J.E., de Oliveira Silva, I. & Boere, V. (2017). Feeding habits of marmosets: A case study of bark anatomy and chemical composition of *Anadenanthera peregrina* gum. *American journal of primatology*, *79*(3), 1-9.

Freeland, W. J., & Janzen, D. H. (1974). Strategies in herbivory by mammals: the role of plant secondary compounds. *The American Naturalist*, *108*(961), 269-289.

Ganzhorn J. U, Rakotondranary & Ratovonamana R.Y. (2011). Habitat description and phenology. *In*: *Field and laboratory methods in primatology: a practical guide*. Setchell, J. M., & Curtis, D. J. (Eds.). Pp 51 – 68. Cambridge University Press.

Garber, P. A. (1987). Foraging strategies among living primates. *Annual review of Anthropology*, *16*(1), 339-364.

Garber, P. A., Righini, N., & Kowalewski, M. M. (2015). Evidence of alternative dietary syndromes and nutritional goals in the genus *Alouatta*. In *Howler Monkeys* (pp. 85-109). Springer New York.

Gautier-Hion, A., & Gautier, J. P. (1976). Croissance, maturité sexuelle et sociale, reproduction chez les cercopithécinés forestiers africains. *Folia Primatologica*, *26*(3), 165-184.

Glander, K. E. (1982). The impact of plant secondary compounds on primate feeding behavior. *American Journal of Physical Anthropology*, *25*(S3), 1-18.

Gunst, N., Leca, J.B., Boinski, S., & Fragaszy, D., (2010). The ontogeny of handling hard-to-process food in wild brown capuchins (*Cebus apella apella*): evidence from foraging on the fruit of *Maximiliana maripa*. *American journal of primatology*, *72*(11), 960-973.

Hanson, A. M., Hodge, K. T., & Porter, L. M. (2003). Mycophagy among primates. *Mycologist*, *17*(1), 6-10.

Hanya, G., Kiyono, M., Takafumi, H., Tsujino, R., & Agetsuma, N. (2007). Mature leaf selection of Japanese macaques: effects of availability and chemical content. *Journal of Zoology*, *273*(2), 140-147.

Harding, R. S. (1981). An order of omnivores: nonhuman primate diets in the wild. *Omnivorous primates: gathering and hunting in human evolution*, 191-214.

Hill, R. A., & Dunbar, R. I. M. (2002). Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary ecology*, *16*(6), 579-593.

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

Huffman, M. A. (1997). Current evidence for self-medication in primates: A multidisciplinary perspective. *American Journal of Physical Anthropology*, *104*(S25), 171-200.

Irwin, M. T., Raharison, J. L., Chapman, C. A., Junge, R. E., & Rothman, J. M. (2017). Minerals in the foods and diet of diademed sifakas: Are they nutritional challenges? *American journal of primatology*, *79*(4), 1-14.

Isbell, L. A., Rothman, J. M., Young, P. J., & Rudolph, K. (2013). Nutritional benefits of *Crematogaster mimosae* ants and *Acacia drepanolobium* gum for patas monkeys and vervets in Laikipia, Kenya. *American journal of physical anthropology*, *150*(2), 286-300.

Jaman, M., & Huffman, M. A. (2010). Age class differences in the feeding behavior of captive Japanese macaques (*Macaca fuscata*) in the forested and nonvegetated enclosure groups. *Zoo biology*, *30*(3), 260-274.

Janson, C. H. (1988). Intra-specific food competition and primate social structure: a synthesis. *Behaviour*, *105*(1), 1-17.

Janson, C. H. & van Schaik, C. P. (2002). Ecological Risk Aversion in juvenile primates: Slow and steady wins the race. In M. E. Pereira & L. A. Fairbanks (Eds.), Juvenile Primates: Life history, Development, and Behavior (pp. 57 -74). Chicago: The University of Chicago Press.

Kent, M., & Coker, P. (1992). *Vegetation description and analysis*. Baffins Lane.

Kinnaird, M. F. (1992). Phenology of flowering and fruiting of an East African riverine forest ecosystem. *Biotropica*, 187-194.

Kivai S. M, Erin E. R. Rothman J.M. Kivasu C. M. & Palombit, R. A. (2017). Extractive foraging in wild Tana River Mangabeys, *Cercocebus galeritus*: Implication of Different Physical Properties of Foods. *Abstract, presented in the 86th Annual Meeting of the American Association of Physical Anthropologists (2017)*. American Association of Physical Anthropologists.

Kivai, S. (2013). Predation on an Endemic and Endangered Tana River Mangabey (*Cercocebus galeritus*) by a Sympatric Yellow Baboon (*Papio cynocephalus*) in Tana River National Primate Reserve, Kenya. *African Primates 8(1),* 59-62.

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

Kool, K. M. (1989). *Behavioural Ecology of the Silver Leaf Monkey, Trachypithecus auratus sondaicus, in the Pangandaran Nature Reserve, West Java, Indonesia.* Ph.D. thesis, University of New South Wales, Sydney.

Krishnamani, R., & Mahaney, W. C. (2000). Geophagy among primates: adaptive significance and ecological consequences. *Animal behaviour*, *59*(5), 899-915.

Kuno, E. (1991). Sampling and analysis of insect populations. *Annual review of entomology*, *36*(1), 285-304.

Lambert, J. E. (2010). Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In: Campell, C., Fuentes, A., Mackinnon, K. C., Panger, M., and Beadner, S. (Eds), *Primates in perspective* (pp. 482-495). Oxford: Oxford University Press.

Lambert J. E., (2011). Primate nutritional ecology: Feeding biology and diet at ecological and evolutionary scales. *In* C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (pp. 512–522). New York: Oxford University Press.

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

Liu, X., Li, F., Jiang, J., Wang, X., & Li, Y. (2016). Age-sex analysis for the diet of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in Shennongjia National Nature Reserve, China. *Primates*, *57*(4), 479-487.

Lonsdorf, E.V., & Ross, S.R., (2012). Socialization and Development of Behavior. In*:* Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.), *The evolution of primate societies* (pp. 245-268). Chicago: University of Chicago Press.

Lucas, P. W., Copes, L., Constantino, P. J., Vogel, E. R., Chalk, J., Talebi, M., Landis, M. & Wagner, M. (2012). Measuring the toughness of primate foods and its ecological value. *International Journal of Primatology*, *33*(3), 598-610.

Lucas, P. W., Omar, R., Al-Fadhalah, K., Almusallam, A. S., Henry, A. G., Michael, S Arockia L. T, Watzke, J, Strait, D.S. & Atkins, A. G. (2013). Mechanisms and causes of wear in tooth enamel: implications for hominin diets. *Journal of the Royal Society Interface*, *10*(80), 20120923.

Mackie, R., & White, B. (2012). *Gastrointestinal Microbiology: Volume 1 Gastrointestinal Ecosystems and Fermentations*. Springer Science & Business Media.

Magliocca, F., & Gautier-Hion, A. (2002). Mineral content as a basis for food selection by western lowland gorillas in a forest clearing. *American Journal of Primatology*, *57*(2), 67-77.

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

Mattson W. J. (1980). Herbivory in relation to plant nitrogen content. *Annual review of ecology and systematics*, *11*(1), 119-161.

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

McGraw, W. S., Vick, A. E., & Daegling, D. J. (2014). Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): Implications for fallback foods and dental adaptation. *American journal of physical anthropology*, *154*(3), 413-423.

McKey, D. B., Gartlan, J. S., Waterman, P. G. & Choo, G. M. (1981). Food selection by black colobus monkeys (*Colobus satanus*) in relation to plant chemistry. *Biological Journal of the Linnean Society*, *16*(2), 115-146.

Medley, K. E. (1993). Extractive forest resources of the Tana River National Primate Reserve, Kenya. *Economic Botany*, *47*(2), 171-183.

Milton, K. (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *The American Naturalist*, *114*(3), 362-378.

Milton, K. (1980). *The Foraging Strategy of Howler Monkeys*. New York: Columbia University Press.

Milton, K. (1984). The role of food-processing factors in primate food choice. *Adaptations for foraging in nonhuman primates*, 249-279.

Milton, K. (1999). Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us? *Nutrition*, *15*(6), 488-498.

Milton, K. & Demment, M. W. (1988). Digestion and Passage Kinetics of Chimpanzees Fed High and Low Fiber Diets and Comparison with Human Data. *Journal of Nutrition,* 118(9):1082-8.

Min, B. R., Barry, T. N., Attwood, G. T., & McNabb, W. C. (2003). The effect of condensed tannins on the nutrition and health of ruminants fed fresh temperate forages: a review. *Animal Feed Science and Technology*, *106*(1), 3-19.

Moinde-Fockler, N. N., Oguge, N. O., Karere, G. M., Otina, D., & Suleman, M. A. (2007). Human and natural impacts on forests along lower Tana River, Kenya: implications towards conservation and management of endemic primate species and their habitat. Biodiversity and Conservation, 16(4), 1161-1173.

Morellato, L. P. C., Camargo, M. G. G., Fernanda, F. D., Luize, B. G., Mantovani, A., & Hudson, I. L. (2010). *The influence of sampling method, sample size, and frequency of observations on plant phenological patterns and interpretation in tropical forest trees* (pp. 99-121). Springer Netherlands.

Mueller-Harvey, I. (2006). Unravelling the conundrum of tannins in animal nutrition and health. *Journal of the Science of Food and Agriculture*, *86*(13), 2010-2037.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853-858.

National Research Council (NRC). (2003). *Nutrient requirements of nonhuman primates*. National Academies Press.

National Research Council. (2010). *Guide for the care and use of laboratory animals*. National Academies Press.

Norconk, M. A., Wright, B. W., Conklin-Brittain, N. L., & Vinyard, C. J. (2009). Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In: Garber, P. A., Estrada, A., Bicca-Marques, J. C., Heymann, E. & Strier, K. B (Eds), *South American Primates* (pp. 279-319). New York: Springer.

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

Oates, J. F. (1978). Water-plant and soil consumption by guereza monkeys (*Colobus guereza*): a relationship with minerals and toxins in the diet? *Biotropica*, 10(4), 241-253.

Oftedal, O. T., Whiten, A., Southgate, D. A. T., & Van Soest, P. (1991). The Nutritional Consequences of Foraging in Primates: The Relationship of Nutrient Intakes to Nutrient Requirements and Discussion. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *334*(1270), 161-170.

Ohwaki, K., Hungate, R. E., Lotter, L., Hofmann, R. R., & Maloiy, G. (1974). Stomach fermentation in East African colobus monkeys in their natural state. *Applied microbiology*, *27*(4), 713-723.

Palombit, R. A. (1997). Inter-and intraspecific variation in the diets of sympatric siamang (*Hylobates syndactylus*) and lar gibbons (*Hylobates lar*). *Folia Primatologica* 68, no. 6 (1997): 321-337.

Pereira, M.E., Fairbanks, L.A., (2002). *Juvenile Primates: Life history, Development, and Behavior*. New York: Oxford University Press.

Porter, L. J., Hrstich, L. N., & Chan, B. G. (1986). The conversion of procyanidins and prodelphinidins to cyanidin and delphinidin. *Phytochemistry*, *25*(1), 223-230.

Power, M. L. (1991). Digestive function, energy intake and the digestive response to dietary gum in captive callitrichids. *Digestive function, energy intake and the digestive response to dietary gum in captive callitrichids*.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Raubenheimer, D. (2011). Toward a quantitative nutritional ecology: the right-angled mixture triangle. *Ecological Monographs*, *81*(3), 407-427.

Raubenheimer, D., Rothman, J. M., Pontzer, H., & Simpson, S. J. (2014). Macronutrient contributions of insects to the diets of hunter–gatherers: a geometric analysis. *Journal of human evolution*, *71*, 70-76.

Righini, N. (2017). Recent advances in primate nutritional ecology. *American journal of primatology*, *79*(4), 1-5.

Righini, N., Garber, P. A., & Rothman, J. M. (2017). The effects of plant nutritional chemistry on food selection of Mexican black howler monkeys (*Alouatta pigra*): the role of lipids. *American journal of primatology*, *79*(4), 1-15.

Robbins, C. (2012). *Wildlife feeding and nutrition*. Elsevier.

Robbins, C. T., Fortin, J. K., Rode, K. D., Farley, S. D., Shipley, L. A., & Felicetti, L. A. (2007). Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos*, *116*(10), 1675-1682.

Robbins, C. T., Hanley, T. A., Hagerman, A. E., Hjeljord, O., Baker, D. L., Schwartz, C. C., & Mautz, W. W. (1987). Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology*, *68*(1), 98-107.

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

Rode, K. D., Chapman, C. A., McDowell, L. R., & Stickler, C. (2006). Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*) 1. *Biotropica*, *38*(5), 625-634.

Ross, C. & Jones, K. E. (1999). Socioecology and the evolution of primate reproductive rates. *Comparative primate socioecology*, 73-110.

Rothman, J. M., Chapman, C. A., & Pell, A. N. (2008b). Fiber-bound nitrogen in gorilla diets: implications for estimating dietary protein intake of primates. *American Journal of Primatology*, *70*(7), 690-694.

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

Rothman, J. M., Chapman, C. A., Struhsaker, T. T., Raubenheimer, D., Twinomugisha, D., & Waterman, P. G. (2015). Long-term declines in nutritional quality of tropical leaves. *Ecology*, *96*(3), 873-878.

Rothman, J. M., Dierenfeld, E. S., Hintz, H. F., & Pell, A. N. (2008a). Nutritional quality of gorilla diets: consequences of age, sex, and season. *Oecologia*, *155*(1), 111-122.

Rothman, J. M., Dierenfeld, E. S., Molina, D. O., Shaw, A. V., Hintz, H. F., & Pell, A. N. (2006). Nutritional chemistry of foods eaten by gorillas in Bwindi Impenetrable National Park, Uganda. *American Journal of Primatology*, *68*(7), 675-691.

Rothman, J. M., Dusinberre, K., & Pell, A. N. (2009). Condensed tannins in the diets of primates: a matter of methods? *American Journal of Primatology*, *71*(1), 70-76.

Rothman, J. M., Raubenheimer, D., Bryer, M. A., Takahashi, M., & Gilbert, C. C. (2014). Nutritional contributions of insects to primate diets: Implications for primate evolution. *Journal of Human Evolution*, *71*, 59-69.

Rothman, J. M., Raubenheimer, D., Bryer, M. A., Takahashi, M., & Gilbert, C. C. (2014). Nutritional contributions of insects to primate diets: Implications for primate evolution. *Journal of Human Evolution*, *71*, 59-69.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual review of ecology and systematics*, *2*(1), 369-404.

Shah, N.F. (2003). Foraging strategies in two sympatric mangabey species (*Cercocebus agilis* and *Lophocebus albigena*). (*Ph.D. dissertation thesis, Stony Brook University, Stony Brook, NY.*

Shimada, T., Saitoh, T., Sasaki, E., Nishitani, Y., & Osawa, R. (2006). Role of tannin-binding salivary proteins and tannase-producing bacteria in the acclimation of the Japanese wood mouse to acorn tannins. *Journal of chemical ecology*, *32*(6), 1165-1180.

Simpson, S. J., Batley, R., & Raubenheimer, D. (2003). Geometric analysis of macronutrient intake in humans: the power of protein? *Appetite*, *41*(2), 123-140.

Stevenson, P. R. (2005). Fruit choice by woolly monkeys in Tinigua National Park, Colombia. *International Journal of Primatology*, *25*(2), 367-381.

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

Strier, K. B. (2016). *Primate behavioral ecology 4th Edition*. Routledge, New York.

Struhsaker, T. T., Cooney, D. O., & Siex, K. S. (1997). Charcoal consumption by Zanzibar red colobus monkeys: function and ecological and demographic consequences. *International Journal of Primatology*, *18*(1), 61-72.

Underwood, J., & Suttle, F. (1999). The detection and correction of mineral imbalances. In *The mineral nutrition of livestock*, Chapter 3 Pp 47 -66. CABI Publishing.

Vogel E.R, Kivai S. M. & Alavi S. (2016). Foraging strategies. *International Encyclopedia of Primatology*. In Press.

Vogel, E. R., Alavi, S. E., Utami-Atmoko, S. S., van Noordwijk, M. A., Bransford, T. D., Erb, W. M., Zulfa, A., Sulistyo, F., Farida, W.R & Rothman, J. M. (2017). Nutritional ecology of wild Bornean orangutans (*Pongo pygmaeus wurmbii*) in a peat swamp habitat: Effects of age, sex, and season. *American journal of primatology*, *79*(4), 1-20.

Vogel, E.R, Zulfa, A., Hardus, M., Wich, S.A. & Dominy, N.J (2014). Food mechanical properties, feeding ecology, and the mandibular morphology of the wild Orangutans. *Journal of Human Evolution*, http://dx.doi.org/10.1016/j.jhevol.2014.05.007.

Voigt, C. C., Capps, K. A., Dechmann, D. K., Michener, R. H., & Kunz, T. H. (2008). Nutrition or detoxification: why bats visit mineral licks of the Amazonian rainforest. *PloS one*, *3*(4), e2011.

Wahungu, G. (1998). Diet and habitat overlap in two sympatric primate species, the Tana crested mangabey *Cercocebus galeritus* and yellow baboon *Papio cynocephalus*. *African Journal of Ecology*, *36*(2), 159-173.

Waterman, P. G. (1984). Food acquisition and processing as a function of plant chemistry. In *Food acquisition and processing in primates* (pp. 177-211). Springer US.

Waterman, P. G., and Kool, K. M. (1994). Colobine food selection and plant chemistry. In Davies, A. G. and Oates, J. F. (eds.), *Colobine Monkeys: Their Ecology, Behaviour, and Evolution*, Cambridge University Press, Cambridge, pp. 251–284.

Wieczkowski J. (2003). *Aspects of the ecological flexibility of the Tana mangabey (Cercocebus galeritus) in its fragmented habitat, Tana River, Keny*a. Ph.D. dissertation thesis. Athens, GA: University of Georgia.

Wieczkowski, J. (2009). Brief communication: Puncture and crushing resistance scores of Tana River mangabey (*Cercocebus galeritus*) diet items. *American journal of physical anthropology*, *140*(3), 572-577.

Wieczkowski, J., & Kinnaird, M. (2008). Shifting forest composition and primate diets: a 13-year comparison of the Tana River mangabey and its habitat. *American Journal of Primatology*, *70*(4), 339-348.

Wrangham, R. W., & Waterman, P. G. (1981). Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. *The Journal of Animal Ecology*, *50(3),* 715-731.

Yamashita, N., Cuozzo, F. P., & Sauther, M. L. (2012). Interpreting food processing through dietary mechanical properties: a Lemur catta case study. *American journal of physical anthropology*, *148*(2), 205-214.

Yeager, C. P., Silver, S. C., & Dierenfeld, E. S. (1997). Mineral and phytochemical influences on foliage selection by the proboscis monkey (*Nasalis larvatus*). *American Journal of Primatology*, *41*(2), 117–128.

Zaller, J. G., Kerschbaumer, G., Rizzoli, R., Tiefenbacher, A., Gruber, E., & Schedl, H. (2015). Monitoring arthropods in protected grasslands: comparing pitfall trapping, quadrat sampling and video monitoring. *Web Ecology*, *15*(1), 15.

CHAPTER FOUR: MECHANICAL PROPERTIES OF FOODS AND THEIR DIETARY IMPLICATIONS ON FORAGING IN JUVENILE TANA RIVER MANGABEYS, *CERCOCEBUS GALERITUS*

Abstract

The mechanical properties of foods provide a significant selective force in dietary adaptations because of the problems they present to potential consumers. Juveniles are more constrained than conspecific adults by such physical defenses due to their foraging incompetence and nutritional demands for growth. Little is known about how juveniles overcome these mechanical barriers, however, as well as how the mechanical and nutritional aspects of foods interact to determine diet selectivity. To address this research gap, I studied Tana River mangabeys (*Cercocebus galeritus*) and tested the following hypotheses. Compared to lactating females: i) *juveniles' diets disproportionately favor foods with fewer mechanical barriers*; and ii) *mechanical and nutritional properties of foods interact to influence dietary decisions during periods of low food abundance*. I measured food fracture toughness and elastic modulus using the portable FLS-tester machine performed laboratory nutritional analyses, and determined the food selectivity using Vanderploeg and Scavia (1979) electivity index. Juveniles consumed foods with significantly lower fracture toughness than lactating females (t = 2.13, df = 1, p = 0.0370), but there was no age class difference in the elastic modulus of the foods ingested (t = 1.68, df = 1, p = 0.0968). Fracture toughness and elastic modulus interacted with protein and metabolizable energy content of food to determine electivity indices and this varied significantly with fruit availability (F = 80.02, df =

14, p < 0.0001) but not age class (F = 0.3, df = 1, p = 0.8713). These findings partially supported the prediction that juveniles consume less physically challenging foods in terms of fracture toughness, but not elastic modulus. The data indicate that mechanical and nutritional properties of foods interact with fruit availability to influence feeding selectivity across seasons, but not across the two age classes.

4.1 Introduction

4.1.1 General Background

The mechanical properties of food are likely to play a significant role in dietary adaptations because of their strong influence on foraging efficiency and food acquisition (Norconk et al., 2009; Constantino et al., 2012; Lambert & Rothman, 2015; Vogel et al., 2014, 2016). The physical properties of foods are outcomes of both internal and external material attributes, particularly toughness, stiffness, hardness, and size (Lucas, 2004; Yamashita et al., 2009; Chalk et al., 2016). Such food properties can act as deterrents to consumers and impose an upper threshold for successful processing and fragmentation strategies (Dominy et al., 2001; Yamashita et al., 2009). Thus, the mechanical properties of food are likely to determine in part the dietary choices of primates (Milton, 1984; Marshall & Wrangham, 2009; Lambert & Rothman, 2015).

Foraging competency to overcome food mechanical defenses is fundamental for ingestion of adequate nutrients necessary for growth and reproduction, which ultimately affects lifetime fitness (Altmann, 1998, 2009; Gunst et al., 2010). The capability to overcome the mechanical problems of foods depends on skeletal and physical maturity, cognitive ability, body size, and energetic requirements (Gunst et al., 2008, 2010; Chapman et al., 2012; Schuppli et al., 2016; Chalk et al., 2016). Such ability also varies with type of food processed and among primate species (Lambert & Rothman, 2015). Because of physical immaturity, foraging inefficiency, and higher nutritional demands compared to adults, juveniles are more vulnerable to the cost imposed by the mechanical challenges of foods (Fragaszy & Boinski, 1995; Marshall

& Wrangham, 2009; Pereira & Fairbanks, 2002; Chapman et al., 2012; Lonsdorf & Ross, 2012). For example, physical properties of foods pose a potential risk of masticatory system damage impeding nutrient acquisition (Yamashita et al., 2012; Lucas et al., 2013). Thus, adult-juvenile foraging differences are likely to emerge prominently in primates, which engage in processing and consumption of difficult-to-process foods and which are often confronted with pronounced seasonality in resource availability (Silk, 1978; Gunst et al., 2010).

Primate foods are not only packed with mechanical deterrents or impurities, but also chemical barriers, which further limit foraging efficiency (Lambert & Rothman 2015; Vogel et al., 2016). The plant secondary compounds represent the most common plant defense mechanism against predation (Dearling et al., 2005). Other factors that as well may influence foraging competence include food scarcity, intraspecific competition, and predation risks (Pereira & Fairbank, 2002; Lonsdorf & Ross, 2012). However, the mechanical and nutritional properties of food may operate independently or synergistically to limit dietary choice and nutrient intake.

Nutritional and mechanical properties of foods are known to interactively constrain foraging efficiency in adults, but their effects on juveniles are largely unclear. The foraging juveniles is likely to express such interactive effects more than adults because of their relative feeding incompetence and intensified nutritional requirements surrounding growth. A handful studies focusing on juvenile primates have explored the feeding implications of nutritional (Altmann, 1998; Pereira & Fairbanks, 2002; Rothman et al., 2008a) or mechanical (Fragaszy & Adams-Curtis,

1998; Chalk, 2011, Gunst et al., 2008; 2010; Resende et al., 2014) properties of food separately, but none has addressed explicitly the interactive role of *both* on juvenile dietary choice. Here I describe the mechanical properties of foods and examine how they interact with nutritional properties reported in preceding chapters to influence the foraging competency of juveniles.

4.1.2 Mechanical Properties of Primate Foods and Their Ecological Implications

4.1.2.1 Food mechanical properties and consequences of primate foraging

One important factor limiting successful foraging in primates is the proficiency to navigate the physical barriers of food (Lucas et al., 2008; Lawn et al., 2009; Gunst et al., 2010). The size, shape, and texture of foods dictate the loading capacity in the oral cavity (Yamashita, 2003; Norconk et al., 2009; Perry et al., 2015). For instance, teeth loading capacity in food fragmentation is limited by enamel susceptibility to fracture and deformation (Lucas et al., 2008). Also, there is evidence that food harvesting, pre-oral processing, and mastication are influenced by manual strength, dextral manipulation, cognitive skill, and jaw force (Gunst et al., 2010; Strait et al., 2013).

The mechanical properties of foods have been increasingly invoked to explain the morphological and dietary adaptations of primates (Norconk et al., 2009; Strait et al., 2013). For instance, species that include tough, hard, and abrasive foods in their diet such as sooty mangabeys (*Cercocebus atys*) and ring-tailed lemur (*Lemur catta*) are likely to be characterized by dietary adaptations or traits such as enlarged premolars and thick enamel, robust jaws, high dental microwear, and

craniofacial buttressing (Cuozzo & Sauther, 2012; McGraw et al., 2014). The interpretation of data from nonhuman primates, however, is characterized by controversies relating to the relevance of mechanical food properties for understanding dietary adaptations (Berthaume, 2016; Chalk et al., 2016; Coiner-Coiller et al., 2016). For instance, in the ring-tailed lemur (*Lemur catta*), patterns of dental micro-wear do not obviously reflect morphological adaptations (Cuozzo & Sauther, 2012). Its diet includes mechanically challenging foods, such as the fruits of *Tamarindus indica* (Sauther & Cuozzo, 2009), which predicts the thick enamel and robust cranium. On the contrary, dental microwear analyses show that the species exhibits a thin enamel and significant antemortem tooth loss and wear (Cuozzo & Sauther, 2012; Yamashita et al., 2012). Surprisingly, the sympatric white-footed sportive lemur (*Lepilemur leucopus*)*, which is folivorous and also consumes tamarind fruits, does not exhibit similar dental loss or wear patterns. These results suggest that the mechanical properties of food may have different evolutionary consequences, possibly because of the existence of alternative strategies for surmounting these mechanical challenges.

On the other hand, substantial evidence linking food properties to dental morphology has emerged from a recent comparative study of orangutans (*Pongo pygmaeus wurmbii*) and chimpanzees (*Pan troglodytes schweinfurthii*) (Vogel et al., 2008). In both great apes, tooth enamel reflected the hardness, toughness or stiffness of the foods they consume, but the orangutan, which possesses thicker enamel, consumed fruits with tough mesocarps that were almost twice as high in fracture toughness as those eaten by the chimpanzee. Thus, thick enamel is an

apparent adaptation to reduce the tooth damage resulting from masticating tough dietary material (Strait et al., 2013).

Food mechanics and interaction with body size play a significant role in primate food choice, handling, processing time, and eventually, energy intake. This is consistent with a recent analysis of 31 wild primates by Coiner-Coiller et al. (2016), which found that the mechanical properties of foods were correlated with time spent in their processing and ingestion depending on body size. In small primates, feeding time increased with food toughness, while larger primates fed for shorter periods as food toughness increased. On the basis of these associations, it can be predicted that feeding time on tough foods potentially increase with body size in primates.

Food differences in mechanical properties across primate species are likely shape various dietary adaptations (Norkonk et al., 2009). For instance, hardness has been found to explain primate dietary adaptations (Kinzey & Norconk, 1990; Wieczkowski, 2009). The diets of the black spider monkeys (*Ateles paniscus*) and bearded saki monkeys (*Chiropotes satanas*) differed in fruit hardness as a measure of mechanical constraint (Kinzey & Norconk, 1990). On average, the hardness of the pericarp opened by the saki monkeys was about 15-times greater than fruits exploited by the spider monkeys. Lambert et al. (2004) reported similar findings on sympatric species dietary differences in physical properties between the grey-cheeked mangabeys (*Lophocebus albigena*) and red-tailed (*Cercopithecus ascanius*)

in Kibale National Park, Uganda. The former included bark and seeds in the diet, which the latter could not puncture or crush.

The mechanical properties of food may influence the ingestive behaviors employed by primates. This is supported by data from food processing by the sympatric verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemur (*Lemur catta*), which indicated that the two species did not differ in toughness of their diet but in their ingestive behavior (Yamashita, 2003). The sifakas ingested tougher food materials such as leaves more posteriorly than the ring-tailed lemur. These studies demonstrate the how food mechanical properties can limit food resource exploitation across sympatric species, giving one species and advantage over the other in resource use especially when food is limited. In addition, they show how resource portioning may be imposed by food mechanics.

1.2.2 Juvenile-adult feeding differences

Primate foods present physical impediments to individuals in all ages, but feeding competence depends on attainment of foraging skills and maturity, which disadvantage juveniles in foraging success (Koenig, 1997; Gunst et al., 2010; Chalk et al., 2016). Thus, body size is likely to play a significant role in deriving the juvenile-adult feeding differences because of the energy requirements to maintain it, strength, and time taken in food processing and ingestion (Schuppli et al., 2016). This is consistent with research findings on juvenile- adult feeding differences in Japanese macaques (*Macaca fuscata*) that the small bodied juveniles ate less fibrous

food materials, processed it at a lower speed, and took more time ingest compared to adults (Hanya, 2003).

Juvenile-feeding differences are likely to vary across species and nature of food consumed. This is well illustrated in a comparison of juveniles feeding behavior in bearded capuchin *(Sapajus libidinosus)* and Phayre's leaf monkey *(Trachypithecus phayrei crepusculus*) (Chalk et al., 2016). Small-bodied juveniles in the two species were generally less efficient in foraging than the adults but differences and similarities existed in juvenile-adult feeding behavior. Compared to adults, juveniles of the Phayre's leaf monkey exhibited disproportionately longer feeding bouts than adults especially when consuming tough foods but there was no significant difference in bout length for juveniles in bearded capuchin. However, juvenile efficiency for both species decrease with increased food size unlike in adults.

Juvenile-adult differences in feeding behavior appear to be pronounced in species in which feeding relies on mechanically challenging foods that are often tough or hard, difficult to locate, harvest, and process (Gunst et al., 2010). Skills and experience required for efficient exploitation of such challenging food resources take time to be achieved as argued by Need-To-Learn hypothesis. As expected, however, such differences are not salient in species that feed on easy-to-process foods (Fragaszy, 1986). Field observations of primates that are hard object feeders (such as sooty mangabeys, orangutans, bearded capuchins, and chimpanzees) show that juveniles differ from adults in feeding and they: spent more time feeding, exhibit lower ingestion rates, and are less efficient in performing complex food

processing behaviors or tasks that require strength (Boinski & Fragaszy, 1989; Janson & van Schaik, 1993; Corp & Bryne, 2002; Hanya, 2003; Jonson & Cock, 2004; Gunst, et al., 2008, 2010; Jaeggi, et al., 2010; Chalk et al., 2015; Taniguchi et al., 2015). Alternatively, as illustrated in mountain gorillas and common squirrel monkeys (*Saimiri sciureus*) (Stone, 2006; Nowell & Fletcher, 2008; Rothman et al., 2008a), when feeding focuses on abundant and easy-to-process fallback foods, such as mature leaves, elaborate juvenile-adult foraging differences are uncommon. These mixed observations underscore the need for more data elucidating the underlying sources of variation in juvenile-adult foraging differences.

1.3 Fallback Foods: Nutritional, Mechanical and Ecological Significance

Primate foods vary not only in their physical and nutritional characteristics, but also in their distribution in space and time (Janson & van Schaik, 1993; Marshall et al., 2009). The increasing quest for the ecological role of diet in driving the evolution of dietary adaptations has given birth to a functional classification of primate diets that emphasizes "fallback foods" (Lambert, 2004; Marshall & Wrangham, 2007). While a precise definition of this term is debated, several recognized key diagnostic features of these foods concern abundance, chemical/mechanical defenses, nutrient density, and preference (Lambert & Rothman, 2015). A widely accepted operational definition of "fallback foods" is those foods whose use is negatively correlated with the availability of preferred foods (Marshall & Wrangham, 2007). The definition for "preferred foods" is foods those selected disproportionately and consumed regularly relative to their abundance in the species environment (Leighton 1993; Manly et al. 2002; Marshall

et al., 2007). These authors further distinguish between "staple fallback foods" (i.e., those available throughout the year and that can be utilized in periods of seasonal food shortage, thereby constituting a majority of the primate diet), and "filler fallback foods" (i.e., foods that are seasonally or annually available, but never constitute a majority of the primate diet). Thus, fallback foods may be of high or low nutritional value, abundant year-round or rare, difficult or easy to process, but they only become dietetically crucial during periods of scarcity in the preferred foods (Laden & Wrangham, 2005). This means the ability to efficiently exploit high-quality fallback foods confers a key survival benefit.

In recent years, the classification of primate fallback foods has been extended beyond considerations of phenology, anatomy, and behavior to include greater emphasis on nutritional return. Lambert (2007) separates fallback foods into two dietary categories. First, those foods that are abundant, low in nutritional density and energetic return, but require long processing time are argued to be responsible for driving the evolution of anatomical adaptations, such as gut anatomy and craniodental morphology. Second, foods that are high in nutritional density and energetic returns, but are rare and heavily protected (either chemically or mechanically) are suggested to select for the cognitive abilities underpinning extractive foraging and tool use. Lambert's classification scheme reinforces the idea that both mechanical and nutritional properties interact as significant selective pressures in primate foraging adaptations.

The majority of primates live in environments with at least some seasonal unpredictability that produces "ecological crunch periods" characterized by extreme resource scarcity and heightened intra-and inter-specific feeding competition (Peres, 1996). The metabolic and physiological disruptions caused by impairments to energy intake may increase the risk of mortality at an individual level. At the demographic level, population bottlenecks and even extinctions may result (Marshall et al., 2009). Ecological crunch periods are argued to exert disproportionately high selective pressure on species morphology, socio-ecology, and macroevolution (Wrangham, 1980; Rosenberger, 1992; Lambert et al., 2004; Potts, 1998; Laden & Wrangham, 2005). Long-term field studies of Darwin's Finches (*Geospiza* spp.) on the Galápagos Islands (Lack, 1947; Schluter & Grant, 1984; Grant & Grant, 2006) have supported this view by establishing that diet and food competition are the fundamental underlying mechanisms driving the evolution of beak morphology. For instance, exploitation of the abundant hard seeds of *Tribulis cistoides* during periods of severe drought favored the evolution of larger beak in the *Geospiza fortis* (Grant & Grant, 2006). Only populations of finches (especially *Geospiza magnirostris*) capable of exploiting the hard *Tribulis* seeds survived the famous drought of 1977, which caused population bottlenecks to other finch species.

Given the different categories of fallback foods, it is crucial to determine whether the observed concomitant behavioral or morphological adaptations arise due to consumption of hard food during fallback periods or throughout the year. Although data to answer this question are extremely limited, studies on the sooty

mangabeys (*Cercocebus atys*) indicate that frequent and year-round reliance on the hard food *Sacoglottis gabonensis* explains the evolution of the thick enamel in this species (McGraw et al., 2014) as opposed to consumption of fallback foods only in periods of food scarcity. However, more data are needed to test these hypotheses rigorously.

4.1.4 Interaction of Mechanical Properties and Nutritional Ecology

Food selection is an important mechanism for achieving nutrient balancing in animals, and thus, a key component in life history strategies (Stephens & Krebs, 1986; Ramamonjisao et al., 2017). Feeding selectivity on the basis of characteristics that overcome chemical and mechanical problems food selectivity can influence individual fitness in different ways, such as, protein-enhanced growth performance, elevated immune function, and accelerated reproduction (Mattson, 1980). Food toughness, stiffness, hardness, and toxicity limit nutrient intake. This increases time spent on food harvesting, handling, and processing, thereby reducing ingestion rates, and also possibly interfering with digestion and nutrient absorption (Clissold et al., 2009; Peeters, 2002; Simpson et al., 2014).

The existing literature suggests that both the mechanical and nutritional properties of foods determine, in part, primate foraging decisions. The interactive effects of these two food properties may exert more impact on diet choice than either acting independently, but there has been no effort to evaluate the synergetic implications of the two food properties. Ostensibly, some food characteristics, that are responsible for mechanical properties are also related to nutritional properties.

For instance, cellulose, hemicellulose, and pectin make up the plant structural component, and the three compounds constitute collectively the fiber part of the plant diet (Chapman et al., 2005). These fiber components are also a key determinant of food toughness, elasticity, and hardness (Lucas et al., 2012), as well as a possible energy source where fermentative digestion is possible (Conklin-Brittain et al., 2006; Rothman et al., 2008b). Although data on interactive effects of nutritional and mechanical properties of foods on primate diet selection are scanty (Dominy et al., 2003; Lucas et al., 2001), there is some consensus among primatologists that, either nutritional or mechanical properties of foods alone are unlikely to fully explain primate diet choice (Irwin et al., 2014).

Compelling evidence of synergetic effects of mechanical and nutritional properties of foods on diet selection has been provided by experimental studies of amphibians (Ramamonjisoa et al., 2017). Through manipulation of toughness and protein level of foods given to tadpoles, Ramamonjisoa and his colleagues found that the two food properties interactively influenced food selection. Food preference increased with protein levels in the diet but decreased with toughness. Nonetheless, food toughness influenced diet selection twice as much as protein level. The tadpoles discriminated food on the basis of protein richness, but when the only available food was tough, protein content did not affect diet choice. Based on these results, it is likely that there are tradeoffs in discriminating food on the basis of interactive effects of both the mechanical and nutritional properties. A similar outcome is expected from primates, mainly when they consume tough fallback foods of varying nutritional value (Lambert & Rothman, 2015).

Primate juveniles are more likely to express the interlinked effects of such food properties more than adults. This is because of their low foraging efficiency of hard foods and the need to ingest sufficient protein and energy for growth and maintenance of their small bodies.

4.1.5 The Tana River Mangabey as a Valuable Study Subject

Mangabeys (*Lophocebus* spp. and *Cercocebus* spp.) have been suggested as appropriate living primate models to test hypotheses on the role of food mechanics in driving the evolution of dietary mechanisms underlying cranial, dental, and facial morphology in fossil hominins (Daegling et al., 2011). This is because both *Lophocebus* and *Cercocebus* have specialized craniodental adaptations for exploiting the mechanically challenging foods, which constitute a majority of their diet (McGraw et al., 2012). For instance, the enlargement of the second premolar (P4), relative to molars is argued to be an adaptation to feeding on hard objects (Fleagle & McGraw, 1999; Gilbert, 2007). The genus *Cercocebus* has a higher P4: M1 ratio than *Lophocebus,* suggesting the former may be more adapted to consumption of harder foods than the latter. The ratio, however, is similar among three species of mangabeys: *Cercocebus galeritus,* red-capped mangabeys (*Cercocebus torquatus*), and *Cercocebus atys* (Weiczkowski, 2009; Cooke & McGraw, 2010; Daegling et al., 2013) suggesting they exploit very tough and hard foods. Other adaptations for feeding on hard objects displayed by these species include thick molar enamel and shortened facial morphology (McGraw et al., 2012).

Among the members of *Cercocebus* and *Lophocebus* groups, the Tana River mangabeys occur in a very unpredictable environment in relation to food resources (Homewood, 1978). Consequently, reliance on tough and hard fallback foods is significant. This may not be less the case with other mangabey species (e.g., *Cercocebus atys, Cercocebus torquatus, Lophocebus albigena, Cercocebus sanjei*), which occupy more productive habitats and experience less severe food scarcity (Wieczkowski, 2009; McCabe et al., 2013; McGraw et al., 2014). Evidence from feeding studies indicates that Tana River mangabeys process and ingest tough seeds and nuts, which other sympatric primates such as Sykes monkeys (*Cercopithecus mitis*), vervet monkeys, and yellow baboons avoid or eat in small quantities (Wahungu, 1998; Wieczkowski, 2009). Thus, the specialized adaptations to utilize hard foods and exist in highly seasonal habitats where consumption of fallback foods may influence survival make the Tana River mangabeys a suitable subject for this study.

The hard fallback foods in the Tana River mangabeys' diet potentially presents mechanical challenges for ingestion to juveniles since they require strength and some cognitive skills. This limits nutrient intake, which juveniles require for sustaining growth and development. Unfortunately, there are no data on how juveniles overcome these mechanical and nutritional constraints to survive in such unpredictable environments. While previous studies have focused on the understanding of the species distribution, general behaviors, and feeding ecology (Homewood, 1978; Kinnaird, 1992; Wahungu, 1998; Wieczkowski, 2003) there are a lack of studies on a species nutritional ecology as well as juvenile-adult feeding

differences. Such information is fundamental to understanding how both juveniles and adults cope with chemical and mechanical problems of foods, and the evolution of dietary adaptation to consumption of hard foods among primates.

4.1.6 Hypotheses Tested

In this chapter, I to examine the mechanical properties of different plant foods consumed by the Tana River mangabeys, and how these properties interact to influence its feeding strategies. To achieve this goal, I compare feeding data from lactating females and juveniles to test the following three hypotheses (H) and predictions (P):

H1: Juveniles' diets differ from those of lactating females in their mechanical properties because lactating females are more efficient foragers than juveniles. Since juveniles are limited by strength, development of masticatory systems, and skills in exploiting hard-to-process foods, I predict that, compared to lactating females, juveniles will select, masticate, and ingest food items that have relatively: **(P1)** lower values of fracture toughness, and **(P2)** lower values of elastic modulus (i.e., Young modulus) during periods of both food abundance and scarcity.

H2: Mechanical and nutritional properties of mangabey foods interact to influence dietary decisions during periods of low fruit abundance. Seasonality influences food availability and quality, and I predict that: (P3) fracture toughness and elastic modulus will interact with protein and metabolizable energy returns of foods to determine feeding such that, during periods of low fruit availability, juveniles select the available foods that are lower in energy and protein, and also higher in fracture

toughness, and elastic modulus, compared to lactating females.

Rationale of the predictions

Compared to adults, juveniles are incompetent feeders on foods that require strength, skeletal maturity, and cognitive skills to process since it takes time to acquire these abilities (Chalk et al., 2016) and these limitations are particularly pronounced in hard foods. Thus, I predict juveniles are incapable of exploiting mechanically challenging foods that require physical strength or specialized manipulation to process and ingest. Because of limited juveniles feeding competence, I expect that most of the foods consumed by juvenile will be characterized by lower fracture toughness and also elastic (young) modulus compared to adults (P1 & P2).

Food resource availability in different primate habitats shows great temporal variation depending on weather, disturbance, and competition among other factors (McGraw et al., 2014). Thus, preferred foods that offer better energetic returns with minimal effort or cost may not be continuously available, suggesting that in the absence of such foods primates have to rely on mechanically challenging foods to meet their daily nutrient intake (Lambert & Rothman et al., 2015). The ability to acquire adequate nutrients, especially in periods of nutritional stress, confers a survival advantage and, food selection may aim to balance the maximization or nutrient intake and minimization of foraging risks posed by mechanical properties

of fallback foods that constitute the sole food source at such times. Consumption of fallback food is unavoidable among the Tana River mangabeys due to the relatively high unpredictability of their food resources. I therefore expect that both nutritional and mechanical properties of foods will interactively influence diet selectivity in this species. Such effects may be more evident during the period of low food availability when mechanically challenging food is utilized. Thus, to test my P3, I assess how intake of available protein, metabolizable energy, fracture toughness, and elastic modulus interact to influence diet selectivity and variation with fruit availability.

4.2 Materials and Methods

4.2.1 Study Area

I conducted this study in the Tana River National Primate Reserve (TRNPR), in Tana River County, Kenya. The reserve lies between 1°40' - 2°15' S and 40°07' - 40°10'E and is 20 - 40 m above sea level (Wieczkowski, 2009) (Fig. 4.1). Mean annual precipitation is 470 mm and ranges from 122 mm to 1020 mm (Decker, 1994). Temperatures range from 17.5°C to 36.5°C with annual mean minimum and maximum temperature of 21.4°C and 33°C, respectively (Wieczkowski, 2003). The lower Tana River floodplain forests are part of the East Africa Coastal Forests biodiversity hotspot (Myers et al., 2000). The forests support two of the globally threatened primate species: the Tana River red colobus (*Procolobus rufomitratus rufomitratus*), and the Tana River mangabeys (*Cercocebus galeritus).* These two species exclusively utilized the riverine forests (Wieczkowski, 2003; Kivai, 2013).
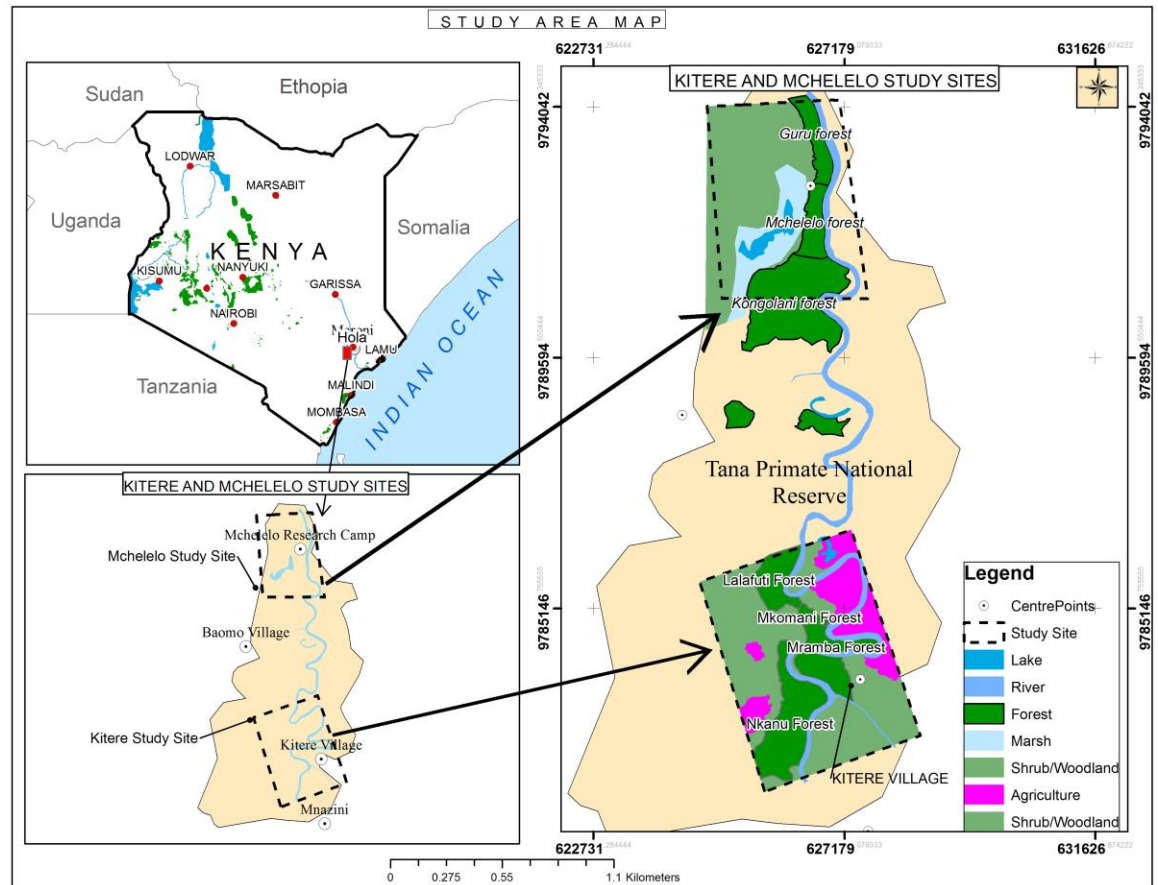
Figure 4.1. Map of the study area showing the location of the Mchelelo and Kitere study sites (indicated by a rectangle with a broken line) within the Tana River Primate National Reserve, Kenya, in Tana River County, Coast Province, Kenya. Mchelelo study site is located in the north while Kitere study site is in the south of the reserve.

I studied the mangabeys at two sites in the TRNPR, designated Mchelelo and Kitere (Fig. 4.1). The study sites offer proper ecological settings to test the role of nutritional and mechanical properties of foods and the likely interactive effects in influencing primate diet selection. This is because the forest fragments experience high seasonality in primate foods and are dominated by important seeds and nut-bearing fallback foods (Homewood, 1978; Kinnaird, 1992; Wieczkowski, 2009). The *Hyphaene compressa* and *Borassus aethiopum* are two palm producing nuts while

Vachellia robusta, Phoenix reclinata, Oncoba spinosa, and *Diaspyros mesipiliformis* constitute some of the tree species producing hard fruits and/or seeds eaten by the mangabeys (Wieczkowski, 2003; Kivai, 2013; Kivai et al., 2017).

4.2.2 Study Subjects

The study subjects consisted of only juveniles and lactating females of one group selected from Mchelelo (N = 45) and one group from Kitere (N = 49) study groups. I habituated both study groups for seven months and positively identified all the individuals before I started data collection. I collected data on 12 lactating females, 10 juvenile males, and 9 juvenile females in Mchelelo group, and 11 lactating females, 12 juvenile males, and 9 juvenile females in the Kitere group. Overall, I had 63 study subjects from both study groups composed of 23 lactating females, and 40 juveniles.

4.2.3 Field Data Collection

4.2.3.1 Feeding behavioral monitoring

I collected field data on feeding behavior, nutrient intake, and food samples for nutritional analysis from October 2014 to December 2015. I collected data for 3 – 5 days each week for approximately 21 days per month. I recorded behavioral data continuously in 10-minute focal animal sampling (Altmann, 1974). I rotated these samples in a manner whereby no individual was repeated before all other subjects were recorded. The focal sessions were separated by rest intervals of approximately 5 minutes.

During the focal sampling, I recorded activity, which was one of these categories: feed, rest, move, social interactions, and other (see Appendix 3.4 for operational definitions), and duration of the activity. When the focal was feeding, I recorded: the food species that was eaten, type of food selected, and transition times feeding on different food types. The foods eaten were categorized into "food type" (i.e., basic or general kind of food) and then into "food class" (i.e., subdivision of food into more specific food item based on state, nature, or developmental status of various foods as follows: i). Fruit – ripe fruit, unripe fruits, fruit buds, pulp, husk, and exocarp; ii). Seed – dry seeds (old seed picked from the ground or extracted from dry fruits or pods), mature seeds (from ripe fruits or pods), and immature seeds (from unripe fruits or pods); iii). Leaf – mature leaves, young leaves, leaf buds, petioles, and grass blades; iv). Flower – open petal and sepal, closed buds; v). Nut fluid – water enclosed in palm nuts; vi). Stem – stem sap, pith, inner bark, and outer bark; and v). Deadwood – non-living dry decaying wood. I operationally defined: "food type" as basic and general foods item e.g., fruit, leaf, seeds, and "food class" as developmental status of various food types i.e., ripe or unripe for fruit, mature and immature for seeds, and mature and young leaves.

To obtain the data needed to estimate intake rates if nutritional variables, I followed each 10-minute focal session with a 5-minute focal period in which I continuously recorded feeding rates. I focused more feeding events scored the number of food units consumed per feeding bout. I defined "Food Unit" as any discrete food item that the focal individual picked and put in the mouth. Typically, this was a discrete food, such as an entire fruit or leaf. In cases where monkeys fed

on large items, the "food unit" was any portion of that item put in the mouth. Thus, feeding rates essentially measured discrete movements to deliver food to the mouth. I operationally defined "feeding bout" as a discrete unit of feeding time starting when the focal individual made its first physical contact with a food item until the time when it terminated contact for at least 5 seconds or switched to another food item or activity.

4.2.3.4 Measurement of mechanical properties of foods

I collected food items consumed by the mangabeys for measuring the mechanical properties during the behavioral focal sampling. I tested foods physical properties at the field research camp using the portable FLS -1 tester machine. I measured the toughness (R), Elastic (Young's) modulus (E), and hardness of the foods eaten by the mangabeys.

a) Food sample collection for tests

During the behavioral observations, I collected at least two fresh samples of each of the food species item consumed by subjects for testing. These samples were collected either from food items discarded by the monkeys or from items at the same feeding spot on the tree or ground where focal animals had fed. I aimed to sample as many mangabey foods as possible, but I mainly focused on the Principal Plant Food species for the mangabeys (i.e., those contributed more than 1% in the annual diet: see chapter 2). Samples collected during focal sampling were stored in moist plastic bags and were measured for fracture toughness and elastic modulus (material stiffness) later in the same day after the focal follows, or within 24 hours of collection. From November 2014 to August 2015, I measured a total of 300 food

plant parts for mechanical properties that consisted of 97 food items tested for elastic (young) modulus, 94 for toughness and 109 for hardness.

b) Measurement of mechanical properties

I measured fracture toughness and elastic modulus, and hardness (see definitions in Chapter 1) using the newly developed FLS-1 tester machine (Lucas et al., 2012). The tester is a fully-USB driven portable mechanical tester that comes equipped with jigs and software for measuring different material physical properties. I measured the mechanical properties of all the food items I collected following the protocols outlined by Lucas et al. (2012), and used by Vogel et al. (2008) and Chalk (2011).

The type of test I performed on each food material dependent on the item size, shape, and symmetry. Based on the nature of the mangabey foods, I measured food toughness using both scissor and wedge tests. For the elastic modulus, I used the blunt test and the sharp indent test, which measured both material hardness and reduced elastic modulus. The scissor test was employed to measure toughness for food materials that were or could be shaped into a sheet form or small cylindrical form, convenient to cut with a scissor. This included leaves, some fruit mesocarps, thin outer stem barks, grass culms, young shoots, and flowers. I ran the scissor test by first loading the scissor program of the software. I then mounted the scissors and the 50N load cells on the FLS tester and placed the food material to be tested on the cutting platform and pushed it in-between the scissors and taped it to avoid any movements during the cutting processes. The tester crosshead was

cranked clockwise using the handle to cut through the food materials for at least 10 mm and the stopped. The cranking handle was then pushed ant-clockwise to allow removal of the material tested. Using veneer-calipers the length of the cut was measured as well as the depth. These measurements were then entered appropriately and as prompted by the scissor program loaded and open on the computer for automatic calibration of the material fracture toughness.

I used the wedge test to measure toughness of food materials that were shapeable into a block form such as large seeds and fruits. To perform this analysis, I cut the food item into a rectangular block with two parallel faces, with the width between them being smaller than the wedge edges. I recorded the width measurements (in mm) and mounted the specimen on the tester platform with the long edges running across the wedge. I attached the 50N load cell and selected it from the already loaded wedge program and entered the width measurement before cranking to cut into the food item to obtain the fracture toughness values.

I measured the elastic modulus (elasticity) of fresh food tissues, such as fruit pulp and seed contents, using the blunt indent test. To perform this test, I shaped the food specimen into a block with a flat horizontal upper surface of 3 mm or more across. The material was then mounted on either a flat or grooved circular brass compression plate screwed on the sliding tester platform. Using the blunt probe indenter attached to the 50N load cell, the crosshead was wound pushing the probe inside the food material for about 10 seconds before stopping to allow the material relaxation to acquire the elastic modulus value.

4.2.3.5 Nutritional analysis and diet selectivity of mangabey foods

To test my prediction (P3) on the interactive effects of mechanical and nutritional properties of foods on diet selectivity, I estimated the available protein (AP) and metabolizable energy (ME) content of foods and also calculated the Vanderploeg and Scavia's 1979 Electivity Index (E*) of the food utilized by mangabeys. This was necessary to estimate protein and metabolizable energy intake across study months and between the two age classes and evaluate how these nutritional properties interacted with mechanical properties of the foods to determine food Electivity index (E*).

To achieve this goal, I collected and processed the food samples consumed by mangabeys in field, analyzed their nutritional content in the laboratory, and estimated intake of available protein and metabolizable energy following standard protocols (Conklin-Brittain et al., 2006; Rothman et al., 2008, 2012) that are described in details in Chapter 2 and 3.

To calculate the Vanderploeg and Scavia (1979) Electivity Index (E*) of the mangabey foods, I estimated the relative abundance of food items in the species diet and in the environment (Manly et al., 2007), and derived the index using the equation described in detail in Chapter 2. For the relative abundance of food in the diet, I used the feeding behavior data, while for the relative abundance of food species consumed in the environment I used nested vegetation plots (Kent & Coker, 1992) (see Chapter 2 for detailed method description). The nutritional analysis of the foods in the laboratory was performed at the Primate Nutrition Ecology Laboratory at Hunter College, New York, from March 2016 to February 2017.

To obtain data on food availability and temporal variations I used phenological data obtained from 542 tagged tree species from 36 plant species that included the Principal Plant Food Species (i.e., food contributing > 1% of the annual diet of juveniles or lactating females), which were score every month following Morellato et al. (2010) to determine the fruit availability index (FAI) (see detailed methodology and calculation of FAI in chapter 3).

4.2.3.6 Data Analysis

To test my predictions (P1 & P2) that juveniles will ingest foods with lower fracture toughness (R) and elastic modulus (E) compared to foods eaten by lactating females, and P3, that such mechanical properties will interact with nutritional properties (protein and metabolizable energy) to influence food electivity, I utilized the mechanical (fracture toughness and elastic modulus), nutritional (available protein, metabolizable energy), phenological (fruit availability), and behavioral (food electivity index) data. For the two measures of mechanical properties (fracture toughness and elastic modulus), I calculated *both* the overall mean (i.e., the mean value obtained by pooling all the test scores or measures from test trials of food material or tissues) and the mean maximum (i.e., the mean value obtained only from the highest test score or measure recorded in each set of test trial done per food material or tissue) fracture toughness and elastic modulus of the foods I measured in assessing juveniles and lactating females feeding differences.

I used a total of 797 and 754 measurements of fracture toughness and elastic modulus, respectively, to descriptively examine the general profile of the

mechanical properties of foods. I focused my analysis on different food types (i.e., the basic food category such as, fruits, leaves, flowers), food classes (i.e., developmental status or state of the food type such as, ripe, unripe or dry seeds, ripe, unripe or dry fruits, young or mature leaves), and food tissues (i.e., the constituent parts of the food type or class such as, fruit exocarp or mesocarp, leaf lamina, midrib, vein or petiole). To test my predictions (P1, P2 & P3), I used the 17,109 feeding events, for which corresponding whose food measurements of mechanical properties were available. Similar to the nutritional data, I matched all the mechanical data to feeding observation data before running the statistical tests in order to understand the effects of mechanical properties on age class and diet intake.

For test the interaction of mechanical properties (R and E) and nutritional properties (ME and AP) in P3, first I obtained metabolizable energy (ME) from the macronutrient intake (Fat, AP, TNC, NDF) using the physiological fuel values of 4 Kcal/g for protein and carbohydrates, 9 Kcal/g for fat, and the NDF digestion coefficient to calculate digestible energy from fiber using 4 Kcal/g. I calculated the ME intake by a focal individual following the procedure described in details in chapter 2 and 3. Second, I calculated the Vanderploeg and Scarvia, 1979 Electivity index (E*) of each food eaten by the mangabeys to determine food selectivity or avoidance. This index ranges from -1 to 1, where values of E* > 0 operationally define food selectivity (i.e., preference) while values of E * < 0 operationally defines food avoidance.

Third, I designated season of fruit availability as high or low based on fruit availability index (FAI) derived from phenological data (see chapter 3 for detailed methodology). Periods (or study months) with more than 50% percentile of FAI (i.e., 43.83) were designated as season of high fruit availability while those less than 50% percentile of FAI as season of low fruit availability. Finally, I matched all the field data with the laboratory nutritional data, electivity index (E*), monthly fruit availability index (FAI), and the mechanical data to facilitate testing of my prediction (P3).

Statistical analysis

I used non-parametric one-way analysis of variance to compare the general mechanical properties of various classes of food type and their constituent tissues. To understand the time feeding on different food type, which potentially vary in mechanical properties and to test predictions relating to nutritional and mechanical properties of foods and dietary intake, I used Generalized Linear Mixed Models (GLMMs). The response, fixed, and random variables used for the GLMMs varied with test prediction or question addressed. Comparison of the general mechanical properties of the food classes and tissues as well as time spent feeding on various food types was not part of the test predictions, but was necessary in understanding the mechanical profile of the foods consumed by mangabeys and potential influence on foraging.

Prior to running any statistical test or model, I checked the data to ensure they met the required assumptions for each particular test used and especially a

normal distribution. I used quantile-quantile (q-q) plots to test data normality where the Shapiro–Wilk test could not be used due to sample size limitations. Where data were not normally distributed, I performed either log or inverse-log transformations. I used nonparametric tests where a normal distribution of data was not possible with transformation. For all the statistical analyses conducted in the analyses, alpha was set at 0.05. I performed all the statistical analysis using R statistical software version 3.3.2 (R Core team (2013). First, I selected the best variable and model to test my prediction test by first constructing full models, which included all variables that were likely to have some effect on the test outcome. Second, I fitted reduce models that eliminated a single variable at a time from the competing model. I then compared the full model with reduced models using analysis of variance (anova) in R, in order to selected the the best model fit to test my predictions. I used the significance level and the lowest Akaike information criterion (AIC) to pick the best model fit (i.e., the significant model ($p < 0.05$) with lowest AIC value).

Before testing my predictions regarding the food mechanics, first, I performed the descriptive analysis of the mechanical properties of various mangabey food type classes and their constituent tissues. I compared both the overall mean and mean maximum value of fracture toughness and elastic modulus across the food classes and tissues using Kruskal Wallis (H) test and Dunn's multiple comparison for post hoc analysis.

Second, I compared the mean time spent (in seconds) feeding on different food types per feeding bout to gain some understanding on time spent exploiting foods with different mechanical properties by both juveniles and lactating females. I used GLMM to test whether time spent feeding varied in response to food type and age class. The model included, time spent feeding as response variable, food type and age class as fixed effects, and I controlled for focal ID as random variable.

To test my predictions I fitted and ran the following models: **P1** - I fitted a GLMM to examine how fracture toughness of the foods eaten by mangabeys varied across the age classes. I selected the overall mean and mean maximum fracture toughness as my response variables, age class as fixed effect, and controlled for focal ID, study group, and food species as random effects. **P2** – I fitted the same model as in P1 but only substitute the response variable with the overall mean and mean maximum elastic modulus. For the two predictions (P1 & P2), First, I ran the model using the mean fracture toughness or mean elastic modulus of the foods, respectively, as response variable and all other variable remaining the same. Second, I repeated the same test using the mean maximum fracture toughness and mean maximum elastic modulus as response variable. **P3** – To test whether the interactive effects of nutritional (available protein & metabolizable energy) and mechanical (fracture toughness & elastic modulus) properties of food on determined food selectivity (i.e., preference) and whether this varied across age class and season of fruit availability, I ran a GLMM model. The model included Vanderploeg & Scavia's Electivity Index (*E) of foods consumed by mangabeys as response variable, available protein (AP), metabolizable energy (ME), fracture

toughness (R), elastic modulus (E), interaction of all four (AP*ME*R*E), age class and fruit availability as fixed effects, and I controlled for focal ID and study group as random effects.

4.3 Results

4.3.1 Mechanical Properties Tana River Mangabey Foods

4.3.1.1 Fracture toughness of plant foods

a) Fracture toughness of food classes

The nine different classes of foods (i.e., dry seeds, mature leaves, young leaves, ripe fruits, unripe fruits, mushrooms, mature seeds, immature seeds, and young stems) considerably varied in fracture toughness (Fig. 4.2). The mean fracture toughness (±SEM) was highest in dry seed (1,531.49 ± 402.74 Jm^2) and lowest in young leaf (229.58 ± 31.25 Jm^2). The absolute fracture toughness of the food classed ranged from 0.06 Jm^2 to 27,313.35 Jm^2, which was reported for unripe fruit food components (Fig. 4.2, Appendix 4.1). The mean fracture toughness differed significantly among the food classes (H = 41.02, df = 8, p < 0.0001, N = 9 food classes, 797 food toughness tests) but there were no differences in mean maximum fracture toughness (H = 13.45, df = 8, p = 0.0973). The post hoc analysis (Dunn's multiple comparison test) revealed that mean fracture toughness of young leaves was significantly lower than mature seeds and ripe fruits (p < 0.05), while mature seeds were tougher compared unripe fruits (p < 0.05). There were no significant differences among the other classes of food type (p > 0.05).
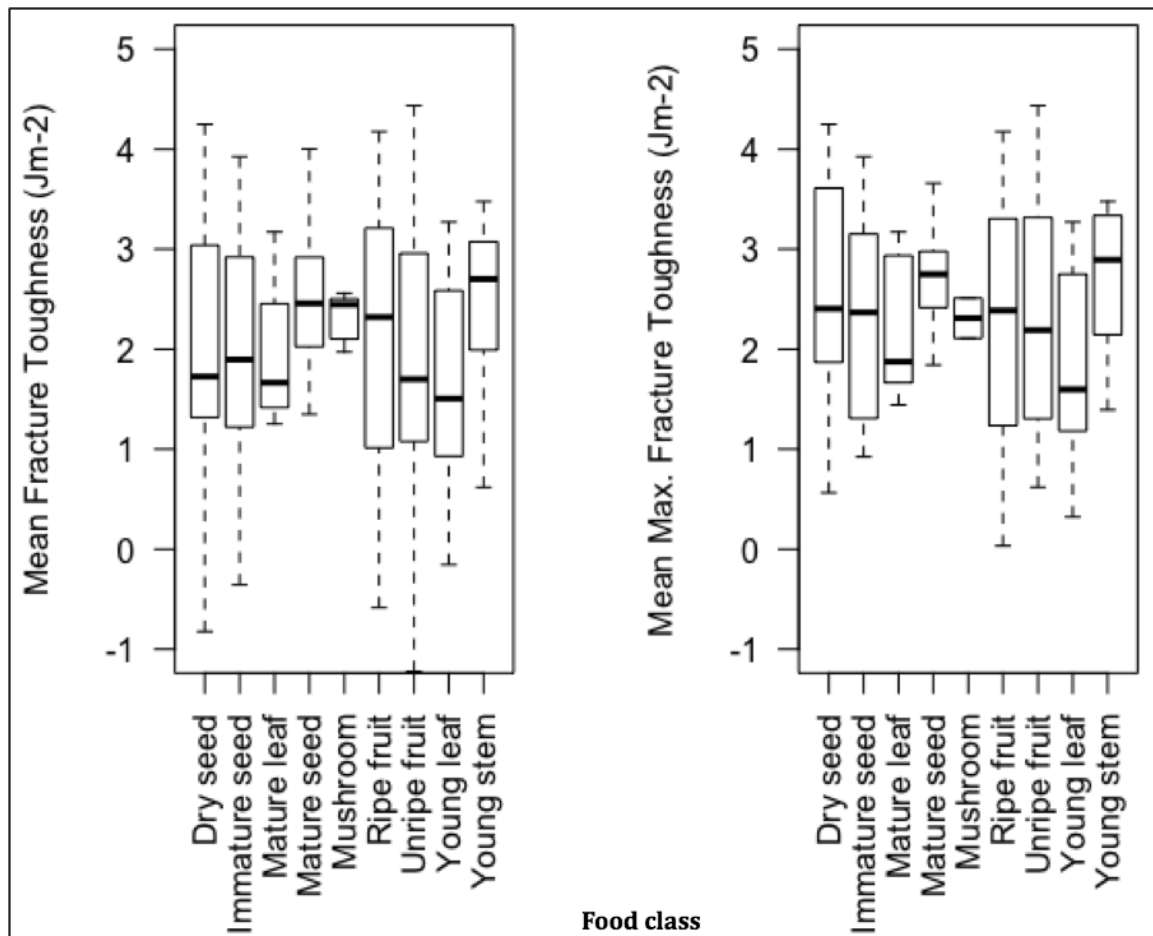
Figure 4.2. Fracture toughness (Jm^{-2}) of foods classes eaten by juveniles and adult females. Shown are overall mean values (left) and the mean maximum values (right). Data log transformed, and error bars indicate standard deviation. N = 9 food classes, 797 food sample tests, and fracture toughness differed significantly across food classes ($p < 0.05$).

b) *Fracture toughness of food tissues*

The food tissues of various classes of food (seed endosperm and coat, fruit mesocarp and exocarp, leaf lamina, midrib, petiole and secondary veins, young shoot, xylem/phloem, and mushroom cap) expressed variable levels of fracture toughness (Fig. 4.3). The mean fracture toughness of the tissues ranged from 36.58

± 8.57 Jm² to 1,473.95 ± 196.39 Jm² in leaf lamina and unripe exocarp, respectively

(Fig. 4.3, Appendix 4.1). The mean fracture toughness of all the ten food tissues

tested varied significantly (H = 122.86, df = 9, p < 0.0001, N = 797), as well as the

mean maximum fracture toughness (F = 38.89, df = 9. p < 0.0001, N = 797).

Figure 4.3. Fracture toughness (Jm⁻²) of tissues of plant foods eaten by juveniles and adult females. Shown are overall mean values (left) and the mean maximum values (right). Data log transformed, and error bars indicate standard deviation. N = 10 food tissues, 797 food sample tests, fracture toughness differed significantly across food tissues (p < 0.05).

The result of post hoc analysis showed that mean fracture toughness of the petiole, xylem/phloem, secondary vein, exocarp, and endosperm was significantly higher when each was compared to lamina and fruit mesocarp ($p < 0.05$), except when the latter was compared to petiole and secondary vein. Fracture toughness of midrib and xylem/phloem was significantly higher compared to exocarp ($p < 0.05$), while toughness of midrib exceeded that of endosperm ($p < 0.05$). The post hoc analysis of the maximum mean fracture toughness indicated that xylem/phloem, seed endosperm, fruit mesocarp, and leaf midrib were significantly tougher than the leaf lamina ($p < 0.05$).

4.3.1.2 Elastic modulus of plant foods

a) *Elastic modulus of the food classes*

The uppermost mean elastic modulus (± SEM) was recorded in dry seeds (105.35 ± 21.02 MPa), while the lowest applied to mushrooms (4.43 ± 0.93 MPa) (Fig. 4.4, Appendix 4.2). Overall, the elastic modulus of mangabey food classes ranged from 0.14 MPa to 972.80 MPa in ripe and unripe fruits, respectively (Appendix 4.2). Across 7 classes of food, there were significant differences in mean elastic modulus (H = 99.77, df = 6, $p < 0.0001$, N = 7, total food measurements = 754 and in mean maximum elastic modulus (H = 28.24, df = 6, $p < 0.0001$, N = 7). The mean elastic modulus of the dry seed was significantly higher compared unripe fruits, ripe fruits mushroom and immature seeds ($p < 0.05$) according to Dunn's multiple paired comparison test. This was also true for mature seeds when compared to mushroom, ripe, and unripe fruits. However, elastic modulus of

mushroom and ripe fruit was significantly lower compared to the food classes (p < 0.05) but the two food classes were not significantly different. The multiple comparison analysis of the food mean maximum elastic modulus also showed that dry seed had higher elastic modulus compared to ripe fruit, unripe fruit, and mushroom (p < 0.05), while mature seeds exceeded ripe fruit in elastic modulus.
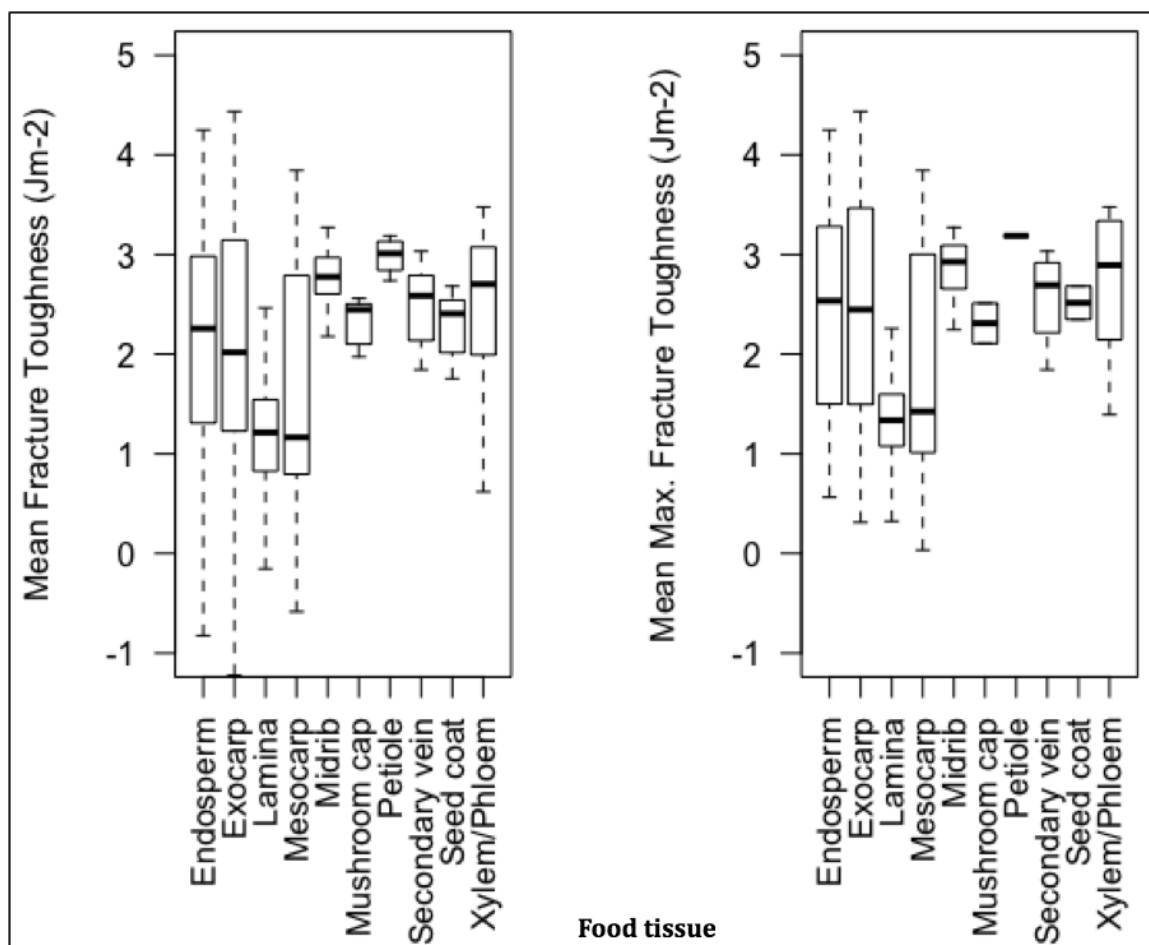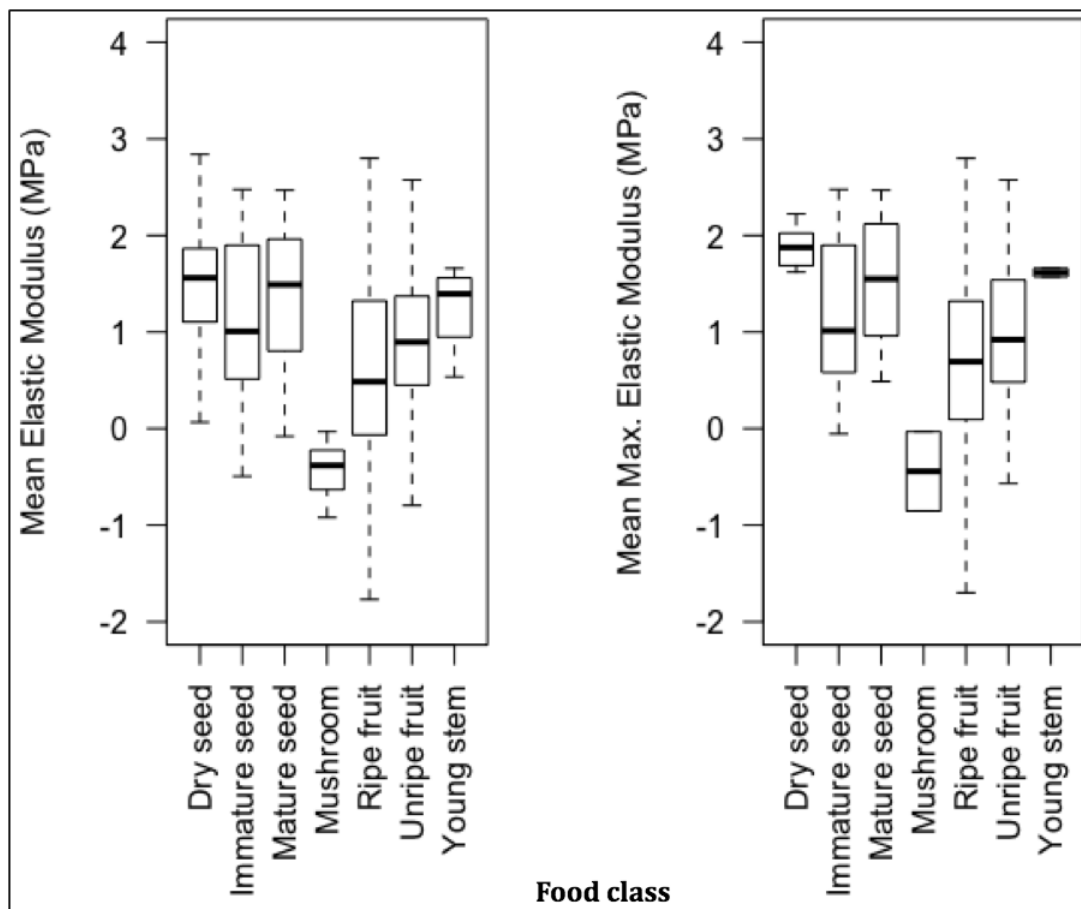

Figure 4.4. Elastic modulus (MPa) of food classes eaten by juveniles and adult females. Shown are overall mean values (left) and the mean maximum values (right). Data log transformed, and error bars indicate standard deviation, N = 7 food classes, 754 food sample tests, elastic modulus differed significantly across food classes (p < 0.05).

b) *Elastic modulus of plant food tissues*

The elastic modulus of 6 tissues (endosperm, exocarp, mesocarp, mushroom cap, seed coat, and young stem) of the foods consumed by the mangabeys is presented inn Figure 4.5 and Appendix 4.2. The mean elastic modulus was highest for seed endosperm (90.21 ± 8.21 MPa) while the lowest for the mushroom cap (4.43 ± 0.93 MPa) (Fig. 4.5).

The 6 tissues differed significantly in mean elastic modulus ($H = 123.06$, df = 5, $p < 0.0001$, N = 6 food tissues, 754 tissue tests) as well as in mean maximum elastic modulus ($H = 32.72$, df = 5, $p < 0.001$). The mean elastic modulus of xylem/phloem, seed coat, exocarp, and endosperm was significantly higher compared to mushroom cap and fruit mesocarp ($p < 0.05$) (Fig. 4.5). The elastic modulus of the endosperm, however, was significantly higher compared to exocarp and mesocarp ($p < 0.05$). The mushroom cap and fruit mesocarp, which had the lowest elastic modulus, did not differ significantly. The post hoc analysis of the mean maximum elastic also indicated that the seed endosperm and fruit mesocarp were significantly higher elastic modulus than the mesocarp ($p < 0.05$).
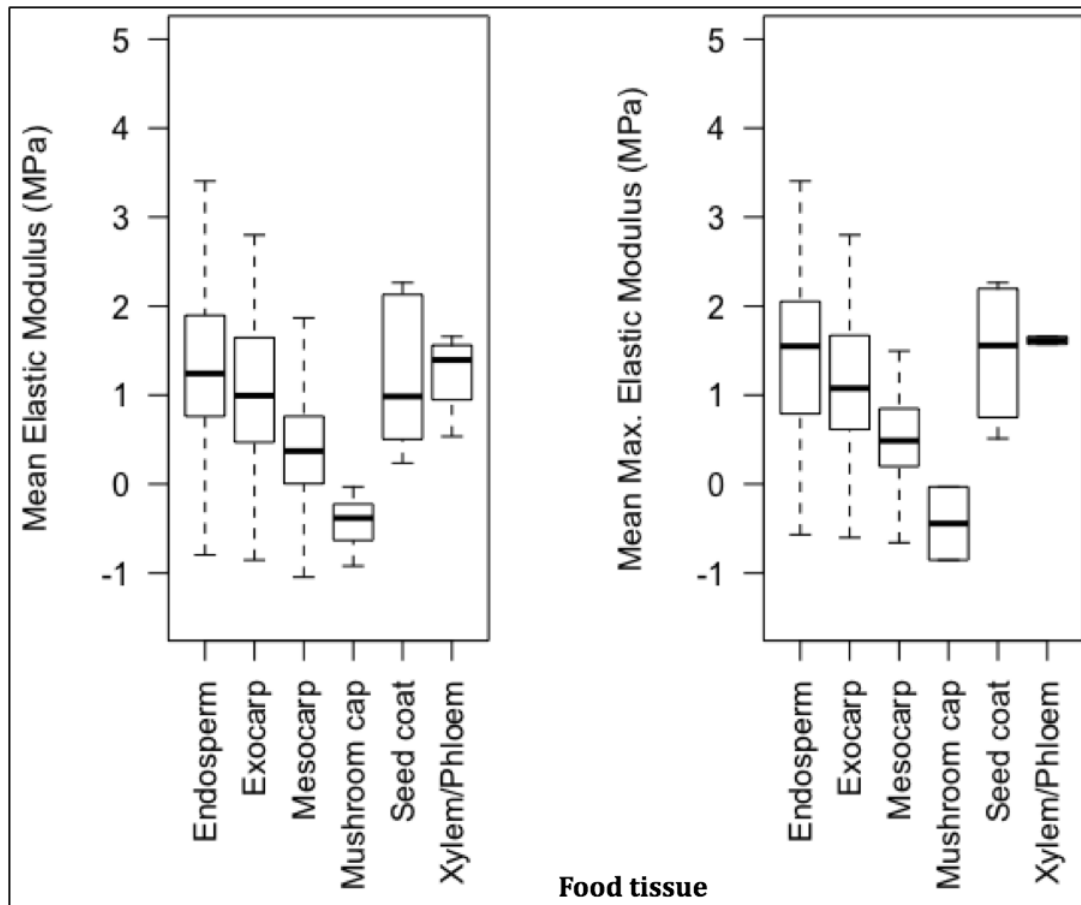
Figure 4.5. Elastic modulus (MPa) of tissues of foods eaten by juveniles and adult females. Shown are overall mean values (left) and the mean maximum values (right). Data log transformed, and error bars indicate standard deviation. N = 6 food classes, 754 food sample tests, elastic modulus differed significantly across food tissues (p < 0.05).

4.3.1.3 Time spent feeding on different foods types of variable mechanical properties

The juveniles and lactating females spent more time (sec) per feeding bout consuming fruits, bark, and seeds (juveniles: 157.35 ± 1.55, 141.07 ± 23.45, 132.78 ± 1.51; lactating females: 150.42 ± 2.38, 134.20 ± 30.84, & 127. ± 2.32, respectively) compared to other foods (Table 4.1).

Table 4.1. Meantime spent feeding (in sec ± standard error of the mean) on different food types eaten by the juveniles and lactating females, which exhibit different mechanical properties.

	Average feeding time (Sec) per bout	
Food type	Juveniles	Lactating females
Bark	141.07 ± 23.45	134.20 ± 30.84
Deadwood	99.00 ± 19.68	80.00 ± 38.85
Flowers	73.60 ±6.97	90.08 ± 13.80
Fruits	157.35 ± 1.55	150.42 ± 2.38
Gum	99.77 ± 5.30	88.13 ± 6.67
Insects	60.75 ± 2.16	58.32 ± 2.68
Leave	83.34 ± 2.14	87.98 ± 3.78
Mushrooms	77.88 ± 2.71	82.35 ± 4.31
Others	69.25 ± 11.77	93.14 ± 23.97
Subterranean structures	61.42 ± 27.48	37.00 ± 23.00
Seed	132.78 ± 1.51	127.70 ± 2.32
Stem	73.21 ± 5.47	68.56 ± 11.71

Time spent feeding on different types of foods per feeding bout differed significantly ($F = 195.59$, $df = 11$, $p < 0.0001$). Compared to bark (intercept), time spent feeding did not differ of consumptions of fruits and seed, but it varied for all other food types ($p < 0.05$). The mangabeys took less time in utilization of flowers, stems, and insects ($p < 0.0001$), leaves and mushrooms ($p < 0.001$), as well as subterranean structures and gum ($p < 0.01$) compared to ingestion of bark. However, time spent feeding did not vary in response to age class ($F = 0.04$, $df = 1$, $p = 0.8373$) and both juveniles and lactating female spent similar amount of time per feeding bout to consume various food types ($t = - 0.10$, $df =1$, $p = 0.9228$).

4.3.2 Age Class Comparisons in Mechanical Properties of Diet

4.3.2.1 Age class differences in fracture toughness and elastic modulus of foods

consumed

To test my predictions (P1 & P2) concerning the mechanical differences in the foods of juveniles and females, I first examined whether ingested food fracture toughness (R) varied in response to age controlling for focal ID. Fracture toughness of the foods consumed by mangabeys varied slightly but was significant with age class, with juveniles consuming foods with lower fracture toughness, both for the overall mean analysis of R (F = 5.15, df = 1, p = 0.0370, t = 2.13, df =1, p = 0.0370, N = 63) and the mean maximum analysis of R (F =4.72, df = 1, p = 0.0335, t = 2,17, df = 1, p = 0.0335, N = 63). The observed differences in food fracture toughness between age classes both for overall mean and mean maximum values were statistically significant, though the magnitude of the difference was not dramatic (Fig. 4.6). These results support my prediction (P1) that juveniles ingest foods with lower fracture toughness compared to those eaten by lactating females.

Second, I examined how the overall mean and mean maximum elastic modulus (E) of the foods consumed by mangabeys varied as a function of age class controlling for the focal ID. There was no effect of age class on mean E (F = 20.83, df = 1, p = 0.0968, N = 63) and the foods eaten by juveniles and lactating females did not differ. However, the mean maximum E was significantly different for the two age classes (F = 4.08, df = 1, p = 0.0473) (Fig. 4.6). Juveniles ingested foods with slightly lower mean maximum E (t = 2.02, df = 1, p = 0.0473). I found no support for my

prediction (P2) when using mean elastic modulus as dependent variable, but there

was weak support for this prediction from the mean maximum elastic modulus.
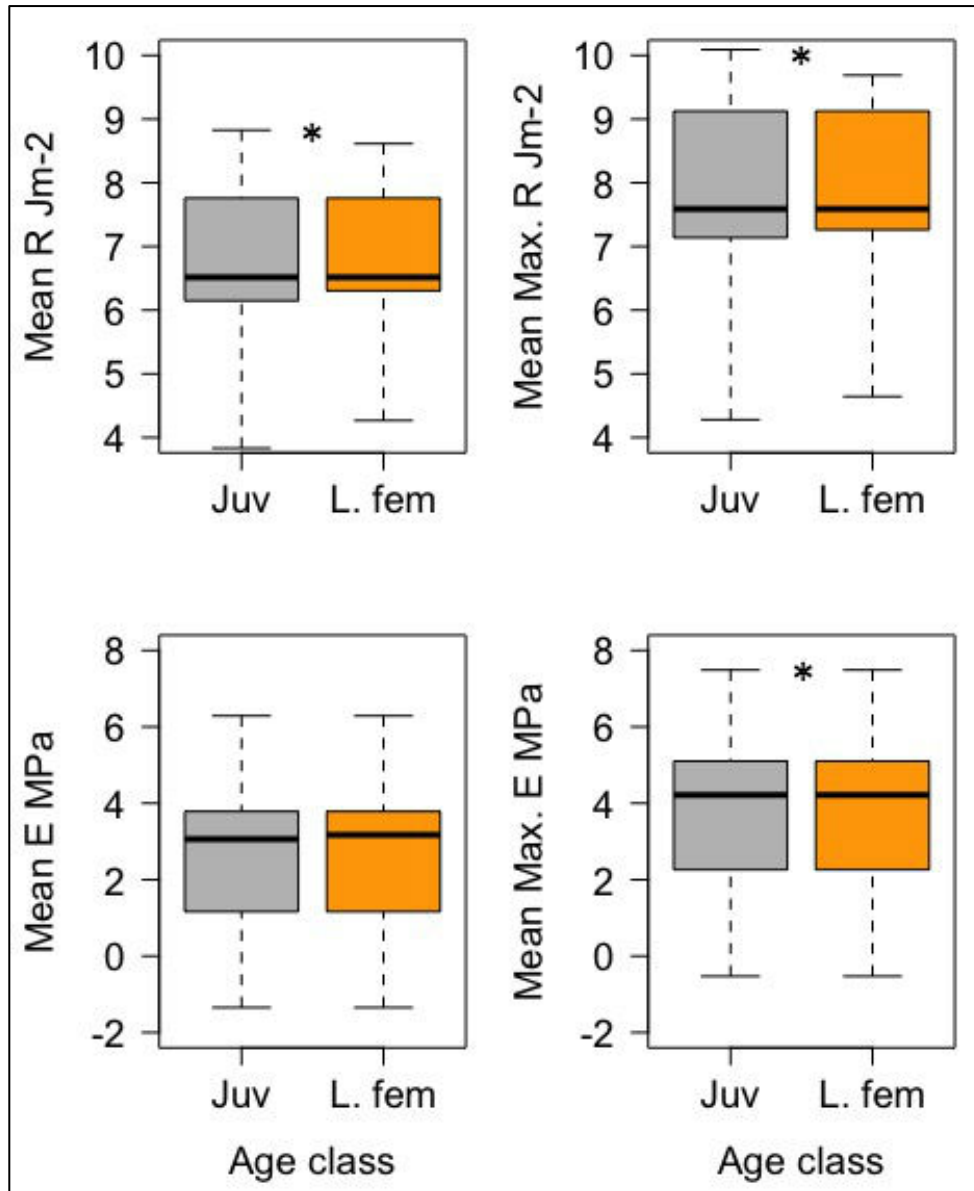
Figure 4.6. Fracture toughness (R) (top row) and elastic modulus (E) (bottom row) of foods eaten by juveniles (Juv) and lactating females (L.Fem). Overall mean is shown on the left and mean maximum (Max.) on the right. Data log transformed, and error bars indicate standard deviation. N = 63 focal individuals, feeding events = 17,109, and asterisk (*) indicates significant results p < 0.05.

4.3.3 Interaction of the Nutritional and Mechanical Properties of Foods

4.3.3.1 Food properties influence on food electivity index (E*)

Food electivity index (E*) changed considerably as a function of the interactive effects of nutritional and mechanical food properties (i.e., available protein - AP and metabolizable energy - ME food returns, or the maximum fracture toughness - *R* and elastic modulus - E) (Table 4.2, 4.3) The electivity index (E*) of the foods consumed by juveniles and lactating females varied significantly in response to fruit availability (F = 80.02, df = 1, p < 0.0001), but not age class (F = 0.03, df = 1, p = 0.8713, N = 63) accounting for interactive effects of nutritional and mechanical properties of foods (Table 4.2). The interactive effects of both nutritional and mechanical properties of foods influenced E* more than each food variable acting alone. Besides *E* (F = -2.11, df = 1, p = 0.0359), independent influence of other food properties (AP, ME, *R*) on E* was insignificant (p > 0.05). However, the following interactions (*) among the four food properties generated to significant influences on food electivity index: AP*ME*R*E (F = 3.85, df = 1, p < 0.0001), AP*ME*R (F = 33.88, df = 1, p = < 0.0001), AP*ME*E (F = 4.01, df = 1, p = 0.0452), AP*ME (F = 24.53, df = 1, p < 0.0001), and ME*E (F = 4.74, df = 1, p = 0.0294).

Food selectivity (E* > 0) by the mangabeys increased significantly with the following food interacting properties: AP*ME (t = 4.95, df = 20,440, p = < 0.0001) and ME*E (t = 2.18, df = 20,450, p = 0.0294) controlling for focal ID and study group. This indicated that selectivity for foods with high elastic modulus occurred if they offered good AP and ME gains. Compared to selectivity, food avoidance (E* < 0) was more influenced by E alone (t = -2.11, df = 20,450, p = 0.0359) and the interactions

of AP*ME*R (t = -5.82, df = 20,440, p = < 0.0001) and AP*ME*R*E (t = 3.85, df = 20,450, p < 0.0001). These results showed that food avoidance ensued when the elastic modulus and fracture toughness were high and the AP and ME gains were low. These results partly support the prediction (P3) that both nutritional and mechanical properties of foods interact to influence diet selection although this did not vary with age class

Table 4.2. Statistical comparison of the interactive effects of nutritional and mechanical properties of foods on food electivity index (preference) of the Tana River mangabeys. The interacting food properties are available protein (AP), metabolizable energy (ME), fracture toughness (R), and Elastic modulus (E), while the asterisk between the variables denote and interaction. Bold-faced values indicate significant differences (p < 0.05) and df = degrees of freedom.

Variables	df	F – value	p – value
Age class	1	0.03	0.8713
Fruit availability	1	80.02	**< 0.0001**
AP	20452	2.21	0.1375
ME	20448	1.89	0.1690
R	20452	0.01	0.9111
E	20451	4.40	**0.0359**
AP*ME	20437	24.53	**< 0.0001**
AP*R	20453	2.50	0.1139
ME*R	20449	0.01	0.9684
AP*E	20451	2.39	0.1223
ME*E	20449	4.74	**0.0294**
R*E	20454	1.78	**0.1818**
AP*ME*R	20442	33.88	**< 0.0001**
AP*ME*E	20432	4.01	0.0452
AP*R*E	20454	2.48	**0.1155**
ME*R*E	20451	1.21	**0.2720**
AP*ME*R*E	20434	14.86	0.0001

4.3.3.2 Interactive effects of food properties and fruit availability (season) on food electivity

The mechanical and nutritional properties of foods synergistically and independently interacted with fruit availability to influenced food electivity (E*) across the study period or seasons (Table 4.2, 4.3). Season of fruit availability significantly influenced how the food properties either acting alone or together determined food electivity (F = 18.03, df = 1, p < 0.0001, N = 2 season of fruit availability, 20,486 feeding events). The interaction of food properties with fruit availability had more effect on food electivity during the season of low fruit availability than it was during high fruit availability (t = -3.99, df =1, p < 0.0001) (Table 4.3).

During the season of low fruit availability metabolizable energy*fracture toughness* elastic modulus (ME*R*E), available protein*Elastic modulus (AP*E), available protein*fracture toughness (AP*R), available protein*metabolizable energy (AP*ME), fracture toughness (R), and available protein (AP) interacted with fruit availability (FA) resulting to significant food electivity (E* > 0, p < 0.05) (Table 4.3). However, fruit availability interacted with AP*ME*R, AP*R*E, ME*R, ME*E, and ME leading to significant food avoidance (E* < 0, p < 0.05).

Fruit availability interaction with AP*ME*R*E, AP*R*E, AP*ME*E, AP*ME*R, R*E, ME*E, ME*R, and ME during the period of high fruit availability yielded significant food electivity (E* > 0, p < 0.5) (Table 4.3). Alternatively, ME*R*E, AP*E, AP*ME, and R associated with fruit availability resulting into food avoidance (E* < 0,

p < 0.05). However, over both season there was no significant interaction of metabolizable energy and fruit availability on food electivity (p > 0.05).

Table 4.3. The interactive effects of nutritional (available protein-AP and metabolizable energy – ME) and mechanical properties (fracture toughness - R and elastic modulus – E) of foods with fruit availability (FA) and the influence on food Electivity index (E*) where p – value < 0.05 indicate significant effect of the interaction, (+) indicates E* > 0 while (-) E* < 0 suggesting the interaction resulted to food selectivity or avoidance, respectively, in corresponding season of fruit availability. (FA) Low fruit availability = fruit availability index (FIA) < 50% percentile, and high fruit availability = FAI > 50% percentile. Asterisk (*) denotes an interaction, while n/a indicates where entries were not applicable.

Food Properties & FA Interaction	t - value (df = 1)	p - value	Electivity (E*)	
			Low FA	High FA
Intercept (High FA)	2.4	0.0163	n/a	n/a
Fruit availability (Low FA)	-3.99	< 0.0001	n/a	n/a
AP*ME*R*E*FA	-1.96	0.0501	-	+
ME*R*E*FA	4.89	< 0.0001	+	-
AP*R*E*FA	-4.49	< 0.0001	-	+
AP*ME*E *FA	-2.42	0.0155	-	+
AP*ME*R*FA	-4.47	< 0.0001	-	+
R*E*FA	-2.32	0.0202	-	+
ME*E*FA	-4.19	< 0.0001	-	+
AP*E*FA	3.72	0.0002	+	-
ME* R*FA	-6.4	< 0.0001	-	+
AP*R*FA	2.42	0.0154	+	-
AP*ME*FA	6.06	< 0.0001	+	-
E*FA	1.78	0.0755	Neutral	Neutral
R*FA	2.87	0.0041	+	-
ME*FA	-3.9	< 0.0001	-	+
AP*FA	7.83	< 0.0001	+	-

4.4 Discussion

Mechanical properties and their implications

The diet composition of the Tana River mangabeys comprised different food classes and constituent tissues that were characterized by variable fracture toughness ranging from 0.06 to 27,313Jm^{-2}, and elastic modulus ranging between 0.14 and 972.8 MPa. The majority of food classes and tissues that had high fracture toughness also displayed high elastic modulus. The of pattern fracture toughness and elastic modulus of food tissues eaten by the Tana River mangabeys mirror that of similar foods ingested by other species. This species ingested tougher and stiffer foods compared to the range of fracture toughness of foods consumed by Japanese macaques (*Macaca fuscata*) (Hill & Lucas, 1996), orangutans (Vogel et al., 2008, 2014), gibbons (*Hylobates albibarbis*) (Vogel et al., 2009), bamboo lemurs (*Haparlemur* sp.) (Yamashita et al., 2009), geladas (*Theropithecus gelada*) (Venkataraman et al., 2014), tufted capuchin monkeys (Chalk et al., 2016), Angola black and white colobus monkeys (*Colobus angolensis palliatus*) (Danhum & Lambert, 2016), and mountain gorilla (Glowacka et al., 2017). Among these species, only the bamboo lemurs consumed foods with higher fracture toughness (66.2 – 19,749.4 Jm^{-2}) close to what mangabeys ate. However, the bamboo lemurs (2.76 – 27,445.17 MPa) and tufted capuchins (0.05 – 10,427.7 MPa) consumed food with higher elastic modulus than the Tana River mangabeys. These results suggest that mangabeys process and consume difficult-to-process foods similar to other hard object feeders like tufted capuchins, orangutans, bamboo lemurs, and geladas.

The differences in fracture toughness and elastic modulus in various food tissues may partly be explained by nature of plant mechanical barriers (Hill & Lucas, 1996). Plants invest in defense mechanisms to protect seed tissues against herbivory, especially before the fruits or the seeds are mature for dispersal. According to Imai & Ohsaki (2004), the growing tissues of plants have been found to be more nutritious and attractive to herbivores. Damage to such tissues, however, has high fitness costs to the plant (Coley, 1983) and consequently, plants have evolved strong mechanical defenses, which include fiber, lignin, and thickened cuticles to deter herbivory (Jazen, 1981; Imai & Ohsaki, 2014). Because of these structural barriers fruit exocarp, mesocarp, and mature seeds are likely to be tough and hard to overcome or minimize predation. This is true for this study since food classes such as mature seeds (that are protected inside fruit pericarp) and dry seed, and constituent tissues such as endosperm and fruit exocarp were among the toughest food components. Tana River mangabeys include high proportions of fruits and seeds in the diet suggesting their food processing and ingestion involved handling foods high fracture toughness and elastic modulus. The costs of consuming food characterized by high fracture toughness or elastic modulus are partly reflected in increased time spent processing such foods (Gunst et al., 200). This study reinforces this observation in that seeds, fruits, and bark, which had significantly higher fracture toughness as well as elastic modulus compared to other food classes, were characterized by longer feeding durations per bout compared to other types of foods. Thus, the mechanical profile of the mangabey foods and time

spent in processing them confirm that mangabeys indeed consume mechanically challenging food materials.

Juveniles-lactating females dietary differences mechanical properties

I found some evidence that juveniles processed and ingested foods with lower mean fracture toughness compared lactating females as I predicted (P1). This was also supported by the mean maximum value analysis. However, there were no age class differences in mean elastic modulus of the foods eaten, contrary to my prediction (P2), but this prediction was weakly supported when I performed the analysis on the mean maximum values. Despite the statistically significant differences in toughness and mean maximum elastic modulus, it is true that the difference was in magnitude. This does not necessarily mean the difference is not biologically significant in foraging. The variation in beak size in the Darwin finches was slight, but determined survival (Grant & Grant, 2006). Data on fracture toughness reflected what is expected of the mangabeys given that they feed on tough diets (Wieczkowski, 2009; McGraw et al., 2014) and juveniles are more likely to be poor foragers as predicted by the need to learn hypothesis (Pereira & Fairbanks, 2002). The findings also support previous studies, which have also demonstrated that adult-juvenile foraging differences occur especially in species that feed on hard-to-process foods, such as yellow baboons, (Altmann, 1998), brown capuchin monkeys, (Gunst et al., 2010; Resende et al., 2014; Chalk et al., 2015), and chimpanzees, (Lonsdorf et al., 2004).

Exploitation of food with higher fracture toughness as well as elastic modulus by juveniles compared to lactating females can be explained by differences dentition development or development in masticatory muscles (Cachel, 1984). Juveniles are characterized by mixed dentitions where deciduous teeth are replaced by adult permanent and stronger set of teeth; thus, they are less efficient in handling difficult food texture. Primate masticatory muscles increase with growth rate (McNamara, 1974; Cachel et al., 1984). Consequently, juveniles have weaker masticatory muscles compared to adults due to lack full development suggesting juvenile may be limited in exploiting foods easily consumed by adults.

Tana River mangabeys engage in extractive foraging behavior that could be cognitively challenging and require coordinated manipulative practices as I observed in the field. This was especially true when they fed on *Oncoba spinosa*, which is among those foods with highest fracture toughness. The fruit processing involves rolling and rubbing it against hard substrates (e.g., tree trunks) coupled with strong canine puncturing. Adults have a high success rate in ingesting the fruit, but juveniles, in many cases, abandon the fruit after unsuccessful trials to break it. Although these observations were not quantified, they reinforce the findings that lactating females in the Tana River mangabeys consumed diets with higher fracture toughness compared to juveniles.

Extractive foraging is often linked to tool use in wild primates (Parker & Gibson, 1977). Majority of primates that use tool use are dexterous extractive foragers (Biro et al., 2003). Theoretically extractive foraging activities and tool

use require development and competency of manual dexterity because such foraging activities require combinational manipulative activities and precision (van Schaik et al., 1999). Thus, extractive foraging has favored the evolution of dexterity in both extant primates and early hominins for the benefit it confers in foraging and nutrient acquisition. However, extractive foraging and tool use behaviors is linked to increased intelligence or cognitive skills and enlarged brain size (McGraw et al., 2014). Therefore, extractive foraging and tool use reflect increased cognitive ability, a evolutionary trait, which partly explain the success of hominins in exploiting different environmental niches compared to other primates (van Schaik et al 1999; Biro et al., 2003). Consequently, the presence of extractive behavior in the Tana River mangabey, competence in manual dexterity and adaptation to exploitation of hard foods make this study relevant to understanding how challenges of mechanical food properties may have favored the evolution of extractive foraging and tool use behavior in hominins as well as in other extant primates.

Overcoming mechanical barriers of fallback foods may require manual strength as found in bamboo foraging in wild capuchin monkey, *Cebus capucinus* (Gunst et al., 2010). Ingestion of *Borassus aethiopum* and *Hyphaene compressa* nuts, which constitute critical fallback foods, requires strength to detach the fruit from the parent plant and to rip off the exocarp. Immature Tana River mangabeys are incapacitated in accomplishing these feeding tasks, as I observed in the field. Findings of this study imply that juveniles utilize a majority of the foods eaten by

adults, including those with high elastic modulus. However, feeding differences occur with foods whose high fracture toughness or large size present handling challenge.

Mangabeys are known to be well adapted to the exploitation of hard food diet (Wieczkowski, 2009; McGraw et al., 2011). Although it is not clear when maturing individuals attaining the ability to exploit such hard foods fully, my findings indicated that older juveniles (> 2 years) were capable of utilizing similar diets as the adults in many cases. This may explain the lack of significant differences in elastic modulus of foods eaten by juveniles and adult females. However, previous studies have also failed to find age class differences in elastic modulus within species known to ingest hard foods, such as the Bornean orangutan (Vogel et al., 2014) and tufted capuchin monkey (Chalk et al., 2016). Although the explanation for this pattern is not entirely clear, the sample size for most of these field studies is small and there is still need for intensive and continuous sampling to test hypotheses on mechanical food properties rigorously.

Interactive effects of mechanical and nutritional properties on diet selectivity

I expected the mangabeys to avoid the physical food barriers and to focus on maximizing protein and energy intake, and due to inefficiency in foraging, that juveniles will avoid foods with high fracture toughness and elastic modulus based on fruit availability. The interaction of mechanical and nutritional properties of foods significantly influenced food selection across the seasons of low or high fruit availability, but there was no significant effect on age class. Fruit availability

determines the quality and quantity of food on basis of nutritional and mechanical aspects (Conklin et al., 1998). During the period of high fruit availability, there is high diversity and abundance of food and dietary choice is wide and it is easy to access food (Palombit, 1997; Vogel et al., 2016). Consequently, the mangabeys are likely to meet their nutritional requirements without challenges unlike in the period of low fruit availability when food resources are likely to be scarce and patchy. This partly explains the variation in food electivity as a function of interacting effects of nutritional and mechanical properties of food. Exploitation of similar food resources, mangabey adaptations to exploit hard foods, younger juvenile's reliance on older experienced individuals to open hard foods, and increased nutritional needs for growth in juveniles and for lactation in females (Altmann, 1998; Pereira & Fairbanks, 2002; Wieczkowski, 2009; Gunst et al., 2010; Chapman et al., 2012) may explain lack of age class differences.

The interaction among available protein, metabolizable energy, fracture toughness and elastic modulus as well as available protein, metabolizable energy and fracture toughness produced the most significant effects on food electivity compared to all other interactions of nutritional and mechanical properties of foods (Table 4.2). Available protein and metabolizable energy, which are only nutritional properties, produced similar significant effects on food electivity. The findings suggest that although nutritional and mechanical properties shape food selection nutritional properties treated separately produce equal effects on diet selectivity. While mechanical properties (Vogel et al., 2008; McGraw et al., 2011; Chalk et al., 2016) and nutritional properties (Rothman et al., 2006; Felton et al., 2009; Vogel et

al., 2017) have been demonstrated to influence primate diet selection, findings from this study illustrate how the two properties interact to influence primate diet selection.

The nutritional and mechanical properties of food interacted with fruit availability producing different patterns of food electivity. The interactive effects of nutritional and mechanical properties of food accounted for about 64% of food avoidance and 36% of food selectivity. The interaction of available protein and metabolizable energy either combined or alone interacted with fracture toughness and elastic modulus produced the highest food avoidance accounting for fruit availability. Equally, available protein and elastic modulus resulted to high food avoided avoidance. Metabolizable energy and fracture toughness acting independently and the interaction of the two food properties with available protein produced strong food selectivity suggesting that tough food rich in energy are selected regardless of the mechanical constraints. However, independent effects of available protein and elastic modulus led to food avoidance. This potentially may indicate that food rich in protein may be associated with other costs that deter their ingestion, as it is the case with elastic food items.

Nutritional (available protein and metabolizable energy) and mechanical (fracture toughness and elastic modulus) properties of food interacted with fruit availability to influence season food electivity. The following interactive effects of food properties resulted in food avoidance during the period of low fruit availability: available protein, metabolizable energy, and fracture toughness;

available protein, fracture toughness and elastic modulus; metabolizable energy and fracture toughness; and metabolizable energy. During the season of high fruit availability interactions yielding food avoidance were: metabolizable energy, fracture toughness, and elastic modulus; available protein and elastic modulus; available protein and metabolizable energy; and fracture toughness alone. These findings suggest that mangabeys potentially avoid foods with high AP, ME, or both and that are difficult to process due to high fracture toughness, elastic modulus or characterized by both traits. Protein is not required in high amounts and the fruits ingested by the Tana River mangabeys were rich in total non-structural carbohydrates indicating that these two macronutrients may be not limited especially during the season of high fruit availability. Thus, either fracture toughness or elastic modulus may be the discriminating factor of food selection especially when resources are not limiting, explaining the pattern of the interactive food properties and food avoidance.

The interaction resulting in food preference during the period of low fruit availability included: metabolizable energy, fracture toughness and elastic modulus; available protein and elastic modulus; available protein and fracture toughness; and available protein and metabolizable energy. Also fracture toughness and available protein acting independently lead to food selectivity. During the season of high fruit availability the following interacting food properties suggested food preference: available protein, metabolizable energy, fracture toughness and elastic modulus; available protein, fracture toughness and elastic modulus; available protein, metabolizable energy, and elastic modulus; available protein, metabolizable energy,

and fracture toughness; fracture toughness and elastic modulus; metabolizable energy and elastic modulus; and metabolizable energy and fracture toughness. Metabolizable energy alone also resulted to food selectivity.

These patterns indicate food selection criteria are based on combination of both nutritional and mechanical properties of foods interacting with fruit availability. According to these interactive patterns, it is clear that depending on fruit availability, mangabeys diet selection is aimed at prioritization of foods that were high in metabolizable energy and available protein, but that are low in fracture toughness and elastic modulus. During the period of low fruit availability available protein was prioritized more than metabolizable energy regardless of food mechanics while during high fruit available metabolizable energy was more targeted than available protein accounting for fracture toughness and elastic modulus. Collectively, based on all the significant interactive effects and the resulting food electivity index, it is clear that mangabeys' food selection is strongly predicted by both nutritional and mechanical properties of foods acting together with fruit availability. This reflects the need to balance the costs and benefits associated with both the nutritional and mechanical traits of foods.

Overall, the combined effects of both nutritional and mechanical properties of foods predicted dietary selection particularly during periods of low fruit availability, when fallback foods are heavily utilized. These results suggest that interactive effects are important during periods of low fruit abundance when preferred foods, when animals potentially switch to ingesting fallback foods.

Although studies focusing on understanding the interactive effects between nutritional and mechanical properties are limited, these results reinforce the findings that fallback foods are ecologically important in periods of low abundance of preferred foods (Marshall & Wrangham, 2007; Lambert & Rothman et al., 2015). The findings mirror those of similar work in amphibians (Ramamonjisoa et al., 2017) whereby food protein content and toughness predicted diet selectivity in tadpoles. While I recognize that amphibians are not comparable to primates, these results strongly suggest nutritional and mechanical properties potentially interact to influence food selection across a broad range of taxa.

In conclusion, my findings fully supported my prediction (P1) that juveniles ingested food with lower fracture toughness than lactating females. However, I did not find support for my second prediction (P2) that juveniles will consume food with lower elastic modulus. However, the analysis of mean maximum values weakly supported P2. Similarly, the interaction between mechanical and nutritional properties of foods together with fruit availability significantly influenced diet selection across the study period as I had predicted (P3), but there were no age class differences opposite of my expectations.

Appendices

Appendix 4.1. Table showing descriptive statistics summary of fracture toughness (R) of different classes of foods and constituent tissues of the mangabey diets. SEM is the standard error of mean, Max. R is the maximum fracture toughness.

Item	Mean ± SEM R (Jm²)	Mean ± SEM Max. R (Jm²)	Range (Min. - Max. R)
Food class			
Dry seed	1,531.49 ± 402.74	3,721.20 ± 1633.51	0.15 - 17,792.23
Mature leaf	314.03 ± 113.26	500.60 ± 293.34	17.90 – 1,488.80
Mushroom	238.26 ± 37.26	226.38 ± 98.00	94.08 - 3,62.60
Ripe fruit	1,385.29 ± 207.58	2,189.95 ± 705.93	0.26 - 15,007.03
Ripe seed	975.61 ± 254.28	1,631.88 ± 842.91	4.06 - 1,0071.68
Stem	943.37 ± 200.50	1,156.46 ± 360.45	4.16 - 3,000.76
Unripe fruit	1,310.34 ± 239.24	2,263.12 ± 712.33	0.06 - 27,313.35
Unripe seed	684.09 ± 135.71	1,188.82 ± 408.48	0.44 - 8,418.20
Young leaf	229.58 ± 31.25	338.08 ± 80.52	0.70 - 1,870.70
Food tissue			
Endosperm	1,116.99 ± 175.76	2,082.82 ± 585.511	0.15 - 17,792.23
Exocarp	1,473.95 ± 196.39	2,647.87 ± 645.62	0.06 - 27,313.35
Lamina	36.58 ± 8.57	61.42 ± 29.49	0.70 - 865.40
Mesocarp	634.60 ± 153.93	874.91 ± 363.14	0.26 - 6,995.24
Midrib	703.42 ± 7096	906.27 ± 163.45	72.10 - 1,870.70
Mushroom cap	238.26 ± 37.26	226.38 ± 98.00	94.08 - 362.60
Petiole	1,040.88 ± 212.65	1,541.50 ± 0.00	545.80 - 1,541.50
Secondary vein	408.58 ± 94.15	541.65 ± 213.32	69.70 - 1,081.20
Seed coat	250.73 ± 64.38	352.15 ± 129.20	56.77 - 481.35
Xylem/Phloem	943.37 ± 200.30	1,156.46 ± 360.45	4.16 - 3,000.76

Appendix 4.2: Table showing descriptive statistics summary of Elastic modulus (E) of different classes of foods and constituent tissues of the mangabey diets. SEM is the standard error of mean, Max. E is the maximum elastic modulus.

Item	Mean ± SEM E (MPa)	Mean Max. ± SEM E (MPa)	Range (Min. - Max. E)
Food class			
Dry seed	105.35 ± 21.02	226.66 ± 73.51	0.88 - 736.40
Mushroom	4.43 ± 0.93	5.24 ± 3.87	1.18 - 9.11
Ripe fruit	47.78 ± 6.93	80.31 ± 22.71	0.14 - 652.70
Ripe seed	95.64 ± 9.72	149.57 ± 25.73	8.13 - 381.70
Stem	24.17 ± 5.48	41.49 ± 4.15	3.43 - 45.64
Unripe fruit	46.87 ± 5.54	81.91 ± 18.07	0.69 - 972.80
Unripe seed	68.61 ± 9.33	101.09 ± 25.22	2.20 - 595.10
Food tissue			
Endosperm	90.21 ± 8.21	153.65 ± 24.10	0.69 - 736.40
Exocarp	56.49 ± 5.73	98.86 ± 19.38	0.14 - 972.80
Mesocarp	24.4.76 ± 4.76	41.64 ± 16.01	0.17 - 652.70
Mushroom cap	4.43 ± 0.93	5.24 ± 3.87	1.18 - 9.11
Seed coat	84.97 ± 16.71	112.23 ± 32.09	16.86 - 183.50
Xylem/Phloem	14.17 ± 5.48	41.49 ± 4.15	3.43 - 45.64

Appendix 4.3. Ethogram of the general behaviors scored during focal sampling

Behavior	Operational definition
Feeding	Food procurement from the source into the mouth, including locating, picking, dextral manipulation, dental processing and finally swallowing it
Moving	Movement by walking on the ground or traveling within and between trees for at least five seconds or by making more than four steps without stopping
Resting	State in which an animal was in inactive position (sitting or lying down) for more than five seconds, and it is not engaged feeding, traveling or in any social activity
Social interaction	Other activities other than feeding, moving, and resting that involved manipulative, communicative, aggressive or friendly engagement behaviors between two individual or independently
Other	Any other behavior, which did not include feeding, moving, resting and social interaction and activities performed when focal individuals are out of sight.

4.5 References

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49(3), 227-267.

Altmann, S. A. (2009). Fallback foods, eclectic omnivores, and the packaging problem. *American journal of physical anthropology*, *140*(4), 615-629.

Altmann, S.A., (1998). *Foraging for survival: yearling baboons in Africa*. Chicago: University of Chicago Press.

Berthaume, M. A. (2016). Food mechanical properties and dietary ecology. *American journal of physical anthropology*, *159*(S61), 79-104.

Boinski, S., & Fragaszy, D. M. (1989). The ontogeny of foraging in squirrel monkeys, *Saimiri oerstedi*. *Animal Behaviour*, *37*, 415-428.

Byrne, R. W. (2002). The ontogeny of manual skill in wild chimpanzees: evidence from feeding on the fruit of Saba florida. *Behaviour*, *139*(1), 137-168.

Chalk-Wilayto, J., Ossi-Lupo, K., & Raguet-Schofield, M. (2016). Growing up tough: Comparing the effects of food toughness on juvenile feeding in *Sapajus libidinosus* and *Trachypithecus phayrei crepusculus*. *Journal of human evolution*, *98*, 76-89.

Chalk, J. (2011). *The effects of feeding strategies and food mechanics on the ontogeny of masticatory function in the Cebus libidinosus cranium.* Doctoral dissertation, The George Washington University.

Chalk, J., Wright, B. W., Lucas, P. W., Schuhmacher, K. D., Vogel, E. R., Fragaszy, D., Visalberghi, E., Izar, P. & Richmond, B. G. (2016). Age-related variation in the mechanical properties of foods processed by *Sapajus libidinosus*. *American journal of physical anthropology*, *159*(2), 199-209.

Chapman, C. A., Chapman, L. J., Struhsaker, T. T., Zanne, A. E., Clark, C. J., & Poulsen, J. R. (2005). A long-term evaluation of fruiting phenology: the importance of climate change. *Journal of Tropical Ecology*, *21*(01), 31-45.

Chapman, C., Rothman, J. M & Lambert E.J (2012). Surviving and growing up in difficult and dangerous world. In *The evolution of primate societies*. Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.). University of Chicago Press.

Clissold, F. J., Sanson, G. D., Read, J., & Simpson, S. J. (2009). Gross vs. net income: how plant toughness affects performance of an insect herbivore. *Ecology*, *90*(12), 3393-3405.

Coiner-Collier, S., Scott, R. S., Chalk-Wilayto, J., Cheyne, S. M., Constantino, P., Dominy, N. J., Elgart, A.A., Glowacka, H., Loyola, L.C., Ossi-Lupo, K. & Raguet-Schofield, M. (2016). Primate dietary ecology in the context of food mechanical properties. *Journal of Human Evolution*, *98*, 103-118.

Coley, P. D. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological monographs*, *53*(2), 209-234.

Conklin-Brittain, N. L., Knott, C. D., & Wrangham, R. W. (2006). Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. *Cambridge Studies in Biological and Evolutionary Anthropology*, *1*(48), 445-472.

Constantino, P. J., Lee, J. J. W., Gerbig, Y., Hartstone-Rose, A., Talebi, M., Lawn, B. R., & Lucas, P. W. (2012). The role of tooth enamel mechanical properties in primate dietary adaptation. *American journal of physical anthropology*, *148*(2), 171-177.

Cooke, C., & McGraw, W. S. (2010). Diet, food hardness, and tooth use in red-capped mangabeys (*Cercocebus torquatus*) from Sette cama, Gabon. *American Journal of primatology*, 72(1), 38.

Cuozzo, F. P., & Sauther, M. L. (2012). What is dental ecology? *American journal of physical anthropology*, *148*(2), 163-170.

Daegling, D. J., Judex, S., Ozcivici, E., Ravosa, M. J., Taylor, A. B., Grine, F. E., Teaford, M. F., & Ungar, P. S. (2013). Viewpoints: Feeding mechanics, diet, and dietary adaptations in early hominins. *American Journal of Physical Anthropology*, *151*(3), 356-371.

Daegling, D. J., McGraw, W. S., Ungar, P. S., Pampush, J. D., Vick, A. E., & Bitty, E. A. (2011). Hard-object feeding in sooty mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. *PloS one*, *6*(8), e23095.

Dearing, M. D., Foley, W. J., & McLean, S. (2005). The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annual review of ecology, evolution, and systematics*, *36 (11)*, 169-89.

Decker, B. S. (1994). Effects of habitat disturbance on the behavioral ecology and demographics of the Tana River red colobus (*Colobus badius rufomitratus*). *International Journal of Primatology*, *15*(5), 703.

Dunham, N. T., & Lambert, A. L. (2016). The role of leaf toughness on foraging efficiency in Angola black and white colobus monkeys (*Colobus angolensis palliatus*). *American journal of physical anthropology*, *161*(2), 343-354.

Fleagle, J. G., & McGraw, W. S. (1999). Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. *Proceedings of the National Academy of Sciences*, *96*(3), 1157-1161.

Fragaszy, D. M., & Boinski, S. (1995). Patterns of individual diet choice and efficiency of foraging in wedge-capped capuchin monkeys (*Cebus olivaceus*). *Journal of Comparative Psychology*, *109*(4), 339.

Fragaszy, D. M., & Adams-Curtis, L. E. (1998). Growth and reproduction in captive tufted capuchins (*Cebus apella*). *American Journal of Primatology*, *44*(3), 197-203.

Fragaszy, D. M. (1986). Time budgets and foraging behavior in wedge-capped capuchins (*Cebus olivaceus*): age and sex differences. In F. King & D. Taub

(Eds.), *Current perspectives in primate social dynamics* (pp. 159-174). New York

Gilbert, C. C. (2007). Craniomandibular morphology supporting the diphyletic origin of mangabeys and a new genus of the *Cercocebus/Mandrillus* clade, *Procercocebus*. *Journal of Human Evolution*, *53*(1), 69-102.

Glowacka, H., McFarlin, S. C., Vogel, E. R., Stoinski, T. S., Ndagijimana, F., Tuyisingize, D. & Schwartz, G. T. (2017). Toughness of the Virunga mountain gorilla (*Gorilla beringei beringei*) diet across an altitudinal gradient. *American Journal of Primatology*.

Grant, P. R., & Grant, B. R. (2006). Evolution of character displacement in Darwin's finches. *Science*, *313*(5784), 224-226.

Gunst, N., Boinski, S., & Fragaszy, D. M., (2008). Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour*, *145*(2), 195-229.

Gunst, N., Leca, J.B., Boinski, S., & Fragaszy, D., (2010). The ontogeny of handling hard-to-process food in wild brown capuchins (*Cebus apella apella*): evidence from foraging on the fruit of *Maximiliana maripa*. *American journal of primatology*, *72*(11), 960-973.

Hanya, G. (2003). Age differences in food intake and dietary selection of wild male Japanese macaques. *Primates*, *44*(4), 333-339.

Hill, D. A., & Lucas, P. W. (1996). Toughness and fiber content of major leaf foods of Japanese macaques (*Macaca fuscata* yakui) in Yakushima. *American Journal of Primatology*, *38*(3), 221-231.

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

Imai, K., & Ohsaki, N. (2004). Internal structure of developing aucuba fruit as a defence increasing oviposition costs of its gall midges Asphondylia aucubae. *Ecological entomology*, *29*(4), 420-428.

Irwin, M. T., Raharison, J. L., Raubenheimer, D. R., Chapman, C. A., & Rothman, J. M. (2014). The nutritional geometry of resource scarcity: effects of lean seasons and habitat disturbance on nutrient intakes and balancing in wild sifakas. *PloS one*, *10*(6), e0128046.

Jaeggi, A. V., Dunkel, L. P., Van Noordwijk, M. A., Wich, S. A., Sura, A. A., & Van Schaik, C. P. (2010). Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *American Journal of Primatology*, *72*(1), 62-71.

Janzen, D. H. (1981). Patterns of herbivory in a tropical deciduous forest. *Biotropica*, 271-282.

Janson C. & van Schaik C. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira M.E. & Fairbanks L.A., (Eds.), *Juvenile primates: life history, development, and behavior* (pp. 57 – 76). New York: Oxford University Press.

Johnson, S. E., & Bock, J. (2004). Trade-offs in skill acquisition and time allocation among juvenile chacma baboons. *Human Nature*, *15*(1), 45-62.

Kent, M., & Coker, P. (1992). *Vegetation description and analysis*. Baffins Lane.

Kinnaird, M. F. (1992). Phenology of flowering and fruiting of an East African riverine forest ecosystem. *Biotropica,* 24 (2), 187–194.

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

Kivai, S. (2013). Predation on an Endemic and Endangered Tana River Mangabey (*Cercocebus galeritus*) by a Sympatric Yellow Baboon (*Papio cynocephalus*) in Tana River National Primate Reserve, Kenya. *African Primates 8(1),* 59-62.

Kivai S. M, Erin E. R. Rothman J.M. Kivasu C. M. & Palombit, R. A. (2017). Extractive foraging in wild Tana River Mangabeys, *Cercocebus galeritus*: Implication of Different Physical Properties of Foods. *Abstract, presented in the 86th Annual Meeting of the American Association of Physical Anthropologists (2017)*. American Association of Physical Anthropologists.

Koenig, A., Borries, C., Chalise, M. K., & Winkler, P. (1997). Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *Journal of Zoology*, *243*(2), 215-235.

Lack, D. (1947). *Darwin's finches*. CUP Archive.

Laden, G., & Wrangham, R. (2005). The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. *Journal of Human Evolution*, *49*(4), 482-498.

Lambert J. E. (2007). Seasonality, fallback strategies, and natural selection: a chimpanzee and cercopithecoid model for inter- preting the evolution of hominin diet. In: Evolution of the human diet. Ungar PS, (ed). Oxford: Oxford University Press. pp. 324–343.

Lambert, J. E. (2010). Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In: Campell, C., Fuentes, A., Mackinnon, K. C., Panger, M., and Beadner, S. (Eds), *Primates in perspective* (pp. 482-495). Oxford: Oxford University Press.

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

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

Lawn, B. R., & Lee, J. J. (2009). Analysis of fracture and deformation modes in teeth subjected to occlusal loading. *Acta Biomaterialia*, *5*(6), 2213-2221.

Lonsdorf, E.V., & Ross, S.R., (2012). Socialization and Development of Behavior. In*:* Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.), *The evolution of primate societies* (pp. 245-268). Chicago: University of Chicago Press.

Lonsdorf, E. V., Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature*, *428*(6984), 715-716.

Lucas, P. W., Copes, L., Constantino, P. J., Vogel, E. R., Chalk, J., Talebi, M., Landis, M. & Wagner, M. (2012). Measuring the toughness of primate foods and its ecological value. *International Journal of Primatology*, *33*(3), 598-610.

Lucas, P. W. (2004). *Dental functional morphology: how teeth work*. Cambridge University Press.

Lucas, P. W., Omar, R., Al-Fadhalah, K., Almusallam, A. S., Henry, A. G., Michael, S Arockia L. T, Watzke, J, Strait, D.S. & Atkins, A. G. (2013). Mechanisms and causes of wear in tooth enamel: implications for hominin diets. *Journal of the Royal Society Interface*, *10*(80), 20120923.

Lucas, P., Constantino, P., Wood, B., & Lawn, B. (2008). Dental enamel as a dietary indicator in mammals. *BioEssays*, *30*(4), 374-385.

Manly, B. F. L., McDonald, L., Thomas, D., McDonald, T. L., & Erickson, W. P. (2007). *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & Business Media.

Marshall, A. J., & Wrangham, R. W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*, *28*(6), 1219.

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

Mattson W. J. (1980). Herbivory in relation to plant nitrogen content. *Annual review of ecology and systematics*, *11*(1), 119-161.

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

McGraw, W. S., & Daegling, D. J., (2012). Primate feeding and foraging: integrating studies of behavior and morphology. *Annual Review of Anthropology*, *41*, 203-219.

McGraw, W. S., Vick, A. E., & Daegling, D. J. (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*(1), 140-153.

McGraw, W. S., Vick, A. E., & Daegling, D. J. (2014). Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): Implications for fallback foods and dental adaptation. *American journal of physical anthropology*, *154*(3), 413-423.

Milton, K. (1984). The role of food-processing factors in primate food choice. *Adaptations for foraging in nonhuman primates*, 249-279.

Norconk, M. A., Wright, B. W., Conklin-Brittain, N. L., & Vinyard, C. J. (2009). Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In: Garber, P. A., Estrada, A., Bicca-Marques, J. C., Heymann, E. & Strier, K. B (Eds), *South American Primates* (pp. 279-319). New York: Springer.

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

Peeters, P. J. (2002). Correlations between leaf structural traits and the densities of herbivorous insect guilds. *Biological Journal of the Linnean Society*, *77*(1), 43-65.

Pereira, M.E., Fairbanks, L.A., (2002). *Juvenile Primates: Life history, Development, and Behavior*. New York: Oxford University Press.

Perry, J. M., Bastian, M. L., St Clair, E., & Hartstone-Rose, A. (2015). Maximum ingested food size in captive anthropoids. *American journal of physical anthropology*, *158*(1), 92-104.

Potts, R. (1998). Variability selection in hominid evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *7*(3), 81-96.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Ramamonjisoa, N., Rakotonoely, H., & Natuhara, Y. (2017). Food Preference in Relation to Resource Toughness and Protein Level in a Pond Dwelling Tadpole. *Journal of Herpetology*, *51*(1), 47-51.

Resende, B. D., Nagy-Reis, M. B., Lacerda, F. N., Pagnotta, M., & Savalli, C. (2014). Tufted capuchin monkeys (*Sapajus* sp) learning how to crack nuts: Does variability decline throughout development?. *Behavioural processes*, *109*, 89-94.

Rosenberger A. L. (1992). The evolution of feeding niches in New World monkeys. *American Journal Physical Anthropology*, *88*(2), 525–562.

Rothman, J. M., Chapman, C. A., & Pell, A. N. (2008b). Fiber-bound nitrogen in gorilla diets: implications for estimating dietary protein intake of primates. *American Journal of Primatology*, *70*(7), 690-694.

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

Rothman, J. M., Dierenfeld, E. S., Hintz, H. F., & Pell, A. N. (2008a). Nutritional quality of gorilla diets: consequences of age, sex, and season. *Oecologia*, *155*(1), 111-122.

Sauther, M. L., & Cuozzo, F. P. (2009). The impact of fallback foods on wild ring-tailed lemur biology: A comparison of intact and anthropogenically disturbed habitats. *American Journal of Physical Anthropology*, *140*(4), 671-686.

Schuppli, C., Forss, S. I., Meulman, E. J., Zweifel, N., Lee, K. C., Rukmana, E., Vogel, E.R., van Noordwijk, M.A. & van Schaik, C. P. (2016). Development of foraging skills in two orangutan populations: needing to learn or needing to grow?. *Frontiers in zoology*, *13*(1), 43.

Schluter, D., & Grant, P. R. (1984). Ecological correlates of morphological evolution in a Darwin's finch, *Geospiza difficilis*. *Evolution*, 856 - 869.

Simpson, S. J., Le Couteur, D. G., & Raubenheimer, D. (2014). Putting the balance back in diet. *Cell*, *161*(1), 18-23.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton University Press.

Stone, A. I. (2006). Foraging ontogeny is not linked to delayed maturation in squirrel monkeys (*Saimiri sciureus*). *Ethology*, *112*(2), 105 - 115.

Strait, D. S., Constantino, P., Lucas, P. W., Richmond, B. G., Spencer, M. A., Dechow, P. C., Callum F. R., Ian R. G., Barth W. W., Bernard A. W., Gerhard W. W., Qian W, Craig B., Dennis E. S., Janine C., Amanda L. S., Leslie C. S., Sarah W., Michael B., Stefano B., Christine D & Ledogar, J. A. (2013). Viewpoints: Diet and dietary adaptations in early hominins: The hard food perspective. *American journal of physical anthropology*, *151*(3), 339-355.

Taniguchi, H. (2015). How the physical properties of food influence its selection by infant Japanese macaques inhabiting a snow-covered area. *American journal of primatology*, *77*(3), 285-295.

Vanderploeg, H. A., & Scavia, D. (1979). Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecological modelling*, *7*(2), 135-149.

Venkataraman, V. V., Glowacka, H., Fritz, J., Clauss, M., Seyoum, C., Nguyen, N., & Fashing, P. J. (2014). Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). *American journal of physical anthropology*, *155*(1), 17-32.

Vogel E.R, Kivai S. M. & Alavi S. (2016). Foraging strategies. *International Encyclopedia of Primatology*. In Press.

Vogel, E. R., Haag, L., Mitra-Setia, T., van Schaik, C. P., & Dominy, N. J. (2009). Foraging and ranging behavior during a fallback episode: *Hylobates albibarbis* and *Pongo*

pygmaeus wurmbii compared. *American Journal of Physical Anthropology*, *140*(4), 716 - 726.

Vogel, E. R., van Woerden, J. T., Lucas, P. W., Utami Atmoko, S. S., van Schaik, C. P., & Dominy, N. J. (2008). Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii. Journal of Human Evolution*, *55*(1), 60 - 74.

Vogel, E.R, Zulfa, A., Hardus, M., Wich, S.A. & Dominy, N.J (2014). Food mechanical properties, feeding ecology, and the mandibular morphology of the wild Orangutans. *Journal of Human Evolution*, http://dx.doi.org/10.1016/j.jhevol.2014.05.007.

Wahungu, G. (1998). Diet and habitat overlap in two sympatric primate species, the Tana crested mangabey *Cercocebus galeritus* and yellow baboon *Papio cynocephalus. African Journal of Ecology*, *36*(2), 159 - 173.

Wieczkowski J. (2003). *Aspects of the ecological flexibility of the Tana mangabey (Cercocebus galeritus) in its fragmented habitat, Tana River, Keny*a. Ph.D. dissertation thesis. Athens, GA: University of Georgia.

Wieczkowski, J. (2009). Brief communication: Puncture and crushing resistance scores of Tana River mangabey (*Cercocebus galeritus*) diet items. *American journal of physical anthropology*, *140*(3), 572 - 577.

Wrangham, R.W. (1980). An ecological model of female bonded primate groups. *Behaviour*, *75*(3), 262 - 300.

Yamashita, N. (2003). Food procurement and tooth use in two sympatric lemur species. *American journal of physical anthropology*, *121*(2), 125 - 133.

Yamashita, N., Cuozzo, F. P., & Sauther, M. L. (2012). Interpreting food processing through dietary mechanical properties: a *Lemur catta* case study. *American journal of physical anthropology*, *148*(2), 205 - 214.

Yamashita, N., Vinyard, C. J., & Tan, C. L. (2009). Food mechanical properties in three sympatric species of Hapalemur in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*, *139*(3), 368 - 381.

CHAPTER FIVE: CONCLUSIONS

5.1 Overall importance of the data generated

Data from this study make an extremely important contribution to juvenile and nutritional ecology studies, which over the past few decades have lagged behind primatological research of other behavioral topics. Juvenile primates to date remain rare foci of both laboratory and field research despite the importance of understanding their behavioral development and natural life histories. This study uniquely integrates both nutritional and mechanical data to understand how food properties interactively determine juvenile feeding behavior and adult foraging. Heretofore, primatologists have generally analyzed the nutritional and mechanical properties of food separately, with little or no effort made to understand how this two food attributes synergistically shape feeding strategies. Consequently, these data provide the first solid evidence of how protein content, metabolizable energy, fracture toughness, and elastic modulus interact to shape diet selectivity in primates.

The quantitative comparison of juvenile-adult feeding differences in dietary choice, macro- and micro-nutrient intake, exploitation of hard-to-extract foods, clarify the behavioral strategies employed by juveniles to overcome foraging challenges and extend significantly the small database on juvenile developmental studies. This growth in knowledge is fundamental to understanding the development of behavioral competence, and the role of nutrition in primate life histories. Above all, these results provide clarification on the ongoing debate regarding the existing hypotheses of juvenile-adult foraging differences, such as the Need-To-Learn (Pereira & Fairbanks, 2002), Ecological Risk Aversion (Janson & van Schaik, 1993), and Nutritional Constraint models (Altmann, 1991, 1998; Ramsay & Houston, 1997).

Significance of the findings

Juvenile primates face particular energetic challenges for growth and development and must balance between consuming a nutritionally balanced diet, learning foraging skills, and overcoming the mechanical and chemical constraints of foods. It is largely unclear what mechanisms foragers employ to achieve such balance in adults, let alone in juveniles, given that no single food meets all nutritional requirements (Righini, 2017). However, as posited by the Need-To-Learn, Ecological Risk Aversion, and Nutritional Constraint hypotheses (Chapman et al., 2012), a trade-off that promotes survival and reproductive fitness amidst feeding challenges is pivotal during the extended juvenile periods that typify primate life histories (Schuppli et al., 2016). Although the debate surrounding the above hypotheses has long established the importance of studying immature primates, doing so has been a daunting task (Pereira & Fairbanks, 2002; Chapman et al., 2012). Research on juvenile primates is confronted by unique problems, such as reliable individual identification, inadequate sample sizes, and an unfounded belief by primatologists that studying juveniles is hard.

Behavioral data of juvenile primates are crucial in understanding the evolution of feeding strategies, particularly the selective forces responsible for the great variety of dietary and anatomical traits observed in primates. This research is particularly important given that the majority of the Old World primates occupy highly unpredictable environments that experience seasonality in food availability

(Hill & Dunbar, 2002) and enormous anthropogenic threats generated by expanding human populations, climate change, industrialization, and agricultural developments (Estrada et al., 2017). Given such natural and anthropogenic effects, Marshall et al. (2009) suggest that the consumption of mechanically challenging fallback foods is an important coping strategy to enhance individual survival during times of nutritional stress. Successfully pursuing this strategy may be difficult for juveniles given that the hard-to-process nature of the majority of fallback foods requires manual strength, learned skills, and spatial knowledge, all of which take time to acquire (Schuppli et al., 2016). In dissertation, I focused on answering questions about how: juveniles make their dietary choices (compared to adult females), how the physical and chemical properties of food influence diet selection; and how juveniles behaviorally overcome food property challenges. Finally, I explore how the data could provide valuable input in the conservation of endangered primates, particularly the Tana River mangabeys.

In chapter 2, I hypothesized that juveniles differ from adult lactating females in their dietary choices because of inefficient foraging resulting partly from relative inexperience. First, I predicted that juveniles have a narrower dietary breadth than lactating females and, second, they have a higher intake of metabolizable energy per metabolic body mass. The data supported both of these predictions. Lactating females had a wider dietary breadth than juveniles. Juveniles included more plant species in their diet overall, but did so in an uneven manner, suggesting a trial and error feeding strategy, perhaps an effort to learn the appropriate food. This outcome was anticipated given that juveniles must learn appropriate foods, and are typically

curious, exploratory, and practicing the necessary foraging skills required to exploit different foods (Pereira & Fairbanks, 2017). These observations were in line with findings that showed juveniles spent more time feeding, relative to lactating females. The results support the Need-To-Learn hypothesis, which argues that primate foraging is complex and, thus, juveniles require time to develop cognitive foraging skills and physical strength to become competent foragers (Gunst et al., 2008; Lonsdorf & Ross, 2012). The data also support the Ecological Risk Aversion hypothesis that proposes that the inefficient foraging of juveniles relative to adult primates, make them more vulnerable to starvation (Lonsdorf & Ross, 2012). Consequently, my data clarify the two hypotheses that explain adult-juveniles foraging differences and the adaptive significance of extended juveniles periods. The evidence that the juvenile Tana River mangabeys ingested more metabolizable energy per metabolic body mass relative to the lactating females also supports the Nutritional Constraint hypothesis via Kleiber's rule (Kleiber, 1947). Energetic intake is determined by basal metabolic rate, activity levels, and specific physiological needs such as reproduction, lactation, and growth, especially in juveniles (Chapman et al., 2012). Consequently, immature individuals require more energy per unit mass than adults, to maintain basal metabolism and other physiological activities (Altmann & Alberts, 2005; Rothman et al., 2008). Juveniles also engage more in physical activities and are more nutritionally compromised by the energetic need for growth and development (Pereira & Fairbank, 2002). These data from Tana River mangabeys support these assertions and shed more light on how nutritional constraints impact juvenile feeding strategies and ontogeny.

Findings from this study reveal that juveniles achieved the elevated energy requirements through prolonged feeding times, targeted consumption of foods that had high energetic content and were easy to process, and scavenging adult leftovers from high-energy foods that were difficult to process. The intake of metabolizable energy varied with food species, and some of the fallback foods, such as *Borassus aethiopum* and *Hypahene compressa,* had high-energy returns. These data suggest that the ability to utilize such foods, especially during periods of food scarcity, confers a significant nutritional benefit, which may be necessary to minimize the exacerbated nutritional stress that juveniles face. Fallback foods are argued to be a significant selective pressure that shaped the masticatory, anatomical, and digestive adaptations among primates (Marshall et al., 2009). These data reinforce the consensus that fallback foods play a significant ecological role in buffering the costs of food scarcity and provide a key selective pressure for the evolution of dietary adaptations in primates (Lambert, 2004; Marshall & Wrangham, 2007; Marshall et al., 2009; Lambert & Rothman, 2015).

This study provides unique data that contribute to the advancement of the developing field of primate nutritional ecology. The availability, spatial-temporal distribution, chemical profile, temporal dynamic, and physical properties of primate foods have a major role in shaping primate ecology and evolution (Norconk et al., 2009; McGraw & Daegling, 2014; Rothman et al., 2015; Righini, 2017). These food attributes also play a pivotal role in primate dietary selection, procurement, processing, and ultimately the efficiency at which individuals meet their nutritional requirements. Primate foraging efficiency and nutrient acquisition at early stages of

development can dictate lifetime fitness (Altmann, 1998). Therefore, knowledge of adult-juvenile differences in macro- and micro-nutrient intake and feeding behavior is fundamental in understanding how food properties impact on juvenile feeding ontogeny, reproductive success, and life history strategies (Garber, 1987; Raubenheimer, 2012).

Consequently, chapter 3 of this dissertation tested hypotheses relating to the food nutritional properties and the influence on Tana River mangabeys dietary selectivity. Based on the Nutritional Constrain hypothesis, I argued juveniles and lactating females differ in their nutritional needs because of contrasting physiological requirements. As a result, I predicted that during periods of preferred food abundance, juveniles would have a higher relative intake of: i) protein; and ii) essential minerals to maximize growth and development, relative to lactating females.

The data supported the Nutritional Constraint hypothesis, as juveniles consumed higher quantities of protein and minerals (i.e., calcium, phosphorus, magnesium, potassium, sodium, iron, zinc, manganese, molybdenum) per metabolic body mass, as compared to lactating females. Protein and minerals have been suggested to be important criteria of food selectivity in primates, due to their importance in growth and physiological functions (Milton, 1984; Rode et al., 2003; Felton et al., 2009; Francisco et al., 2017; Irwin et al., 2017). On the basis of growth rate and protein concentration in milk, however, it is also suggested that primates may not require high protein diets, and perhaps consume more protein than they

need (Oftedal, 1991; Chapman et al., 2012). Protein requirements vary with life stages, and growing individuals require more protein per unit body mass than adults (Rothman et al., 2008). Approximately 3 g of protein per kilogram of metabolic body mass, or 6 - 8% of dietary dry matter, is necessary for primates to meet their daily protein requirements (NRC, 2003). However, meeting such daily protein needs may be challenging partly because tannins can interfere with uptake by binding to protein and partly because of protein utilization by gut microbes. Thus, not all the protein that is ingested is available to the consumer (Rothman et al., 2012). Unfortunately, most studies do not estimate the available protein or quality of protein in primate diets (Chapman et al., 2012). However, estimation of the available protein intake, as opposed to the routine estimate of crude protein in this study, contributes significantly to better understanding of the dietary role of protein in primate foraging. These data indicated that juveniles ingested more protein per metabolic body mass than adults, and importantly, protein interacted with food fracture toughness and elastic modulus to determine diet selectivity. The findings continue to shed light on the role of protein in primate diet selection and uniquely illustrate how other food properties may interact with protein to influence diet selection.

It is clear that mineral composition plays a significant role in juvenile growth, and that mineral deficiencies may have detrimental effects on lifetime fitness (Robbins, 1993; Fashing et al., 2007; Deblauwe & Janssen, 2008; Cancellier et al., 2014; Irwin et al., 2017). Enough data, however, are yet to be accumulated to fully understand how mineral content influences primate foraging strategies. The

estimation of mineral concentrations in the Tana River mangabeys' foods and their intake in both juveniles and lactating females is an important contribution in assembling the much-needed data to inform us how mineral content influences primate foraging. Current data on mineral concentrations in primate foods indicate major deficiencies in essential minerals, and it's unclear how primates cope with such shortfalls (Rode et al., 2003; Deblauwe & Janssen, 2008).

Moreover, plant secondary metabolites occur in primate foods and vary variation in concentration depending on the nature of plant parts and the stage of plant growth or development (Wrangham & Waterman, 1981; Waterman, 1984; Dearing et al., 2005). Thus, to achieve their nutritional goals, primates must balance the costs and benefits of plant consumption. Dietary selection, complete avoidance, and controlled intake are some of the behavioral strategies of primate balancing of the nutrient intake (Johnson et al., 2017; Rightini et al., 2017) and avoidance of chemical and mechanical constraints (Hill & Lucas, 1996; Yamashita et al., 2009). However, studies focusing on how different primates behaviorally overcome food mechanical and chemical constraints remain rare. Such information is critical in understanding primate dietary adaptations and the relevant evolutionary significance. To contribute to this knowledge gap, I tested the hypothesis that mangabeys in general will feed selectively to avoid food with high concentrations of condensed tannins (CT), and where they ingest foods with CT, they will consume foods with low concentration of CT. Thus, mangabeys dietary composition will have more foods free of CT compared to those containing such compounds and will ingest more food with lower concentration of CT among food positive for CT.

I found no differences between the foods that tested positive or negative for condensed tannins among the food consumed by the Tana River mangabeys. However, as I predicted the majority of the foods containing CT that were consumed only had a low or moderate concentration of tannins. These findings suggested that food selection is a potentially important behavioral strategy to overcome chemical problems among the Tana River mangabeys.

I focused on the mechanical properties of foods ingested by the mangabeys, and the interaction with the nutritional properties to determine diet selectivity in Chapter 4. The mechanical properties of foods have been suggested as ecologically significant selective pressures deriving the morphological and anatomical dietary adaptations in both extant and fossil primates (Marshall & Wrangham, 2007). Such adaptations mainly arise from consumption of fallback foods particularly during periods of food scarcity. Exploitation of fallback foods requires physical strength, proficiency in processing, and full development of masticatory system. Consequently, juveniles are inexperienced and their small body size limits their ability to ingest these foods leading to juvenile-adult foraging differences efficiently. Thus, I hypothesized juveniles' diets differ from those of lactating females in their mechanical properties because lactating females are more efficient foragers than juveniles (i.e., Physical Maturation Constraint hypothesis – Gurven et al., 2006; Gunst et al., 2010). As a result, I predicted that juveniles would exploit foods with relatively lower fracture toughness, and elastic modulus, compared to lactating females. I also hypothesized that both mechanical and nutritional properties of foods interact to influence diet selectivity, which I refer to as "Interactive Food

Properties hypothesis." I predicted that during lean periods, juveniles would forage more on less preferred (fallback) foods that are relatively abundant, low in energy and protein, but easy to extract and process, while lactating females would feed on less selected foods that are rich in energy and protein, but are mechanically protected and require longer handling time.

There was partial evidence for the Physical Maturation and Interactive Food Properties hypotheses. Juveniles consumed foods that were lower in fracture toughness than those eaten by lactating females, but there was no age class difference in elastic modulus. This potentially suggests that juvenile competence in consumption of tough food items is not achieved until late in immature stage or near maturity, but juveniles attain adult efficiency in the use of stiff food material earlier in life. Similarly, the interactive effects of mechanical and nutritional properties have a strong influence on diet selectivity during the period of low food availability, but there were no observed juvenile-adult differences at any time of the year. This shows that nutritional and mechanical properties of foods are interlinked (Hill & Lucas, 1996) and both are associated with significant costs and benefits, the balancing of which plays a critical role in diet selection (Lambert & Rothman, 2015).

Evolutionary relevance to dietary adaptations in early hominins

Consumption of mechanically challenging fallback foods has become a focal point of debates concerning early hominin dietary adaptations. The mechanical properties of foods have increasingly been invoked as a driving force for the morphological and dietary adaptations that were posited for early hominins (Ungar, 2004; Van der Merwe et al., 2008; Lee-Thorp et al., 2010, Strait et al., 2013). For

instance, recent biomechanical analyses support the hypothesis that the inclusion of hard foods in the diet influenced the craniodental and facial morphology of the Australopithecines (Strait et al., 2013). The teeth, crania, and facial shape of *Australopithecus africanus*, and other hominins reflect a suite of adaptations for the consumption of hard foods, such as seeds and nuts (Lucas et al., 1985; Peters, 1987). Despite the evidence linking the mechanical properties of food to the evolution of observed craniodental adaptations in early hominins and extant primates (McGraw et al., 2015; Daegling et al., 2013), contradicting results (Strait et al., 2012) continue to emerge and spark debates on the role of mechanical properties of food in shaping dietary adaptations (Ungar et al., 2010; Coiner-Coiller et al., 2016).

Dental microwear texture analysis of *Paranthropus boisei* and *P. robustus,* which are morphologically and functionally similar, have yielded divergent results; with *P. boisei* showing no evidence of exploitation of hard foods (Scott et al., 2005; Ungar et al., 2010). On the other hand, isotopic analyses have revealed differences in the stable carbon isotope signal, suggesting that *P. boisei* ate more C4 plant resources compared to the mixed diet dominated by C3 plants (nut producers) in *P. robustus* and the australopithecines (Sponheimer et al., 2006; Lee-Thorp et al., 2010). Because C4 seeds alone cannot account for the cranio-morphological form observed in *P. boisei,* the inclusion of high proportions of tough and pliable food tissues from C4 sedges and grass are proffered as explanations for the observed morphological adaptations (van der Merwe et al., 2008; Cerling et al., 2011). These studies have led to the conclusion that the craniodental adaptations of *P. robustus* and *P. boisei* have been driven differently by consumption of hard foods and tough-

compliant diets, respectively (Scott et al., 2005). Although these microwear and isotopic analyses indicate an apparent mismatch between the dietary and morphological signatures, both point to the importance of food mechanical properties in driving morphological and dietary adaptations. Data from this study have shown that Tana River mangabeys consumed foods that are characterized by high fracture toughness and elastic modulus. Comparing these data with data on species tooth structure, wear, and craniofacial characteristic may shed more light on the ongoing debate on the role of fallback foods in hominin evolution.

Relevance of the data to primate conservation

Primates are among the most globally threatened groups of mammals, with the majority of species facing extremely high extinction risks in the wild (Estrada et al., 2017). Among the 504 extant primate species, currently 60% of the species are endangered, and about 75% have undergone considerable population declines (Estrada et al., 2017). Habitat degradation, loss, and fragmentation remain the most significant threats that are driving primates towards extinction (Cowlishaw & Dunbar, 2000). The decline of foods resources and concomitant decline in habitat quality is crucially implicated in the crisis.

Tana River mangabeys and the sympatric red colobus (*Procolobus rufomitratus*) overlap in food resource use (Homewood, 1978; Wieczkowski, 2003; Marsh, 1981) and are among the world most endangered primates in dire need of intervention. Efforts to enhance survival of the Tana primates can occur through habitat restoration and the enrichment of nutritionally impoverished habitat

fragments through the growth of plant foods with high nutritional returns. However, such conservation efforts require a keen understanding of the plant food nutritional benefits, mechanical costs, and implications of feeding strategies, upon which, informed decisions can be made about which plant species to use in habitat rehabilitation or restoration efforts (Marshall et al., 2009; DeGabriel et al., 2016).

Data from this study provide details on the nutritional and mechanical properties of the dietary composition of the Tana River mangabeys and how these features influence diet selectivity throughout the year. Such valuable data inform conservation efforts by uniquely integrating laboratory and field studies to understand the nutritional implications for population dynamics. The study responds to calls to translate experimental laboratory information to field application, for the purposes of boosting in-situ species conservation (DeGabriel et al., 2016).

Intellectual contribution & future research directions

This study generated a new dataset that can be utilized for enhancing learning in higher institutions of learning in the field of primatology, particular in the subfields of primate feeding behavior, nutritional ecology, and juvenile feeding strategies. The data improve our theoretical understanding of juvenile primate ecology, how food properties shape feeding behavior, and clarify the primary hypotheses that explain juvenile-adult foraging differences. Such thematic areas are underrepresented in literature.

Importantly, this study stimulates new research questions that warrant further investigation to refine our understanding of juvenile foraging strategies and the implications of food properties in driving dietary adaptations in primates. To begin with, recent studies on orangutans (*Pongo pygmaeus wurmbii*) and sooty mangabeys (*Cercocebus atys*) have shown that foraging strategies across age-sex classes vary greatly (McGraw et al., 2011; Vogel et al., 2017). Thus, to fully understand the nutritional influences on feeding strategies of the Tana River mangabeys, future studies need to focus on comparing both juveniles with adult males and non-lactating females to understand the age-sex differences in nutrient intake and behavioral strategies to overcome food barriers. This will very usefully clarify the implications of physiological status and body size (given sexual dimorphism) on nutrient intake among the Tana River mangabeys. Equally important, there is also a need to estimate energy expenditure based on the daily activity budget of the two age classes. This is critical for understanding the mechanisms that this species employ to balance energy intake and expenditure, especially when resources are limited and daily energy requirements are challenging to meet.

During field observations, I noted that some mothers become very weak after giving birth and their health condition remained poor until the infants were fully weaned. Also, some mothers tended to carry their infants ventrally while others dorsally throughout the lactation period. Some mothers were assisted by male friends or older siblings who carried the infants during foraging. This raises the need to quantify the energetic constraints of lactation and how lactating mothers

cope with it at an individual level. Moreover, the alternative patterns of infant transport and whether the help from other members dissipate lactation costs in mangabeys demands some investigations. Understanding factors that influence the relatively fast weaning of infants (less than seven months) to offset lactational costs is also of interest in understanding the mechanisms of dealing with lactational challenges.

Given the crucial role of minerals and some of the life-threatening effects linked to their deficiencies, it was surprising to observe that the majority of foods eaten by mangabeys were quite deficient in important macro- and micro-minerals. It is imperative, therefore, for researchers to further explore how individuals of this species cope with such a challenge and whether this is a historical, or new, situation. This forms an interesting research question that needs to be pursued to enhance our knowledge on how primates cope with the chemical challenges in their diets.

This study also found that mangabeys ingest foods containing variable quantities of condensed tannins. It is unclear how this mangabey species deals with such chemical constraints even though food selection partly offers a behavioral strategy to this problem. Similarly, the species includes a high proportion of insects in its diet whereby the majority are consumed together with the exoskeleton, which is rich in chitin. Again it is yet to be understood how the species handle the dietary challenges presented by chitin. There is now a growing body of primate literature, which indicate gut microbes and enzymatic mechanisms are some of the ways primates deal with plant secondary metabolites and chitin (Amato et al., 2014;

Janiak, 2016). Thus, future studies should focus on trying to understand the possible role of digestive tract microbes, enzymes, and anatomical adaptations that may aid in coping with tannins and chitin. The possible behavioral observations that I suspect are aimed at mitigating the effects of plant secondary metabolites also require further detailed investigation, and include: eructation, harvesting of unripe fruits, delayed food consumption, and bark chewing.

While this study has clearly demonstrated that Tana River mangabeys forage on foods with extremely high fracture toughness and elastic modulus, there is still a need to understand whether the effects of such foods are reflected in the dental adaptations of this monkey. In this case, further research should strive to understand generally the implications of such diets on tooth microwear, tooth enamel, and craniofacial morphology. Thus, I would like to collect skulls and teeth from the Tana River mangabeys and collaborate with Prof. Robert Scott's laboratory in Department of Anthropology here at Rutgers to understand further implications for physics for dental and masticatory adaptations of mangabeys, particularly the hard food they eat. Moreover, I would like to continue collecting data on mechanical properties of foods of a wider variety of primates to understand how environmental variables may influence such properties and what the implications may be for foraging strategies.

Last but not the least, with the realization of the value of laboratory research to field efforts to save threatened species, I will plan to apply my results to practical field conservation practices to mitigate the serious threats that face the endangered

Tana River mangabeys. The next phase of this study will focus on careful consideration of the nutritional and mechanical properties of mangabeys' foods to identify and select the most valuable foods at any given time of the year. I will then recommend the species to be adopted for habitat restoration and nutritional enrichment of degraded habitat that have a potential of supporting the species. Such interventions will be critical in promoting the survival of all the Tana River primate community that is threatened by habitat loss and degradation.

References

Altmann, J., & Alberts, S. C. (2005). Growth rates in a wild primate population: ecological influences and maternal effects. *Behavioral Ecology and Sociobiology*, *57*(5), 490-501.

Altmann, S. A. (1991). Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. *Proceedings of the National Academy of Sciences*, *88*(2), 420-423.

Altmann, S.A., (1998). *Foraging for survival: yearling baboons in Africa*. Chicago: University of Chicago Press.

Amato, K. R., Leigh, S. R., Kent, A., Mackie, R. I., Yeoman, C. J., Stumpf, R. M., Wilson, B.A., Nelson, K.E., White, B.A. & Garber, P. A. (2014). The role of gut microbes in satisfying the nutritional demands of adult and juvenile wild, black howler monkeys (*Alouatta pigra*). *American journal of physical anthropology*, *155*(4), 652-664.

Cancelliere, E. C., DeAngelis, N., Nkurunungi, J. B., Raubenheimer, D., & Rothman, J. M. (2014). Minerals in the Foods Eaten by Mountain Gorillas (*Gorilla beringei*). *PloS one*, *9*(11), e112117.

Cerling, T. E., Mbua, E., Kirera, F. M., Manthi, F. K., Grine, F. E., Leakey, M. G., Sponheimer, M. & Uno, K. T. (2011). Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proceedings of the National Academy of Sciences*, *108*(23), 9337-9341.

Chapman, C., Rothman, J. M & Lambert E.J (2012). Surviving and growing up in difficult and dangerous world. In *The evolution of primate societies*. Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds). University of Chicago Press.

Coiner-Collier, S., Scott, R. S., Chalk-Wilayto, J., Cheyne, S. M., Constantino, P., Dominy, N. J., Elgart, A.A., Glowacka, H., Loyola, L.C., Ossi-Lupo, K. & Raguet-Schofield, M. (2016). Primate dietary ecology in the context of food mechanical properties. *Journal of Human Evolution*, *98*, 103-118.

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

Daegling, D. J., McGraw, W. S., Ungar, P. S., Pampush, J. D., Vick, A. E., & Bitty, E. A. (2011). Hard-object feeding in sooty mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. *PloS one*, *6*(8), e23095.

Deblauwe, I., & Janssens, G. P. (2008). New insights in insect prey choice by chimpanzees and gorillas in southeast Cameroon: the role of nutritional value. *American Journal of Physical Anthropology*, *135*(1), 42-55.

DeGabriel, J. L., Moore, B. D., Felton, A. M., Ganzhorn, J. U., Stolter, C., Wallis, I. R., Christopher N. Johnson & Foley, W. J. (2014). Translating nutritional ecology from the laboratory to the field: milestones in linking plant chemistry to population regulation in mammalian browsers. *Oikos*, *123*(3), 298-308.

Dearing, M. D., Foley, W. J., & McLean, S. (2005). The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annual review of ecology, evolution, and systematics*, *36*(1), 69-189

Dominy, N. J., Lucas, P. W., & Wright, S. J. (2003). Mechanics and chemistry of rain forest leaves: canopy and understorey compared. *Journal of Experimental Botany*, *54*(390), 2007-2014.

Lucas, P. W., Beta, T., Darvell, B. W., Dominy, N. J., Essackjee, H. C., Lee, P. K. D., Osorio, D., RamsdenL., Yamashita N. & Yuen, T. D. B. (2001). Field kit to characterize physical, chemical and spatial aspects of potential primate foods. *Folia Primatologica*, *72*(1), 11-25.

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K.A.I., Nijman, V., Heymann, E.W., Lambert, J.E & Rovero, F. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, *3*(1), e1600946.

Fashing, P. J., Dierenfeld, E. S., & Mowry, C. B. (2007). Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of *Colobus guereza* in Kakamega Forest, Kenya. *International Journal of Primatology*, *28*(3), 673-703.

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

Felton, A. M., Felton, A., Wood, J. T., & Lindenmayer, D. B. (2008). Diet and feeding ecology of *Ateles chamek* in a Bolivian semi humid forest: the importance of Ficus as a staple food resource. *International Journal of Primatology*, *29*(2), 379-403.

Francisco, T. M., Lopes-Mattos, K. L. B., Picoli, E. A. D. T., Couto, D. R., Oliveira, J. A., Zanuncio, J. C., Serrão J. E., Silva I. O. & Boere, V. (2017). Feeding habits of marmosets: A case study of bark anatomy and chemical composition of *Anadenanthera peregrina* gum. *American journal of primatology*, *79*(3), 1-9.

Gunst, N., Boinski, S., & Fragaszy, D. M. (2008). Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour*, *145*(2), 195-229.

Gunst, N., Leca, J.B., Boinski, S., & Fragaszy, D., (2010). The ontogeny of handling hard-to-process food in wild brown capuchins (*Cebus apella apella*): evidence from foraging on the fruit of *Maximiliana maripa*. *American journal of primatology*, *72*(11), 960-973.

Gurven, M., Kaplan, H., & Gutierrez, M. (2006). How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span. *Journal of human evolution*, *51*(5), 454-470.

Hill, D. A., & Lucas, P. W. (1996). Toughness and fiber content of major leaf foods of Japanese macaques (*Macaca fuscata yakui*) in Yakushima. *American Journal of Primatology*, *38*(3), 221-231.

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

Irwin, M. T., Raharison, J. L., Chapman, C. A., Junge, R. E., & Rothman, J. M. (2017). Minerals in the foods and diet of diademed sifakas: Are they nutritional challenges?. *American journal of primatology*, *79*(4), 1-14.

Johnson, C. A., Raubenheimer, D., Chapman, C. A., Tombak, K. J., Reid, A. J., & Rothman, J. M. (2017). Macronutrient balancing affects patch departure by guerezas (*Colobus guereza*). *American journal of primatology*, *79*(4), 1-9.

Janiak, M. C. (2016). Digestive enzymes of human and nonhuman primates. *Evolutionary Anthropology: Issues, News, and Reviews*, *25*(5), 253-266.

Kleiber, M. (1947). Body size and metabolic rate. *Physiological reviews*, *27*(4), 511-541.

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

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

Lee-Thorp, J. A., Sponheimer, M., Passey, B. H., De Ruiter, D. J., & Cerling, T. E. (2010). Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift in the Pliocene. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1556), 3389-3396.

Lonsdorf, E.V., & Ross, S.R., (2012). Socialization and Development of Behavior. In*:* Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.), *The evolution of primate societies* (pp. 245-268). Chicago: University of Chicago Press.

Lucas, P. W., Copes, L., Constantino, P. J., Vogel, E. R., Chalk, J., Talebi, M., Landis, M. & Wagner, M. (2012). Measuring the toughness of primate foods and its ecological value. *International Journal of Primatology*, *33*(3), 598-610.

Lucas, P. W., Corlett, R. T., & Luke, D. A. (1985). Plio-Pleistocene hominid diets: an approach combining masticatory and ecological analysis. *Journal of Human Evolution*, *14*(2), 187-20

Marsh, C. W. (1981). Ranging behaviour and its relation to diet selection in Tana River red colobus (*Colobus badius rufomitratus*). *Journal of Zoology*, *195*(4), 473-492.

Marshall, A. J., & Wrangham, R. W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*, *28*(6), 1219.

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

McGraw, W. S., Vick, A. E., & Daegling, D. J. (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*(1), 140-153.

McGraw, W. S., Vick, A. E., & Daegling, D. J. (2014). Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): Implications for fallback foods and dental adaptation. *American journal of physical anthropology*, *154*(3), 413-423.

Milton, K. (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *The American Naturalist*, *114*(3), 362-378.

Milton, K. (1984). The role of food-processing factors in primate food choice. *Adaptations for foraging in nonhuman primates*, 249-279.

National Research Council. (2003). *Nutrient requirements of nonhuman primates*. National Academies Press.

Norconk, M. A., Wright, B. W., Conklin-Brittain, N. L., & Vinyard, C. J. (2009). Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In: Garber, P. A., Estrada, A., Bicca-Marques, J. C., Heymann, E. & Strier, K. B (Eds), *South American Primates* (pp. 279-319). New York: Springer.

Oftedal, O. T., Whiten, A., Southgate, D. A. T., & Van Soest, P. (1991). The Nutritional Consequences of Foraging in Primates: The Relationship of Nutrient Intakes to Nutrient Requirements and Discussion. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *334*(1270), 161-170.

Pereira, M.E., Fairbanks, L.A., (2002). *Juvenile Primates: Life history, Development, and Behavior*. New York: Oxford University Press.

Peters, C. R. (1987). Nut-like oil seeds: Food for monkeys, chimpanzees, humans, and probably ape-men. *American Journal of Physical Anthropology*, *73*(3), 333-363.

Ramsay, S. L., & Houston, D. C. (1997). Nutritional constraints on egg production in the blue tit: a supplementary feeding study. *Journal of Animal Ecology*, 649-657.

Righini, N. (2017). Recent advances in primate nutritional ecology. *American journal of primatology*, *79*(4), 1-5.

Righini, N., Garber, P. A., & Rothman, J. M. (2017). The effects of plant nutritional chemistry on food selection of Mexican black howler monkeys (Alouatta pigra): the role of lipids. *American journal of primatology*, *79*(4), 1-15.

Robbins, C. T. (1993). *Wildlife nutrition and feeding*. New York Academic Press.

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

Rothman, J. M., Chapman, C. A., & Pell, A. N. (2008b). Fiber-bound nitrogen in gorilla diets: implications for estimating dietary protein intake of primates. *American Journal of Primatology*, *70*(7), 690-694.

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

Rothman, J. M., Chapman, C. A., Struhsaker, T. T., Raubenheimer, D., Twinomugisha, D., & Waterman, P. G. (2015). Long-term declines in nutritional quality of tropical leaves. *Ecology*, *96*(3), 873-878.

Rothman, J. M., Dierenfeld, E. S., Hintz, H. F., & Pell, A. N. (2008a). Nutritional quality of gorilla diets: consequences of age, sex, and season. *Oecologia*, *155*(1), 111-122.

Schuppli, C., Meulman, E. J., Forss, S. I., Aprilinayati, F., van Noordwijk, M. A., & van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87-98.

Scott, R. S., Ungar, P. S., Bergstrom, T. S., Brown, C. A., Grine, F. E., Teaford, M. F., & Walker, A. (2005). Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature*, *436*(7051), 693-695.

Sphonheimer, M., Lee-Thorp, J. & de Rutier, D (2016). Icarus, Isotopes, and Australopiths Diets. In: Ungar, P. S. (Ed). *Evolution of the human diet: The known, the unknown, and the unknowable* (pp. 132-149). Oxford: Oxford University Press.

Strait, D. S., Constantino, P., Lucas, P. W., Richmond, B. G., Spencer, M. A., Dechow, P. C., Callum F. R., Ian R. G., Barth W. W., Bernard A. W., Gerhard W. W., Qian W, Craig B., Dennis E. S., Janine C., Amanda L. S., Leslie C. S., Sarah W., Michael B., Stefano B., Christine D & Ledogar, J. A. (2013). Viewpoints: Diet and dietary adaptations in early hominins: The hard food perspective. *American journal of physical anthropology*, *151*(3), 339-355.

Ungar, P. (2004). Dental topography and diets of *Australopithecus afarensis* and early Homo. *Journal of Human Evolution*, *46*(5), 605-622.

Ungar, P. S., Scott, R. S., Grine, F. E., & Teaford, M. F. (2010). Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis. Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1556), 3345-3354.

van der Merwe, N. J., Masao, F. T., & Bamford, M. K. (2008). Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. *South African Journal of Science*, *104*(3-4), 153-155.

Vogel, E. R., Alavi, S. E., Utami-Atmoko, S. S., van Noordwijk, M. A., Bransford, T. D., Erb, W. M., Zulfa, A., Sulistyo, F., Farida, W.R & Rothman, J. M. (2017). Nutritional ecology of wild Bornean orangutans (Pongo pygmaeus wurmbii) in a peat swamp habitat: Effects of age, sex, and season. *American journal of primatology*, *79*(4), 1-20.

Waterman, P. G. (1984). Food acquisition and processing as a function of plant chemistry. In *Food acquisition and processing in primates* (pp. 177-211). Springer US.

Wrangham, R. W., & Waterman, P. G. (1981). Feeding behaviour of vervet monkeys on Acacia tortilis and Acacia xanthophloea: with special reference to reproductive strategies and tannin production. *The Journal of Animal Ecology*, 715-731.

Wieczkowski J. (2003). *Aspects of the ecological flexibility of the Tana mangabey (Cercocebus galeritus) in its fragmented habitat, Tana River, Keny*a. Ph.D. dissertation thesis. Athens, GA: University of Georgia.

Yamashita, N., Vinyard, C. J., & Tan, C. L. (2009). Food mechanical properties in three sympatric species of Hapalemur in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*, *139*(3), 368-381.