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Coping with Forest Fragmentation: A Comparison of Colobus angolensis palliatus dietary diversity and behavioral plasticity in the East Sagara Forest, Tanzania.

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Abstract

Habitat destruction and forest fragmentation are perhaps the largest threats to primate species around the world. While national parks, games reserves, and primate sanctuaries are instrumental in primate conservation, research suggests that some non-governmentally protected forest fragments may also serve as viable habitats for primates. Of course not all primates respond to fragmentation in the same way, but a species' ability to survive in a fragment relates to 1) home range size 2) degree of frugivory 3) dietary flexibility and behavioral plasticity and 4) ability to utilize matrix habitats. Here I describe these variables in relation to black and white colobus monkeys while focusing on dietary and behavioral plasticity. In general, black and white colobus monkeys seem well adapted to cope with forest fragmentation compared to other primate species because of their small home ranges, predominantly folivorous diets, and dietary and behavioral flexibility. For 15 days during October and November 2009, I observed two troops of *Colobus angolensis palliatus* in a small encroached forest fragment in the Western Usambara Mountains of northeastern Tanzania. Utilizing past studies from Preston (2002), Fox (2004), Heinen (2006), and Olsen (2007), this study monitors behavioral changes in terms of activity budgets and feeding effort to analyze stress levels associated with fragmentation. Furthermore, this study explores black and white colobus monkey dietary diversity in terms of tree species and selection ratios. This study suggests *Colobus angolensis palliatus* exhibit remarkable dietary diversity and may be altering their behavior to cope with increasing food scarcity over time. These characteristics likely contribute to primates' ability to persist in this forest fragment.

Introduction

Roughly 90% of all primate species rely on the tropical forests of Africa, Asia, and South America for survival (Mittermeir and Cheney 1987). For centuries these forests have been shrinking due largely to human population increases and the associated higher demand for timber and agricultural land. According to the United Nations Global Forest Resource Assessment of 2010, the planet lost roughly 160,000 km^2 of forest per year from 1991 to 2000. Countries containing indigenous primate populations are believed to contribute roughly 125,000 km^2 (78%) of this annual forest loss (Chapman and Peres 2001). As a result of this devastating deforestation, primates around the globe are now largely limited to isolated forest patches (fragments[1]) that are under varying levels of protection. Primates inhabiting small (less than 1 km^2) unprotected forest fragments are particularly vulnerable to the adverse effects of habitat destruction with some species facing threat of local extinction.

With deforestation and habitat loss as the greatest threats to primate species, the establishment of national parks, forests reserves, and primate sanctuaries is instrumental in conserving primates and their habitats. In theory, these areas protect primate populations by limiting not only habitat degradation, but also exposure to hunters and human and livestock transmitted diseases (Arroyo-Rodriguez and Dias 2010). These areas are also well suited for meaningful long-term study of primates. Unfortunately, parks and reserves typically require extensive resources to effectively manage and maintain. In addition, these gazetted areas often exclude or even displace indigenous peoples, making the areas extremely controversial and contested (Adams and Hutton 2007).

[1] Forest fragmentation is defined as the splitting of contiguous forest into isolated patches.

While establishing national parks and forests reserves may seem the most effective avenue to conserve forests and primates, some small non-governmentally protected forest fragments have the potential for meaningful gains in primate conservation (Marsh 2003; Chapman et al. 2007; Chapman et al. in press). The conservation of fragments is particularly worthwhile when a particular fragment contains primate species whose ranges span only a few protected areas or none at all. The combination of secondary growth and non-indigenous plant species characteristic of fragments provide greater abundances of exploitable food sources for some primate species (Coley 1983). Furthermore, the absence of major predators in small forest fragments may actually make these environments better for some species compared to larger forests capable of sustaining large predators (Isabirye-Basuta and Lwanga 2008). While most unprotected forest fragments are rapidly diminishing due to anthropogenic disturbances, some fragments have the potential to provide viable primate habitats under indigenous community management (Persha and Blomley 2009; Chapman et al. in press).

Not all primate species react to habitat fragmentation in the same way, as some seem more likely to persist in fragments than others. Examining the literature of primate studies in fragments, Marsh (2003) recognized that 1), home range size[2] 2), degree of frugivory in diet 3), dietary flexibility and behavioral plasticity and 4), ability to utilize matrix habitat[3] are general variables influencing a particular species' ability to survive in forest fragments. The aim of this study is to assess these aforementioned characteristics with regard to black and white colobus

[2] Home range is defined as the area occupied and traversed by a primate group over one year.

[3] Matrix habitat is the area immediately adjacent to the forest fragment. In terms of this paper, the matrix consists of a large variety of landscapes including human settlements, cleared forests, and agricultural fields that directly border forest fragments and separate patches of forest from each other. Matrix habitats can be part of primate groups' home ranges.

monkeys in general,[4] and particularly for Angola black and white colobus monkeys (*Colobus angolensis palliatus*) inhabiting a small forest fragment in the Western Usambara Mountains of Tanzania. By examining the fragment composition and characteristics, the activity budgets and feeding ecology of *C.a. palliatus* within the fragment, and studies of black and white colobus monkeys conducted throughout Africa, I will assess whether or not these monkeys are likely to survive in this fragment. I believe this study to be significant because *C. a. palliatus* range includes only two large protected forests, the Shimba Hills National Forest Reserve in Kenya and the Mikumi National Park in Tanzania (Rodgers 1981; Anderson et al. 2007c). Assessing the conservation potential of small fragments like the East Sagara Forest will help ensure which, based on the characteristics of the fragment, if any, forest fragments have the potential to remain viable habitats for these primates. Determining the potential success and persistence of these fragments as habitats for this monkey species will inform which fragments are likely to be sites of local extinction, and thus which, if any, are truly worth conservation efforts and funding.

Literature Review

I. Home Range

Studies have suggested that primate species exhibiting large home ranges are poor candidates to exist in small forest fragments (Estada and Coates-Estrada 1996; Lovejoy et al. 1986). For instance, Onderdonk and Chapman (2000) found that blue monkeys (home range=

[4] The five species of black and white colobus monkey include mantled guereza (*Colobus guereza*), Angola colobus (*Colobus angolensis*), king colobus (*Colobus polykomos*), ursine colobus (*Colobus vellerosus*) and black colobus (*Colobus satanas*). The term "black and white colobus monkeys" will henceforth refer to all five species in general terms. When referring to a particular species, either the genus and species names will be used or the common names such as "Angola colobus" or "king colobus."

approximately 0.61 km²) and grey cheeked mangabeys (home range of approximately 4.1 km²) inhabiting Kibale National Park, Uganda, were absent from all 20 forest fragments (average fragment size of 0.047 km²) surveyed just outside the park. In contrast, species with smaller average home ranges like red-tail guenons (home range of approximately 0.24 km²) and black and white colobus monkeys (home range of approximately 0.16 km²) were found in Kibale National Park and almost every neighboring fragment (Onderdonk and Chapman 2000). The most extensively studied primate species with regard to habitat fragmentation, and perhaps some of the most successful primates in forest fragments, are howler monkeys (genus *Alouatta*). These primates are common in fragments likely due in part because their home ranges are frequently less than .10 km² (Bicca-Marques 2003).[5] Home range size is one key variable that likely contributes to a suite of factors influencing primates' success in forest fragments.

Black and white colobus monkeys are characterized by relatively small home ranges compared to most primate species. It is well accepted that home range size relates to primate behavioral ecology and correlates directly with troop size, as larger groups require more resources, and thus larger ranging areas (Milton and May 1976). The most extensively studied of the five black and white colobus species, *Colobus guereza*, typically belongs to troops ranging from 2-15 individuals. Correspondingly, *C. guereza* home ranges usually range from 0.05-0.25 km² (Estes 1991). Similar to *C. guereza*, *C. angolensis* troops generally range from 2-20 individuals, with home ranges similar to mantled guerezas. This species sometimes forms massive troops consisting of more than 300 members (Fashing 2001; Fashing et al. 2007c). These "super troops" documented in the Nyungwe Forest of Rwanda utilize markedly larger

[5] It is important to note that home range size analyzed independently under logistic regression does not predict ability of species to live in fragments (Onderdonk and Chapman 2000).

home ranges approaching 25 km² (Fashing et al. 2007c). It is important to note that these massive troops are atypical, with black and white colobus usually maintaining small troops and home ranges.[6]

II. Degree of Frugivory

Diet and body size are also good predictors of home range size with folivorous primates exhibiting smaller home ranges than frugivores of similar body size (Milton and May 1976). Because fruits are heterogeneously dispersed throughout forests, frugivores typically must travel greater distances to satisfy their dietary requirements (Marsh 2003). The need to travel further to find adequate food supplies translates not only into larger home ranges, but also greater daily path lengths[7] (Milton and May 1976). Unless a particular frugivorous species incorporates multiple fragments within their range, it is unlikely to persist in a fragment (Johns and Skorupa 1987; Turner 1996). Gilbert and Setz (2001) revealed that large bodied frugivores like black spider monkeys (*Ateles paniscus*), bearded sakis (*Chiropotes chiropotes*), and brown capuchins (*Cebus paella*) disappeared from small fragments (0.1 km²-1 km²) almost immediately after their isolation from a larger forest reserve in Central Amazonia. In contrast, the more folivorous red howling monkey (*Alouatta seniculus*) persisted in each of the eight fragments analyzed.

Unlike fruits, leaves are ubiquitous and homogeneously distributed throughout forests (Milton and May 1976). This provides folivores with more food per unit area than frugivores. Some of the earliest studies of black and white colobus monkeys recognize the taxon simply as

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[6] The unusually large troop sizes at Nyungwe Forest are believed to be attributed to an abundance of highly nutritious mature leaves unique to this forest. Higher abundances of nutritious food are believed to severely mitigate intragroup competition and allow groups sizes to become very large (Fimbel et al 2001).

[7] Daily path length is defined as the average distance traveled by a troop each day.

arboreal ruminants "subject to the constraints of folivory" (Ripley 1984). Somewhat similar to ruminants, black and white colobus monkeys possess a complex multi-chambered stomach equipped with symbiotic microbes that function in digestive fermentation (McKey and Gartlan 1981). This colobine digestive fermentation allows for conversion of primary plant compounds like cellulose into readily digestible material (Davies and Oates 1994). More than any other primates, members of the sub-family Colobinae are able to process large quantities of leaves. Furthermore, black and white colobus monkeys, particularly *C. guereza*, are believed to be the most proficient digesters of leaves (Davies and Oates 1994). Leaves constitute more than 85% of the diet for certain troops of this species (Chapman et al 2007; Harris and Chapman 2007; Wasserman and Chapman 2003).

Not all black and white colobus groups rely so heavily on leaves though. In fact, fruits sometimes constitute significant portions of black and white colobus diets (Dasilva 1994). Degree of frugivory[8] ranges widely from 2-60% for black and white colobus monkeys. While leaves generally make up the bulk of the *C. guereza* diet, researchers suggest fruits and seeds are a more integral part of the lesser studied *C. satanas* (Gautier-Hion et al. 1993; Fluery and Gautier Hion 1999; Harrison 1986) and *C. polykomos* (Dasilva 1992). See Appendix II for black and white colobus diet composition by food type.

III. Dietary Flexibility and Behavioral Plasticity

Primate species particularly dependent on one or a few food items and/or tree species are less likely to persist in forest fragments than species with highly diversified diets. Because fragments are often encroached on or occupied by humans, typical primate food tree species may

[8] Degree of frugivory is defined as the sum percentage of fruits and seeds contributing to dietary composition.

become scarce due to logging, agricultural clearing, changes in micro-climate associated with edge effects, and competition with non-indigenous species (Isabirye-Basuta and Lwanga 2008). Once again howler monkeys are a prime example of a species well equipped to cope with fragmentation. Dietary diversity undoubtedly contributes to their ability to survive in fragments smaller than 0.05 km². While dietary diversity in terms of food items (i.e. folivory in addition to frugivory) is influential in this success, the variety of trees species is also important. For instance, Silver and Marsh (2003) showed that howler monkeys' (*Aloutatta pigra*) top food tree species accounts for only 22% of their diet in fragments of southern Belize. Other studies indicate that howlers can utilize nearly 200 plant species in their diet (*Alouatta seniculus*; Julliot 1994) and can also exploit non-indigenous trees species for as much as 38% of their diet (*Alouatta caraya*; Bicca-Marques and Calegaro-Marques 1994).

Although most groups are predominantly folivorous, some black and white colobus groups will opportunistically select whole fruits and seeds when they are available (Dasilva 1994; Fashing 2001). In addition, colobus monkeys consume both young and mature leaves. Young leaves are preferred to mature leaves, as the former are lower in fiber, more nutritious, and easier to digest (McKey and Gartlan 1981). While preferred foods like fruits and young leaves are seasonal, mature leaves are available year round (McKey and Gartlan 1981). Thus in times of preferred-food scarcity, black and white colobus monkeys often rely heavily on mature leaves as fallback foods, more so than any other African colobines (Fashing 2007a). Mature leaves with high protein to fiber ratios are preferred by black and white colobus and seem to be a good predictor of colobine abundance (Wasserman and Chapman 2003). Certain groups of monkeys also incorporate varying levels of flowers, lianas, lichens, and occasionally insects into their diets as well (Fashing et al. 2007c).

Black and white colobus species also exhibit varying levels of dietary flexibility in terms of tree species. When preferred food trees are abundant, some troops feed almost exclusively on a few species. For instance, it is well documented that *C. guereza* inhabiting Kibale National Park, Uganda, rely heavily on *Celtis durandii* and *Albizia grandibracleala* for their dietary intake (Clutton-Brock 1975; Harris and Chapman 2007; Harris et al. 2009). In fact, Clutton-Brock (1975) observed 88% of a troop's total feeding behaviors from *Celtis durandii* leaves alone. Similarly, McKey and Waternab (1982) found that 65% of a troop of *C. satanas* diet came from just three species of trees (see Appendix IV). When preferred food trees are scarce, however, black and white colobus generally decrease their reliance on preferred species and greatly increase their dietary diversity by selecting fallback foods (Harris et al. 2009). For example, *Colobus angolensis* has been observed to utilize 116 food tree species, some non-indigenous, in response to food scarcity in forest fragments of southern Kenya (Anderson et al. 2007a; Donaldson pers. comm. 2010).

Related to dietary flexibility, behavioral plasticity is a means of reacting to food scarcity and stress associated with fragmentation. Howler monkeys seem highly adaptable to shifts in food abundance by altering their activity levels while most primate species apparently cannot (Silver and Marsh 2003). Silver and Marsh (2003) suggested that howler monkeys are well suited to cope with forest fragmentation because they are able to increase their time spent resting to compensate for the lower caloric intake attributed to food scarcity.

Black and white colobus utilize varying strategies to cope with food scarcity. In some instances, they react by increasing their daily path lengths, number of food patches visited and time spent feeding per day (*C. guereza*: Harris et al. 2009; *C. satanas*: McKey and Gartlan 1981). In other words, they increase their feeding effort, traveling greater distances than normal to find food and satisfy their dietary requirements (Dunn et al. 2010). Similar to howler monkeys, black and white colobus monkeys may also react to food scarcity through energy conservation. Numerous studies have documented black and white colobus practicing thermoregulation to conserve energy (Dasilva 1992; Fashing 2001; Groves 1973). This often involves sun-bathing during the day and hunching during bouts of cold weather and rain (Groves 1973).

IV. Ability to Utilize Matrix Habitat

The ability for primate species to establish and sustain viable populations within forest fragments is strongly related to the composition of the matrix habitat.[9] Matrices can consist of a variety of landscapes from agricultural fields, cleared forests, agro-forests, non-indigenous woodlots, human settlements and various other habitats. Often resources within forest fragments are insufficient to support primate populations, thus forcing them to utilize matrix habitats for food or as corridors linking to another fragment or contiguous forest. Umapathy and Kumar (2003) found that Niligiri langurs (*Trachypithecus johnii*) were present in more forest fragments in southwestern India than lion-tailed macaques (*Macaca silenus*) due in part to the greater utilization of the matrix habitat by the former. Similarly, chimpanzees are common in fragmented forests because they frequently travel from one forest patch to another via the matrix (Onderdonk and Chapman 2000; Reynolds et al. 2003). Of course just because chimpanzees can utilize matrix habitats, particularly agricultural fields for food and dispersal does not mean they are safe in these habitats. In fact, chimpanzees inhabiting a small fragment outside the Budongo

Forest in Uganda, are often killed by farmers if caught crop raiding sugarcane fields (Reynolds et al. 2003).

It is important to stress that whether a species will effectively utilize the matrix depends on the composition of the matrix habitat. For instance, grey-cheeked mangabeys (*Cercocebus albigena*) inhabiting the Lopé Forest Reserve in Gabon are found in similar densities in neighboring fragments outside the reserve (Tutin et al. 1997). In contrast, this same species found in Kibale National Park in Uganda are absent from all of the forest fragments just outside the park (Chapman and Onderdonk 2000). This phenomenon could be explained by the fact that at Lopé humans are virtually absent from the matrix habitats surrounding the fragments, while at Kibale humans living in high population densities may deter grey-cheeked mangabeys from utilizing the matrix.

It is difficult to generalize whether or not black and white colobus will exploit matrix habitats. Because black and white colobus are highly arboreal it is logical to think they would be hesitant to traverse long distances through some matrix habitats such as agricultural fields. These monkeys are extremely vulnerable on the ground as their large bodies and clumsy locomotion make them easy prey for dogs and other predators (Fashing 2007b). Mantled guerezas do not move amongst forest fragments outside Kibale National Park due likely to this reason (Chapman et al. in press). In contrast, Angola colobus in southern Kenya utilize a variety of matrix habitats including wooded shrublands, agricultural plantations, and mangroves. These primates generally use these matrix habitats as corridors connecting to other forest patches, but will occasionally feed from unripe mangos, oranges, leaves of cassava, sweet potato, and cow peas found in the matrix (Anderson et al. 2007b). Undoubtedly, matrix characteristics are extremely influential in determining the likelihood of primates sustainably inhabiting fragments and must be assessed on a case by case basis.

V. Black and White Colobus Monkeys in Fragments

Studies of black and white colobus monkeys in fragments (*C. guereza*: Onderdonk and Chapman 2000; Chapman et al. 2003; Chapman et al. 2007; Chapman et al. in press; *C. vellerosus*: Wong et al. 2006; Wong and Sicotte 2007; *C. angolensis*: Anderson et al. 2007a; Anderson et al. 2007b) have produced somewhat conflicting results. In general, the combination of small home ranges, predominance of folivory over frugivory, and high degree of behavioral and dietary flexibility make black and white colobus monkeys more likely to succeed in forest fragments (Onderdonk and Chapman 2000). Of course it is very difficult to generalize across different species of black and white colobus and harder still to account for the many variables of fragmentation. Studies from forest fragments near the Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana concluded the patches seemed to be viable habitats for *C. vellerosus* (Wong and Sicotte 2007). Similarly, the ability for *C. angolensis* populations in southern Kenya to effectively utilize matrix habitat for dispersal and food sources greatly increased their chance of persisting in the fragmented ecosystem (Anderson et al. 2007b).

Monkeys inhabiting fragments outside Kibale National Park (KNP) have been far less successful in forest fragments. A 15-year analysis of mantled guerezas in these fragments revealed that in 1995 sixteen of twenty fragments analyzed contained *C. guereza* (Chapman et al. 2007). Subsequent studies in 2000, 2003, and 2010 showed that only three of these fragments contained mantled guerezas by 2010 (Chapman et al. in press). Furthermore, *C. guereza* populations have declined by 65% in these fragments since 1995 (Chapman et al. in press).

Local extinctions in most of these fragments are due predominantly to habitat destruction as most of the fragments in this study (mean area of 0.047 km² in 1995) were completely cleared by 2010 (Chapman et al. in press). *C. guereza* seem unable to effectively utilize the matrix habitat around KNP because of extensive human activity in the area (Chapman et al. in press).

Study Site

The East Sagara Forest is a montane forest located in the eastern arm of the Western Usambara Mountains of Tanzania. Rainfall in the area averages approximately 1230 mm, but is highly seasonal (Redhead 1981).[10] The elevation ranges from 1400-1500 m and slopes gradually from south to north. The forest is divided into six sections: Shambangulowy Shekalage, Mashimba, Mtungi, Papata, Bondeni, and Kwajega. In total, these six areas along with interspersed matrix habitat of felled land and agricultural fields amount to approximately 0.40 km² (Freierman 2008). The forest is home to a variety of trees and animals, many of which are endemic. Black and white colobus monkeys (*C. angolensis palliatus*) and Syke's (blue) monkeys (*Cecopithecus mitis kibonotensis*) are the only primate species found here.

Management of the forest has varied greatly over the past century. Swiss immigrant John Tanner purchased 7.5 km² of forest in Western Usambara Mountains during the early twentieth century (Persha and Blomley 2009). He converted much of the land into tea plantations, hiring 103 indigenous Sambaa workers, known as the Sagara Group (Persha and Blomley 2009). Roughly 3 km² of Tanner's estate was gazetted as the Mazumbai Forest Reserve

[10] Rainfall data collected from neighboring Mazumbai Forest Reserve and assumed to be comparable to the East Sagara Forest.

and placed under the jurisdiction of the University of Dar es Salaam in 1968 and later given to the Sokoine University of Agriculture (Mrecha pers. comm. 2009). Another portion of forest, the Sagara Forest, remained under Tanner's management plan. Tanner returned to Switzerland in 1982 severely indebted to the Sagara Group. In attempt to pay them for their labor, Tanner gave them ownership of the tea plantations and the Sagara Forest.

The forest experienced intense logging, particularly for East African Camphorwood (*Ocotea usambarensis*), throughout the 1980s (Persha and Blomley 2009). By the 1990s, the Sagara Group adopted a more conservational approach to forest management, recognizing the forest's value as a watershed (Mrecha pers. comm. 2009). Around the turn of the 21st century, the forest was officially designated as a Village Forest and all collection from the forest except that of deadwood was outlawed (Mrecha pers. comm. 2009; Persha and Blomley 2009).

Although the Sagara Groups remains dedicated to the theory of protecting the forest because of its watershed value, deforestation is still a common occurrence. Most of the Sambaa people inhabiting the area are subsistence-level agriculturalists and the vast majority use fuel wood as their only energy source (Mrecha pers. comm. 2009). Furthermore, the area exhibits some of the highest populations densities, average family size, and populations growth rates (3.8-4.2% annually) in all of Tanzania (Mrecha pers. comm. 2009). Combining these factors with the reality that only one unpaid forest guard protects the area, it is not surprising that Sagara Forest continues to thin and shrink (Persha and Blomley 2009). Currently, the forest is highly disturbed with agricultural plots, numerous footpaths, and a 3 m-wide road bisecting the forest that is frequented by pedestrians and automobiles.

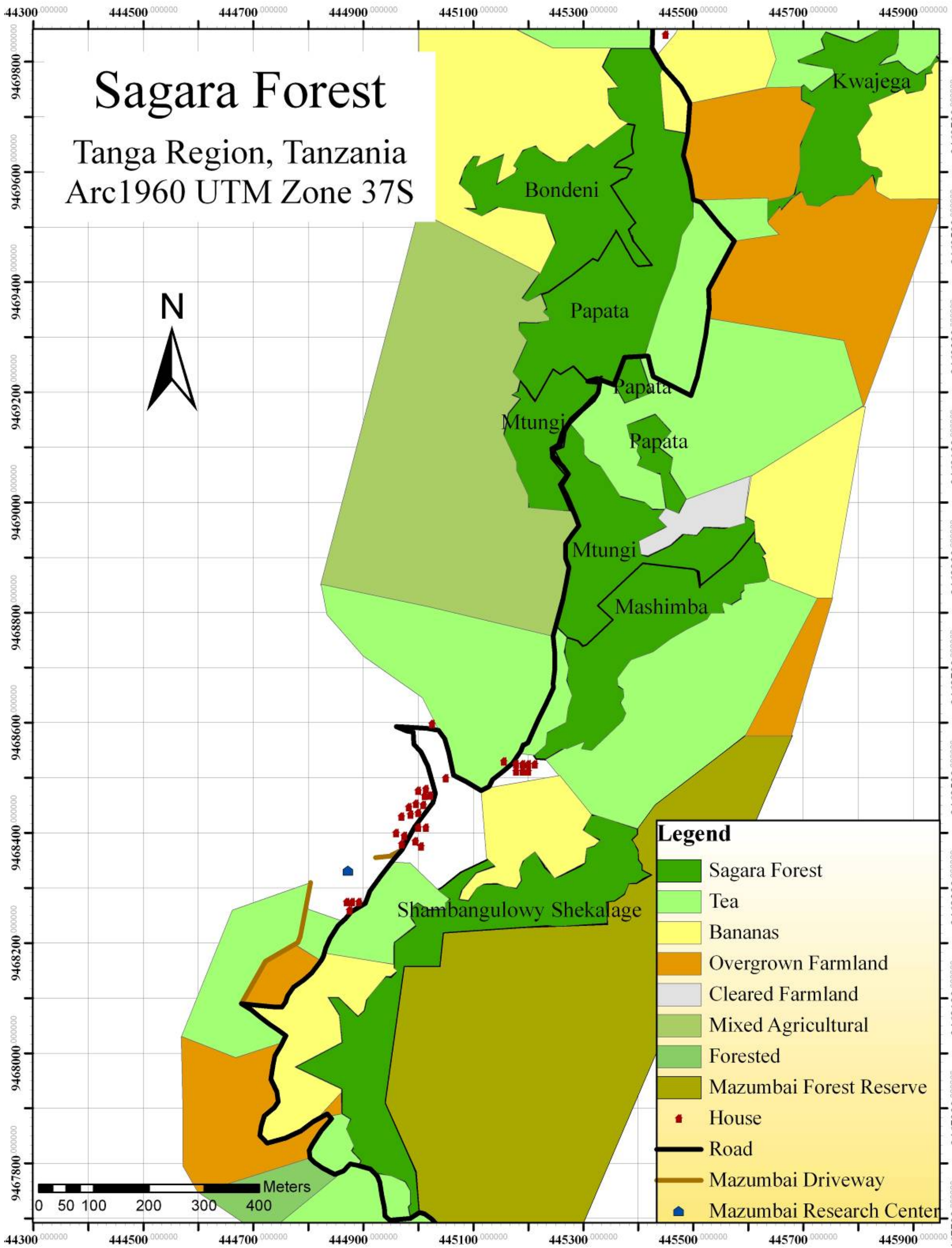

Figure 1: Map of the East Sagara Forest and the surrounding agricultural lands. Created using the Arc1960 datum in UTM Zone 37S. GPS data collected using Garmin GPS 12XL in the Sagara Forest, Tanzania, April 2008. Used with permission from Freierman (2008).

Methods

I. Sample Time Plan

I studied two troops of *Colobus angolensis palliatus* in the East Sagara Forest for 15 days in October and November of 2009. In order to remain consistent with past studies of the East Sagara Angola colobus (Preston 2002; Fox 2004; Heinen 2006; Olsen 2007), I collected behavioral data at two time intervals each day, from 6-10am and 2-6pm. I kept these time intervals so that I could compare my behavioral data to past studies. Furthermore, the time gap between the observation periods helped combat observer fatigue. Since my study focused on the feeding ecology of the monkeys, these time intervals were also ideal as they coincide with the peak feeding hours of other documented black and white colobus monkeys groups (Oates 1977; McKey and Waternab 1982; Boican 1997; Teichroeb et al. 2003).

II. Activity Budgets

Like in the previous studies of the East Sagara colobines, I utilized the instantaneous focal method first described by Clutton-Brock (1977). This method involves selecting one individual (focal animal) and recording its behavior at the beginning of each time interval. I used two-minute time intervals to remain consistent with the observation schedule of past studies. Behaviors were defined as inactive (sleeping, sitting, laying, or static without interaction), moving (walking, running, climbing, or leaping), feeding (bringing food to mouth, chewing, and swallowing), social grooming (grooming another individual), self-cleaning (grooming oneself), and *other* (remaining behaviors not characterized by previous categories). If at any time the focal animal moved out of my line of sight and could not be located by the start of the next interval, I randomly selected a new focal animal. This was performed by generating a number list from 1-5 and counting the monkeys in my view from right to left until I reached the number. In addition, I chose to observe only adults to eliminate behaviors that might be unique to juveniles.

III. Feeding Tree Identification

Using the instantaneous focal method, I recorded the tree species in which the focal animal was present during each two-minute interval. With limited knowledge of the native tree species, I relied on the knowledge of my forest guide, Said Mtali, who provided me with the common Sambaa names; these were later translated into their genus and species equivalents.

Data Analysis

I. Activity Budget and Feeding Effort

I created an activity budget based on all focal animal observations and assumed these were indicative of the troop in general. I then converted the frequencies of these behaviors into percentages and compared these values with previous studies of the East Sagara troops. Linear regressions were used to analyze the relationship between the activity budgets in each study.

Feeding effort was calculated using the formula described by Cavigelli (1999) in which feeding effort equaled (time spent feeding and moving) / time spent inactive. Feeding efforts from previous studies in the East Sagara Forest were also derived from activity budgets to serve as comparisons. Linear regressions were used to analyze the relationship between feeding efforts in each study.

II. Selection Ratios

I compiled all of the feeding behaviors by tree species and converted these frequencies into percentages. Using the survey of the East Sagara Forest created by Freierman (2008), I compared the ratio of percentage of time spent feeding by tree species with the abundance of the tree species in the forest. This ratio first described by Clutton-Brock (1975) is known as the selection ratio and is calculated by [(% of total feeding records made on species) / (% of tree species in the vegetation sample)] x 10. Selection ratios larger than 10 suggest a particular species is chosen more often than its abundance would predict if food is chosen at random. Similarly, selection ratios lower than 10 suggest the opposite.

Results

I. Sample Time Plan

In October and November of 2009, I spent 15 days in the East Sagara Village Forest, logging 96.6 hours of contact time with two troops of *Colobus angolensis palliatus*. Reconnaissance days used locating the troops and preparing for the study are not included in this 15 day period. The distribution of observation time is listed below in Table I.

	Morning Observation Period (6:00am-10:00am)	Afternoon Observation Period (2:00pm-6:00pm)	Totals
Number of Observation Periods	15	15	30
Total Time in Field	60 hours	60 hours	120 hours
Total Contact	49.1 hours	47.5 hours	96.6 hours
Total Number of Observations	1474	1424	2898
Average Contact per Observation	3.27 hours	3.17 hours	3.22 hours
Percent of Time in Contact	81.8%	79.2%	80.5%

Table I: The distribution of observation time of *Colobus angolensis palliatus* in the East Sagara Village Forest, Tanzania, October-November 2009.

II. Activity Budget and Feeding Effort

Of the 96.6 hours of contact I had with *C. angolensis palliatus*, 68.5% (1984/2898 observations) of the time was spent inactive. Feeding was noted 16.3% (472/2898) of the time. Moving constituted 8.9% (258/2898) of the colobus' activity. Lastly, self-cleaning (2.9%; 83/2898), social grooming (3.2%; 94/2898), and *other* (0.4%; 11/2898) comprised smaller portions of daily activity. The time activity budget is represented in Figure 2. Figure 3 shows the activity budget of inactivity, feeding, and moving since 2002. Feeding effort was calculated to be 0.36. Figure 4 displays feeding effort values from 2002-2009.

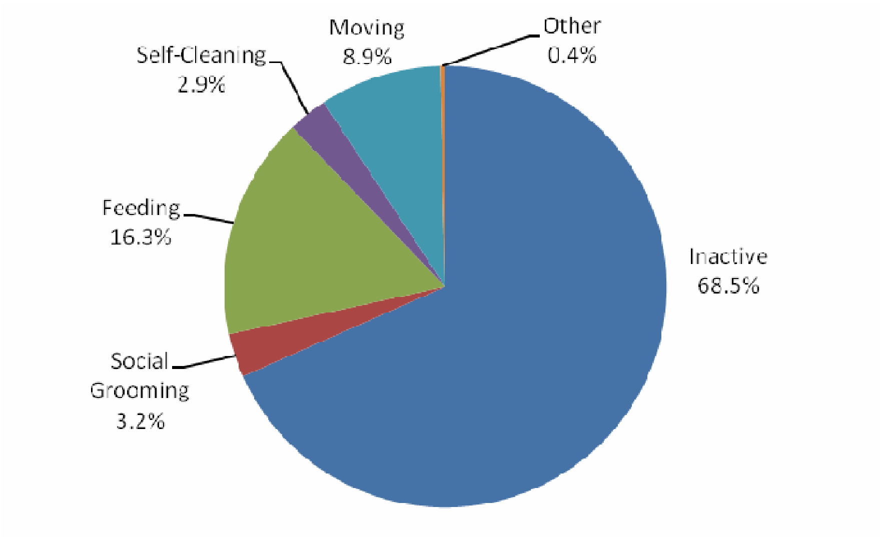

Figure 2: Time activity budget of *Colobus angolensis palliatus* in the East Sagara Forest, Tanzania, October-November 2009.

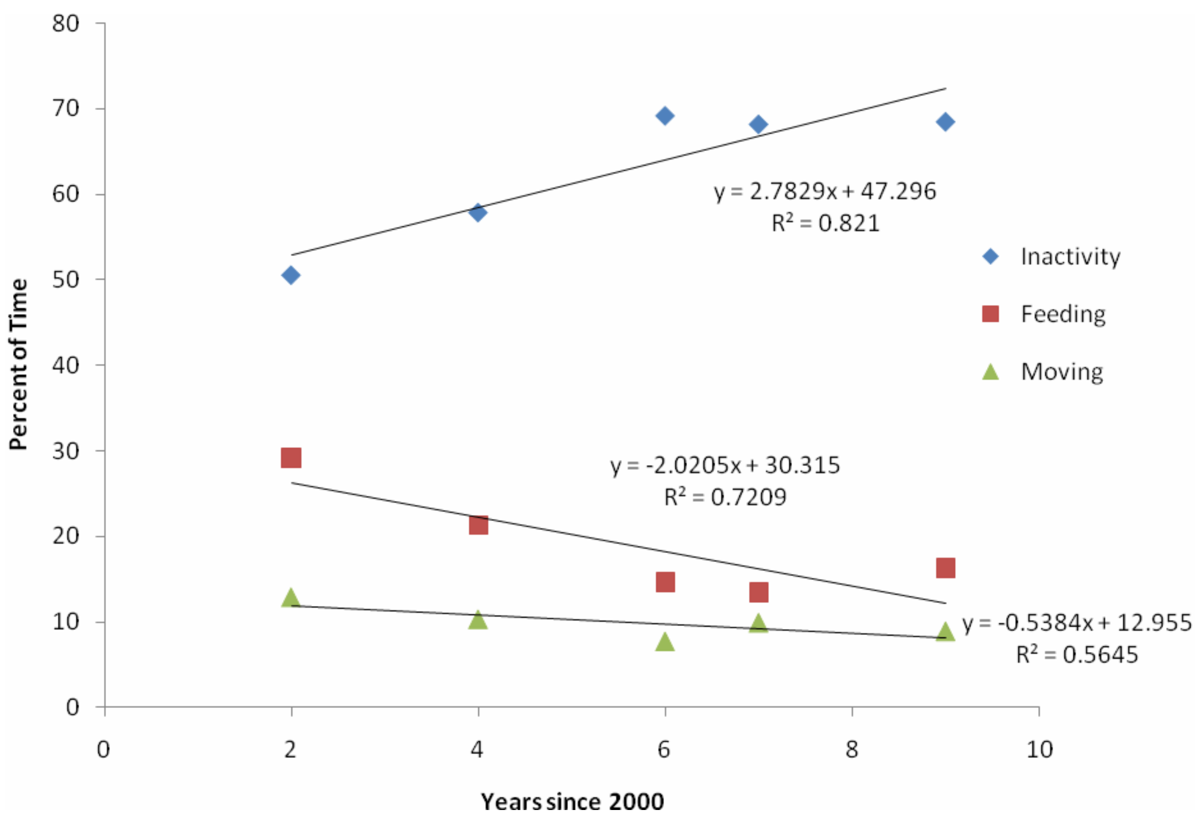

Figure 3: Activity Budget of *Colobus angolensis palliatus* in the East Sagara Forest from the fall of 2002 to the fall of 2009.

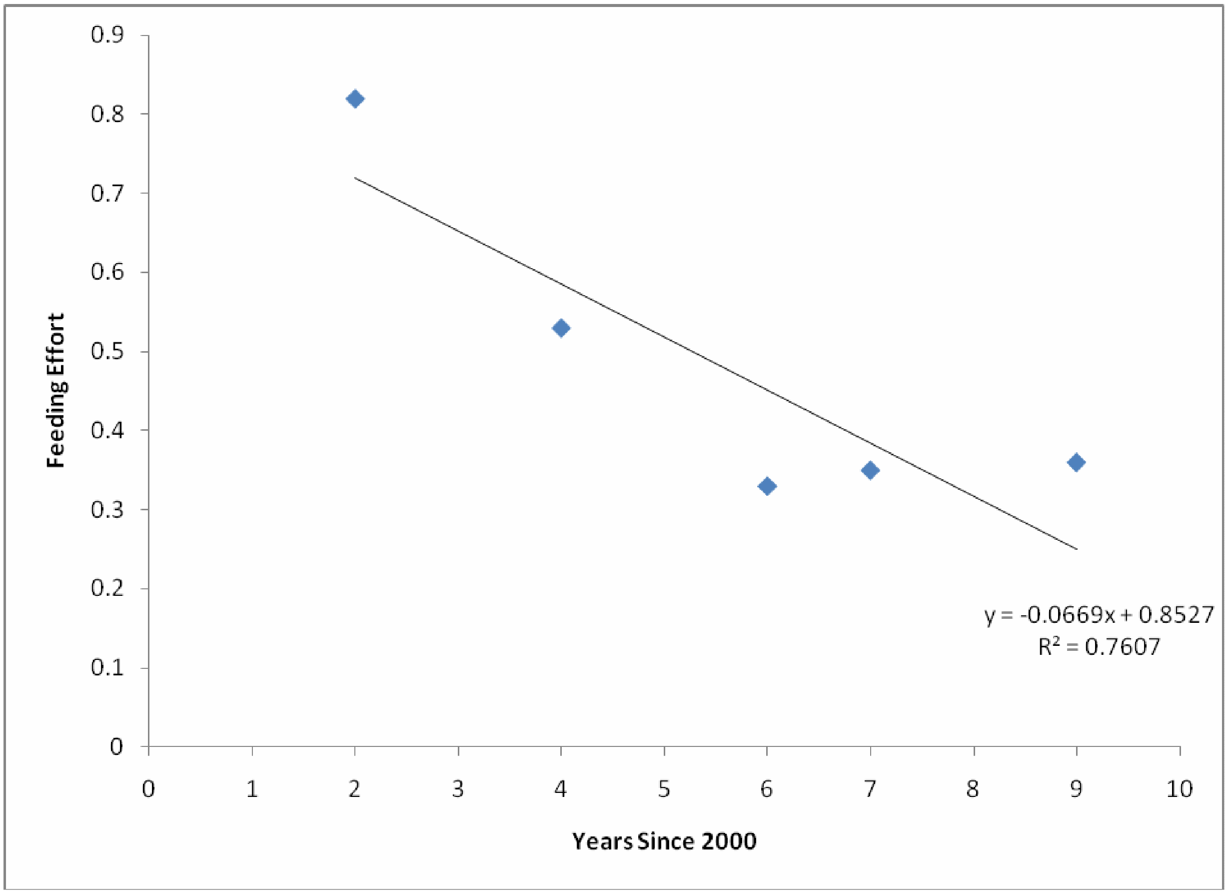

Figure 4: Feeding Effort of *Colobus angolensis palliatus* in the East Sagara Forest from the fall of 2002 to the fall of 2009.

III. Feeding Tree Identification and Selection Ratios

The colobus monkeys were observed feeding at 472 intervals on 22 different tree species from at least 15 families within the East Sagara Forest. The top five most frequently utilized feeding trees were *Albizia gummifera* (16.1%; 76/472 observations), *Syzygium guinense* (12.5%; 59/472), *Sorindeia usambarensis* (8.1%; 38/472), *Newtonia buchananii* (7.8%; 37/472), and *Cassipourea malosana* (7.6%; 36/472). Percentages of feeding and abundance for all 22 food tree species are reported in Table II. Selection ratios for food tree species are listed in Figure 4; the six food tree species not recorded in the forest survey lack selection ratios.

Tree Species	Sambaa Name	Family	% of Feeding	% Frequency in Forest[11]	Selection Ratio
Albizia gummifera	mshai	Leguminosae	16.1	4.76	33.8
Syzygium guinense	mshiwi	Myrtaceae	12.5	14.03	8.9
Sorindeia usambarensis	mkunguma	Anacardiaceae	8.1	8.11	10.0
Newtonia buchananii	mnyasa	Leguminosae	7.8	30.12	2.6
Cassipourea malosana	nekazito	Rhizophoraceae	7.6	2.19	34.7
Cynometra sp.	kimungwe	Caesalpinioideae	7.2	0.51	141.2
Ficus thonningii	mvumo	Moraceae	6.6	1.16	56.9
Parinaria excelsa	muula	Chrysobalanaceae	6.4	19.69	3.3
Trema orientalis	mshinga	Ulmaceae	4.4	0.64	68.8
Croton sylvaticus	kogho	Euphorbiaceae	4.0	2.57	15.6
Casearia englerii	mkokoko	Flacourtiaceae	3.8	3.47	11.0
Allophylus sp.	mbombwe	Sapindaceae	3.0	0.26	115.4
Ficus capensis	mkuyu	Moraceae	2.8	-	-
Grevillea robusta	mkabela	Proteaceae	2.2	-	-
N/A[12]	papata	N/A[11]	1.9	-	-
Odyendea zimmermanni	kuti	Simroubaceae	1.3	1.80	7.2
N/A[11]	ugoloto	N/A[11]	1.1	-	-
N/A[11]	mvuma	N/A[11]	0.8	-	-
Allanblackia stuhlmanii	msambu	Guttiferae	0.6	4.38	1.4
Strombosia scheffleri	sangana	Olacaceae	0.6	0.39	15.4
Acrocarpus fraxinifolius	acrocarpus	Caesalpinioideae	0.4	-	-
Margaritaria discoides/ Ochna holstii	tondoti	Euphorbiaceae/ Ochnaceae	0.4	0.39	10.3

Table II: Feeding trees by percent of feeding observations and abundance for *Colobus angolensis palliatus* in the East Sagara Village Forest, Tanzania, October-November 2009.

[11] These values are taken from the East Sagara Forest survey performed by Freierman (2008).

[12] These tree species names and family names could not be determined from their Sambaa common names.

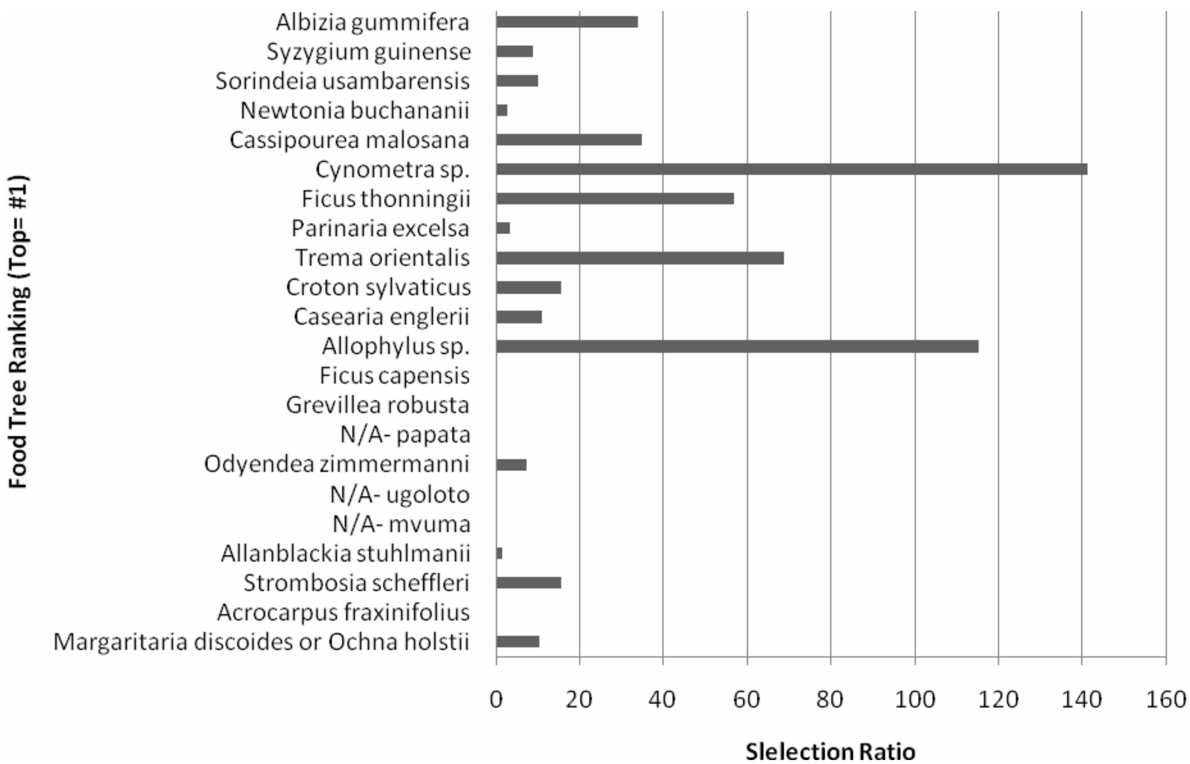

Figure 5: Selection Ratios for 22 food tree species utilized by *Colobus angolensis palliatus* in the East Sagara Village Forest, Tanzania, October-November 2009.

Discussion

I. Activity Budgets and Feeding Effort

Inactivity accounted for the largest percentage (68.5%) of *C. angolensis pallilatus*' behavior. Like most colobines, these monkeys must be inactive for long periods to digest their complex leafy diet. Also, since this folivorous diet is low in caloric content, colobus monkeys compensate by resting frequently, often for long periods of time.

Feeding was the second most frequent activity in my study (16.3%), as well as all of the previous studies. Usually the monkeys had one or two major periods of feeding per observation session. The rate of feeding, however, varied greatly. The monkeys were often noted feeding almost continuously for up to thirty minutes at a time, and other occasions alternated brief periods of feeding with inactivity for more than an hour at a time.

Moving constituted 8.9% of the troops' behavior. Moving was almost always noted just before feeding, or just before long periods of inactivity. This can be attributed to searching for feeding trees or traveling to sleeping trees.

Self-cleaning represented 2.9% of the troops' activity. This behavior was often observed while other monkeys were social grooming. The behavior usually involved scratching, especially the back and forearms, and picking through the white tip of the tail.

The percent of time spent social grooming (3.2%) lies within the range of past studies of 1.4% (Preston 2002) and 5.7% (Heinen 2006). Individuals often took turns grooming one another. In addition, social grooming usually involved cleaning areas around the anus, the large tufts of fur around the shoulders, and other areas that may be difficult to self-clean.

Activities classified as *other* constituted 0.4% of black and white colobus activity. Previous studies used the term "playing," and also noted percentages of 0.2% (Heinen 2006)- to 0.4% (Preston 2002). The term *other* was chosen to include activities that could not be considered as inactive, feeding, moving, self-cleaning, or social grooming. Activities such as: roaring and branch shaking, fighting/playing, mating, and female nursing juvenile were observed.

Since 2002, the East Sagara black and white colobus activity budgets have demonstrated general trends of increased inactivity, decreased feeding, and relatively stable movement (see

Figure 3). Of these trends, inactivity significantly increased over time ($p= .034$), feeding did not significantly decrease over time ($p= .069$), and moving stayed relatively constant ($p= .143$). Corresponding to these trends, feeding effort has largely declined since 2002, although this decrease was not significant ($p= .053$) (see Figure 4). Decreasing feeding effort could correspond with decreasing stress levels (Sapolsky 1986; Cavigelly 1999). It is possible that decreasing stress and feeding effort correlate with increasing food availability or availability of higher quality food. Since the forest officially banned the cutting of trees at the start of the twenty-first century, it is plausible to consider that in 2002 food availability could have been relatively low because of the recent widespread forest extraction. By 2009, the forest had approximately nine years to regenerate under the new management plan and seven years to recover from the first behavioral study of *C. a. palliatus* in East Sagara.

Without accurate knowledge of the extent of deforestation or regeneration occurring in East Sagara since 2002, it difficult to claim that the forest has recovered. In fact, according to locals, it is more likely that the forest has actually decreased in size since 2002 despite the new conservation oriented management plan (Mrecha pers. comm. 2009). A study by Persha and Blomley (2009) indicated illegal cutting and collecting from the East Sagara Forest is commonplace and forest guards rarely impose the monetary fines ascribed to these illegal activities. During my 15 day study alone, my forest guide and I discovered local people illegally logging on four separate occasions. Furthermore, Perhsa and Blomley (2009) report that the three most frequently harvested tree species from East Sagara are *Strombosia scheffleri, Cassipourea malosana,* and *Syzygium guineense*. The latter two species rank in the top five most frequently utilized food trees for the East Sagara colobus. If the forest is indeed shrinking and important colobus food trees are disappearing, perhaps it is more likely that the East Sagara troops are eating less as an adaptation to cope with decreasing food availability.

The phenomenon of decreasing feeding effort over the years may actually translate to higher stress levels associated with food scarcity. While this hypothesis is counter to the findings of Sapolsky (1986) and Cavigelly (1999), it is in fact consistent with findings of other primate species. Howler monkeys demonstrate the ability to cope with the stress of food scarcity by increasing their feeding effort (Dunn et al. 2010) or by decreasing their feeding effort (Silver and Marsh 2003). Black and white colobus may be similar to howlers in their ability to either seek distant food sources (*C. satanas*: McKey and Gartlan 1982; *C. guereza*: Harris et al. 2009) or adopt an energy-conserving existence to survive periods of food scarcity. It seems that forest area is likely a crucial variable in whether or not primates increase or decrease their feeding effort in response to food scarcity. Primates inhabiting small forest fragments are likely to be constrained by the size of the fragment. Without access to new food sources, primates living in forest fragments likely have little option but to decrease their feeding effort while primates in larger forests can expand their ranges to incorporate more food sources.

Onderdonk and Chapman (2000) found that the feeding effort of *C. guereza* was lower in fragments than in neighboring KNP. Similarly, Wong and Sicotte (2007) demonstrate that *C. vellerosus* feeding effort was markedly lower in fragments compared to the adjacent BFMS. Although these smaller feeding efforts outside KNP and BFMS could be the result of a disproportionately large amount of high quality food in the fragments, it seems more likely that colobine food sources are scarcer in these fragments. Extensive nutritional analysis on colobine food quality and caloric intake could help clarify this issue. Furthermore, analyzing the fecal cortisol levels of these fragment populations, including the East Sagara troops, could show whether decreased feeding efforts correlate with stress.

II. Dietary Diversity and Selection Ratios

The East Sagara black and white colobus exhibit remarkable dietary diversity. The tree species making up the largest percentage of feeding observations, *Albizia gummifera*, constitutes just 16.1% of the diet. Compared to other species of black and white colobus, particularly *C. guereza* which has been observed feeding almost exclusively on one or two tree species, these *C. angolensis* troops rely relatively equally on many species (see Appendix IV). In fact, each of the twelve most utilized food tree species account for at least 3% of the diet (see Table II). This level of dietary diversity is an asset for primates coping with forest fragmentation and food scarcity. If the data suggested that the monkeys were feeding almost exclusively on one or a few rare tree species in the forest, this would make the primates highly vulnerable to experiencing food scarcity caused by continued deforestation.

Examining the selection ratios, it is evident that the data show just the opposite response. In fact the three most abundant trees in the forest, *Newtonia buchananii*, *Parinaria excelsa*, and *Syzygium guinense*, all constitute significant portions of the Angola colobus diet (see Table II). The monkeys exhibited selection ratios of less than ten for all of these species though. In other words, the Angola colobus fed from these species less often than predicted, assuming purely random feeding behavior.

In contrast, *C. a. palliatus* utilized six species, *Albizia gummifera* (selection ratio= 33.8), *Cassipourea malsosana* (34.7), *Cynometra* sp. (141.2), *Ficus thonningii* (56.9), *Trema oreintalis* (68.8), and *Allophylus* sp. (115.4), disproportionately higher than their abundances would predict based on random selection (see Figure 5). The primates fed from *Ficus capensis*, *Grevillea robusta*, and "papata" for a combined 6.9% of feeding observations. As none of these species were recorded in the forest survey in 2008, it is safe to assume that these species are rare within Sagara and that the monkeys exhibit significantly high selection ratios for these tree species. These findings suggest that Angola colobus are highly selective feeders, choosing some species more often and avoiding others.

Primates may select certain foods based on accessibility, economic exploitation, availability throughout the year, nutritional content, or simply preference. It is likely that the East Sagara black and white colobus select certain species based on a combination of these factors. It would very interesting to discover why the monkeys acquire roughly 7.2% of their diet from *Cynometra* sp., a tree species that constitutes just 0.51% of the forest. It is likely the leaves from this tree are especially nutritious, easy to digest, and or contain a high protein to fiber ratio. Chemical analysis of the leaves could reveal why this species is so highly selected. Likewise, this analysis could reveal why species like *Allanblackia stuhlmanii*, comprising 4.38% of the forest and attributing to only 0.6% of the colobus diet, are not often selected. It is also important to note that because of the short duration of the study, the selection ratios could be misleading. A year-long analysis of *C. a. palliatus* selection ratios would be more meaningful and also account for dietary variances in relation to seasonality.

III. Future of the East Sagara Forest and its colobus monkeys

Based on the activity budgets and feeding behavior of the East Sagara black and white colobus, it is reasonable to suggest that they exhibit sufficient behavioral plasticity and dietary diversity to persist in this forest fragment. Although the other three variables (home range size, degree of frugivory, and ability to utilize matrix habitat) proposed by Marsh (2003) were not officially analyzed, it would be worthwhile to examine them, particularly whether or not the primates are utilizing the matrix habitat and if so, in what manner. The long term success of primates in fragments like the East Sagara Forest may ultimately depend on whether or not they can utilize interspersed agricultural lands as food sources and corridors to other forest patches. During my study, I witnessed two occasions when Angola colobus monkeys were running on the ground, but never across matrix habitats. Furthermore, locals reported "mbega"[13] occasionally venturing into their farmlands, but that Syke's monkeys (*Cercopithecus mitis*) were far more common and likely to utilize these habitats for food (crop raiding) and travel (Mtali pers. comm. 2009).

One of the best indicators that the East Sagara Forest is indeed a viable habitat for black and white colobus monkeys is simply that they continue to live and reproduce in the forest. Olsen (2007) observed three infants easily discernible by their characteristic all-white coats. One of the troops I observed in 2009 contained three juveniles, most likely the same three individuals observed by Olsen a year and a half earlier.

Ensuring the long term conservation of *C. a. palliatus* in the East Sagara Forest will likely foremost depend on the preservation of this forest fragment. Despite the regulations of the recently adopted forest management plan banning the cutting of trees, it is obvious that the forest is still losing trees, but at an unknown rate. It is difficult to assess the conservation value of the East Sagara Forest, as, on one hand, it is part of the East Arc Mountain Forests renown as one of the world's twenty-five hot-spots for biodiversity and surely a place worth conservation efforts. On the other hand, it sits adjacent to the much larger (3 km²) and protected Mazumbai Forest

[13] "Mbega" is the Sambaa name for Anogla colobus monkeys.

Reserve, which presumably contains every species, including black and white colobus, inhabiting the East Sagara Forest. In this regard the 0.40 km^2 East Sagara Forest fragment may unfortunately be viewed as a lost cause, destined to gradually shrink until only a few trees remain, similar to the forest fragments containing *C. guereza* outside KNP in Uganda.

Whether through large scale woodlots composed of fast growing species like *Eucalyptus* or the development of alternatives to fuel wood, significant changes will undoubtedly need to be implemented to reduce the indigenous peoples' dependency on the forest if it is to be preserved. Future ethnographic studies of the Sambaa in the area would be instrumental in better understanding how people use and think about the East Sagara Forest. Knowing what items are regularly taken from the forest and their specific functional and cultural uses will be helpful in developing better conservation policies. For instance, it may be that some items are essential to the transmission of Sambaa livelihood, while more sustainable alternatives could be devised for certain forest items. In addition, ethnoprimatological[14] studies could reveal the attitudes of locals with regard to Angola colobus. Better understanding the dynamics between people and non-human primates can help focus primate conservation initiatives.

There is reason to be optimistic as some locals do recognize the value in preserving montane forest fragments as watersheds. The neighboring Sokoine University of Agriculture-run Mazumbai Forest Reserve employs and educates about a dozen locals in the fields of forestry and conservation. Future studies analyzing locals' (Sagara Group members and those outside the group) views and opinions of forest conservation and biodiversity could reveal misconception and shortcomings with the current conservation education programs. Furthermore, analysis of existing and development of new and sustainable children's education programs will be vital in

[14] Ethnoprimatology is the study of human and non-human primate interactions.

the potential long term preservation of the East Sagara Forest. NGOs like the Tanzania Forest Conservation Group and Protect the Forest are beginning to make significant contributions to forest preservation education and practices throughout the Western Usambara Mountains. Thus, the tools and incentives are in place for the conservation of the East Sagara Forest and surely the preservation of even the smallest forest fragments are worthwhile conservation investments.

Conclusion

As primate species continue to decline across the globe, it becomes increasingly essential that primatologists discover novel means toward primate conservation. Research in fragments suggests that some forest patches may serve as vital refuges for primate populations coping with habitat destruction. Still, the reality is that many forest fragments, particularly those with large human populations nearby, are likely to be cleared and rendered inhospitable for primates.

It is well understood that primate species react differently to fragmentation and achieve varying levels of success in forest fragments. Home range size, level of frugivory, behavioral plasticity/ dietary flexibility, and ability to utilize matrix habitats are the key variables influencing the likelihood of a primate species inhabiting and persisting in forest fragments (Marsh 2003). Studies suggest black and white colobus monkeys, like South American howler monkeys, are well-equipped to persist in fragments as small as .05 km^2 because of their small home ranges, high degree of folivory, and dietary flexibility/ behavioral plasticity. This study in the East Sagara Forest of Tanzania affirms that *C. a. palliatus* exhibit remarkable dietary diversity and may be altering their behavior to cope with food scarcity. Long term follow-up studies are required to better analyze these variables and thus more accurately assess the likelihood of this forest fragment sustaining Angola colobus.

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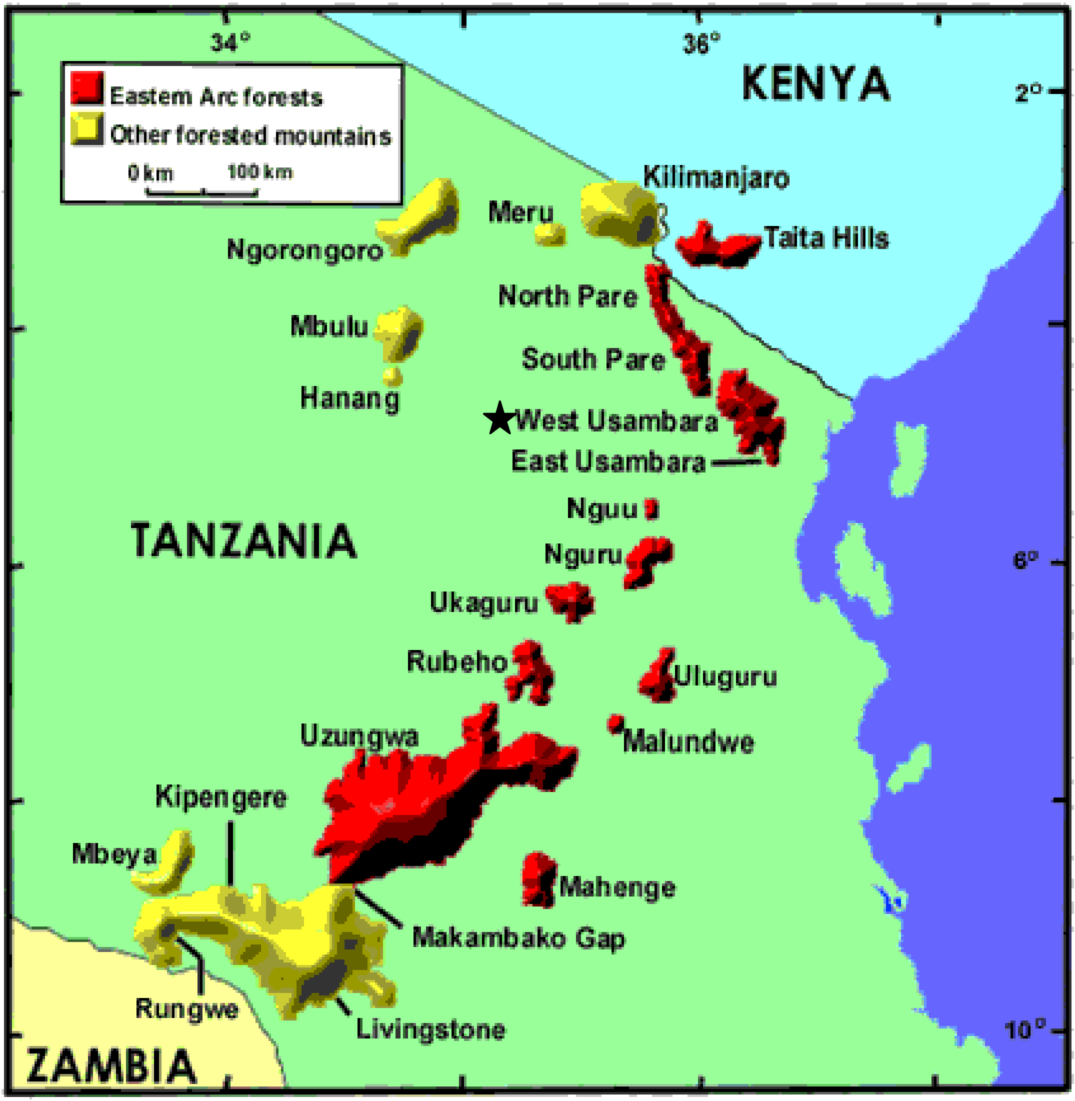
Appendix 1- Map of the Eastern Arc Mountains



Source: Eastern Arc Mountains Conservation Endowment Fund. www.easternarc.or.tz/eastarc

Appendix II- Diet Composition by Food Part for Black and White Colobus Monkeys

Species	Study Site	YL	ML	UL	TL	FR/SD	Other	Reference
C. angolensis	Ituri, D.R. Congo	26	2	22	50	28	22	Bocian (1997)
C. angolensis	Nyungwe, Rwanda	30	7	1	38	23	38*	Fashing et al (2007)
C. angolensis	Nyungwe, Rwanda	25	40	7	72	17	11	Fimbel et al (2001)
C. angolensis	Diani Beach, Kenya	-	-	57	57	32	11	Moreno-Black and Naples (1977)
C. guereza	Ituri, D.R. Congo	30	4	24	58	25	18	Bocian (1997)
C. guereza	Kibale (big group), Uganda	85	4	0	89	7	3	Chapman et al 2007, Chapman pers. comm.
C. guereza	Kibale (small group), Uganda	78	6	0	84	10	7	Chapman et al 2007, Chapman pers. comm.
C. guereza	Kibale (fragment), Uganda	65	14	0	79	12	9	Chapman et al 2007, Chapman pers. comm.
C. guereza	Kakamega, Kenya	24	7	23	54	39	9	Fashing (2001)
C. guereza	Kibale, Uganda- Batekaine	52	27	12	91	2	7	Harris and Chapman (2007)
C. guereza	Kibale, Uganda- Basaijia	69	21	4	94	3	3	Harris and Chapman (2007)
C. guereza	Kibale, Uganda- Mzee	55	28	3	89	4	7	Harris and Chapman (2007)
C. guereza	Kibale, Uganda- Kasembo	42	42	6	90	4	6	Harris and Chapman (2007)
C. guereza	Kibale, Uganda- Bwango	59	26	5	90	7	3	Harris and Chapman (2007)
C. guereza	Kibale, Uganda- Zikuru	67	13	4	84	11	5	Harris and Chapman (2007)
C. guereza	Kibale, Uganda- Birungi	67	15	1	84	11	5	Harris and Chapman (2007)
C. guereza	Kiblae, Uganda- Mugenyi	65	9	5	79	19	2	Harris and Chapman (2007)
C. guereza	Kibale, Uganda	65	13	3	81	15	4	Oates (1977a,b)
C. guereza	Kiblae, Uganda- Rutoma 1	56	4	18	83*	15	2	Onderdonk and Chapman (2000)
C. guereza	Budongo (unlogged), Uganda	-	-	63	63	29	8	Plumptre (2006)
C. guereza	Budongo (logged), Uganda	-	-	51	51	40	9	Plumptre (2006)
C. guereza	Kibale (logged), Uganda	79	7	0	86	6	8	Wasserman and Chapman (2003)
C. guereza	Kibale (Kanywara), Uganda	76	6	0	80	7	12	Wasserman and Chapman (2003)
C. guereza	Kibale (fragment), Uganda	60	22	0	82	7	10	Wasserman and Chapman (2003)
C. guereza	Kibale (Kanywara), Uganda	64	13	0	77	8	14	Wasserman and Chapman (2003)
C. polykomos	Tiwai, Sierra Leone	30	26	2	58	35	6	Dasilva (1989,1992)
C. polykomos	Tai, Ivory Coast	28	20	0	49	48	4	Korstjens et al (2006)
C. satanas	Foret des Abeilles, Gabon	35	3	0	38	50	12	Gautier-Hion et al (1993)
C. satanas	Lope, Gabon	23	3	0	26	60	8	Harrison (1986)
C. satanas	Douala-Edea, Cameroon	21	18	0	39	53	8	McKey and Waternab(1982)
C. vellerosus	Boabeng-Fiema, Ghana (B1)	40	34	0	74	16	10	Wong and Sicotte (2007)

YL= young leaves, ML= mature leaves, UL= unidentified leaves, TL= total leaves, FR/SD= fruits and seeds, Other= flowers, insects, lianas, lichens, and other foods.

Appendix III- Activity Budgets and Feeding Effort of Black and White Colobus Monkeys

Species	Study Site	Group Size (mean)	Home Range (km²)	Feed (%)	Move (%)	Rest (%)	Social (%)	Other (%)	Feed Effort -	Reference
C. angolensis	East Sagara, Tanzania	-	-	14	10	68	-	-	0.35	Olsen (2007)
C. angolensis	East Sagara, Tanzania	-	-	15	8	69	-	-	0.33	Heinen (2006)
C. angolensis	East Sagara, Tanzania	-	-	16	9	69	-	-	0.36	This Study (2009)
C. angolensis	East Sagara, Tanzania	-	-	21	10	58	-	-	0.53	Fox (2004)
C. angolensis	East Sagara, Tanzania	-	-	29	13	51	-	-	0.82	Preston (2002)
C. angolensis	Ituri, D.R. Congo	14	3.71	27	24	43	5	1	1.19	Bocian (1997)
C. angolensis	Nyungwe, Rwanda	>300	24.40	42	20	32	5	1	1.94	Fashing et al (2007)
C. guereza	Entebbe, Uganda	7	.08	20	12	58	10	1	0.55	Grimes (2000)
C. guereza	Ituri, D.R. Congo	8	1.00	19	22	52	5	2	0.79	Bocian (1997)
C. guereza	Kakamega, Kenya	13	.18	26	2	63	7	2	0.44	Fashing (2001)
C. guereza	Kibale (big group), Uganda	9	-	42	3	47	6	1	0.96	Chapman et al 2007, Chapman pers. comm.
C. guereza	Kibale (fragment), Uganda	6.5	-	30	8	54	8	1	0.70	Chapman et al 2007, Chapman pers. comm.
C. guereza	Kibale (logged), Uganda	-	-	32	8	53	6	1	0.75	Chapman et al 2007, Chapman pers. comm.
C. guereza	Kibale (small group), Uganda	6	-	28	17	50	5	1	0.90	Chapman et al 2007, Chapman pers. comm.
C. guereza	Kibale, Uganda	11	.28	20	5	57	11	7	0.44	Oates (1977)
C. guereza	Kiblae, Uganda- Rutoma 1	5	-	17	6	69	6	2	0.33	Onderdonk and Chapman (2000)
C. polykomos	Tiwai, Sierra Leone	11	.24	28	9	61	1	1	0.61	Dasilva (1989,1992)
C. satanas	Douala-Edea, Cameroon	15	.60	23	4	60	14	0	0.45	McKey and Waternab(1982)
C. vellerosus	Boabeng-Fiema, Ghana (B1)	14	-	24	15	59	2	0	0.66	Teichroeb et al (2003); Wong and Sicotte (2007)
C. vellerosus	Boabeng-Fiema, Ghana (B2)	-	-	23	17	58	2	0	0.69	Teichroeb et al (2003); Wong and Sicotte (2007)
C. vellerosus	Boabeng-Fiema, Ghana (fragments (AK)	14	-	19	8	71	2	0	0.38	Wong and Sicotte (2007)
C. vellerosus	Boabeng-Fiema, Ghana (fragments (BS)	-	-	23	8	66	3	0	0.47	Wong and Sicotte (2007)
C. vellerosus	Boabeng-Fiema, Ghana (fragments (BT)	-	-	23	5	68	3	0	0.41	Wong and Sicotte (2007)
C. vellerosus	Boabeng-Fiema, Ghana (WW)	-	-	24	12	60	4	0	0.60	Teichroeb et al (2003); Wong and Sicotte (2007)

Appendix IV- Dietary Diversity by Top Tree Species for Black and White Colobus Monkeys

Species	Top Tree Species	% of diet	Location	Reference
C. angolensis	*Albizia gummifera*	16%	Sagara, Tanzania	This Study
C. guereza	*Celtis durandii*	71%	Bigodi, Uganda	Clutton-Brock (1975)
C. guereza	*Celtis durandii*	88%	Kanywara, Uganda	Clutton-Brock (1975)
C. guereza	*Celtis durandii*	42%	Kibale, Uganda	Harris and Chapman (2007)
C. guereza	*Celtis durandii* and *Albizia grandibracleala*	70%	Kibale, Uganda	Harris et al (2009)
C. guereza	*Celtis durandii* and *Albizia grandibracleala*	75%	Kibale, Uganda	Harris et al (2009)
C. satanas	3 species	65%	Douala-Edea, Cameroon	McKey and Waternab (1982)