THE UNIVERSITY OF CALGARY

Guereza Dietary and Behavioural Patterns at the Entebbe Botanical Gardens

by

Kristin H. Grimes

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE

DEGREE OF MASTER OF ARTS

DEPARTMENT OF ANTHROPOLOGY

CALGARY, ALBERTA

March, 2000

0-612-49567-1

Abstract

This study investigated the utilization of a human altered environment by *Colobus guereza* living in the Entebbe Botanical Gardens, Uganda. The dietary options available to the three troops of guerezas included a broad range of novel and exotic foods. The guerezas fed on eighty-one identified species of trees, shrubs, and vines. Of these 25.9% are exotics. The study revealed a 50 to 60% overlap in species eaten by the individual troops. Instantaneous feeding samples were found to be significantly different between the three troops. All leaf types (including mature and new leaves, and shoots) made up 83% of the overall diet. Plant part consumption was found to differ significantly between the troops. These results, in comparison to published data on guereza diet, indicate that the species is more adaptable than previously estimated.

Acknowledgments

I would like to thank all of the people who provided time, energy, laughter, and support in helping me complete this thesis. Dr. James D. Paterson, my advisor and friend who encouraged and supported me, Thank you. I am grateful to all of the members of my thesis and proposal committees for their ideas and support: Dr. Pascale Sicotte, Dr. Rob Longair, Dr. Mary S.M. Pavelka, and Brian Keating.

I am indebted to Myrna Haglund, May Ives, and Jill Ogle the amazing staff in the Department of Anthropology, without whom the other students and I would spend many hours lost. You made the process easier and more fun.

In Uganda, I would like to thank: John Mulumbg Wasswa, Curator of the Entebbe Botanical Gardens, Rose Mutonyi Masaaba, Resident District Commissioner, Mipigi District, and the Uganda National Council for Science and Technology for giving me permission to collect data in the Botanical Gardens; Lynn Nakayenze provided invaluable information about the Gardens; Mary Namaganda and Olivia W. Maganyi, the wonderful staff at the Makerere University Herbarium for helping me identify plants. I am also indebted to Debby Cox, Uganda Chapter of the Jane Goodall Institute for her support and friendship and to Keith, Barb, Jim, Mary, and the girls who opened their homes and provided invaluable friendship during the study.

I am grateful to the Primate Information Center, Washington for providing the initial guereza bibliography to get me started on this project; to Dr. David Paterson and Janette Latta at the Royal Botanical Gardens Edinburgh for allowing me access to a previous survey; to Katie Fawcett at the Scottish Primate Research Group for her help; Gisela Engels, Dr. John Oates, Dr. Colin Chapman, Noel Rowe, Dr. Tom Struhsaker, and Kirstin Siex for sharing their knowledge.

I would like to acknowledge the Department for financial support in the form of a University of Calgary Research Scholarship and an initial travel grant to facilitate the preliminary study completed at the San Diego Zoo; the Faculty of Graduate Studies for a Thesis Travel Grant; and the University of Calgary International Centre for an International Scholarship.

I would like to thank my parents for enthusiasm, motivation, scholarship, and editing; Shawna, Dave, and Kara for opening their home to me; Diane, Randy, Paul, and Karla; the other primatology students at the University of Calgary who shared this process - Sarah Jazrawi, Brad McVittie, Hugh Notman, Sera Parsons-Blair, Tania Saj, Tamaini Snaith, and Julie Teichroeb. Lastly, I would like to especially thank Donna Sheppard whose friendship, ideas, and laughter was and is invaluable.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

CHAPTER ONE

INTRODUCTION

Home range size, population density, social behaviour, group size, and composition of primates are all affected by diet (Chapman and Chapman 1999, Fleagle 1999, Altmann 1998, Yeager and Kirkpatrick 1998, Oates 1987, Chapman 1985, Struhsaker 1975). Dietary specializations allow animals to exploit a certain food type, which in turn affects many aspects of an animal's life. For example, the readily abundant leaves allow folivores to live in smaller home ranges and have a greater overall population density than frugivores who, due to the seasonal variation in individual fruit trees, need to travel greater distances to obtain enough food. In addition, the lower digestibility of leaves results in folivores spending more time resting than do primates that feed on high energy, easily digested fruit (Oates 1987).

The study of dietary and behavioural plasticity is of prime importance if we are to understand a primate's ability to adapt to their ever-changing environment (Chapman and Lambert 2000, Lowe and Sturrock 1998). To date, there have been very few studies conducted to examine the differences between neighboring primate troops in a similar habitat (Chapman and Chapman 1999, Chapman and Fedigan 1990).

Habitat destruction has the greatest influence on primate populations (Oates 1977c), resulting in many species becoming endangered. Although guerezas (*Colobus guereza*) are not listed presently as an endangered species and seem to prefer disturbed habitats (thereby allowing them to be more ecologically flexible), Altmann and Muruthi (1988) state that even species that seem to be successful may have long term conservation problems. By increasing our knowledge of the ways in which primates adapt to novel foods and habitats, we will better understand future changes that groups may go through to survive, and thus we can improve the management of these groups (Chapman and Lambert 2000, Siex and Struhsaker 1999, Saj 1998, Altmann and Muruthi 1988).

One way habitat is changing is through the introduction of exotic species. Traditionally, in native habitats, there are few circumstances in which nonhuman primates have had access to exotic plants. However, due to the encroachment of humans upon game parks, national parks, wildlife preserves, and other animal habitats the effects of humans on wildlife are escalating. In many areas of Africa the use of exotic species by humans is increasing. For example, individual exotic tree species are being incorporated into small-scale farms and, in some cases, large areas of native habitat are being taken over for plantations of exotic trees. In Uganda, Oates (1977a) records the native flora in the Mafuga Forest Reserve as having been entirely replaced with exotic conifers and eucalyptus species. In Kenya, Moreno-Black (1974) found the anthropogenic effects on the natural forest of her study site to include the introduction of ornamental plants. In Tanzania, Siex and Struhsaker (1998, 1999) record half the Zanzibar red colobus (*Procolobus kirkii*) residing in agriculture areas, outside the native forest preserves.

At the time this research was being carried out, no previous field research had been undertaken to examine guerezas in unusual habitats or the use of exotic foods in their diets. As well, there are few studies available on the use of exotic plant species by any other primate species (see Siex and Struhsaker 1999, Rowe 1996, Bicca-Marques and Calegaro-Marques 1994, Ganzhorn 1987).

Original guereza studies were completed by Clutton-Brock (1975), Dunbar and Dunbar (1974), Marler (1969, 1972), Oates (1974, 1977a, 1977b, 1977c, and 1978), and Struhsaker (1978). The research work conducted after these initial studies, was limited in both depth and study duration. Many of the researchers focused on a specific aspect of guerezas' life (i.e., Morbeck's studies on positional behaviour and the use of substrates 1974, 1977, and 1979). While important data is revealed, the parameters of these studies allow few overall comparisons to be made with regard to feeding and social behaviour. The exception to this is the 1994 book 'Colobine Monkeys: Their Ecology, Behaviour, and Evolution' edited by A.G. Davies and J.F. Oates. This book provides an overview of colobine populations both in Asia and Africa, including general social organization, diet, activities, and ranging patterns. While *Procolobus badius* and *Colobus guereza* have been the two species most focused on in previous African colobine studies, research on other black and white colobus species include Davies, et *al.* (1999), Lowe and Sturrock (1998), Bocian (1997), Gautier-Hion, et *al.* (1997), Dasilva (1992, 1994), Oates, et *al.* (1994), Baranga (1986), Gautier-Hion (1983), Oates and Trocco (1983), McKey and Waterman (1982), Moreno-Black and Bent (1982), McKey, et *al.* (1981), and Groves (1973).

RESEARCH OBJECTIVES

In this thesis, I presented the dietary and behavioural activities of three troops of guereza monkeys residing in the human altered habitat of the Entebbe Botanical Gardens, Uganda. I described what food choices are made by guerezas when exposed to both native and exotic plants and how a seemingly highly adapted folivorous primate lives in a human modified environment. In addition, I documented differences among three troops inhabiting a limited area (35 hectares) to expose small-scale variation.

In order to accomplish this I examined five components that included: diet, ranging patterns, activity budget, group composition, and social behaviour. Descriptions were made between these three guereza troops and compared with the existing data on troops living in natural habitats. Inter-troop descriptions were made to determine if dietary and activity patterns were altered in a similar manner by the three troops.

The five research objectives examined in this thesis include:

1. A description of the diet of the three troops, including the breakdown of food parts eaten will be provided. I examine the relationship between the consumption of exotic and native plants by exploring any changes made to the guereza diet when exposed to a human modified environment and exotic plants.

2. I investigate day range, home range size, and sites of inter-troop conflict. This will indicate how the available resources in the Entebbe Botanical Gardens influence the guereza's ranging behaviour.

3. I examine the connection between diet and the proportion of time spent in different activities (both between the individual troops as well as within age-sex categories).

4. Size and composition of the troops at the Botanical Gardens will be reported. I will describe the demographic changes during the course of the study.

5. Finally, I will compare inter- and intra- troop encounters in the human modified environment of the Botanical Gardens to what is known of *Colobus guereza* in the wild, in order to identify differences in "behavioural adjustments". In addition, I make comparisons between the studies on diet and social behaviour in native habitats and the guerezas residing in the Entebbe Botanical Gardens. This study provides preliminary exploration into the options guerezas have when exposed to new foods and habitats.

I will also compare these three troops amongst each other. Examining three troops reveals the guerezas ability to survive in different habitats and exposes dietary options available to guerezas when presented with novel foods. Comparisons are made that indicate variability and flexibility in previously perceived fixed-diet species. Although it should be noted that the perceived notion of the guereza's lack of dietary variation may be due to a shortage of existing dietary data.

CHAPTER TWO

OVERVIEW OF GUEREZAS AND ADJUSTMENT TO EXOTIC FOODS AND HABITATS

Introduction

This chapter provides a review of the existing data on guereza habitat and ranging behaviour, social structure, diet, and the interactions between other troops and species. In addition, the relevant literature on the use of exotic foods and primates residing in a human altered habitat is presented. Finally, a history of the study site is provided.

A Review of The Literature On Guerezas

Members of the subfamily Colobinae are adapted to a folivorous diet that is generally inadequate for other primates (Altmann 1998). Colobines include approximately 30 species found in both Asia and Africa (Oates and Davies 1994, Oates 1977a, Leskes and Acheson 1970). There are two distinct subgroups of African colobus monkeys including *Procolobus* (the red and olive colobus) and *Colobus* (the black and white colobus). There are five species of black and white colobus (including - *Colobus angolensis*, *C. guereza*, *C. polykomos*, *C. satanas*, and *C. vellerosus*) (Lowe and Sturrock 1998, Rowe 1996, Oates et *al*. 1994, Oates and Trocco 1983, Oates 1977a and c). Physiological and anatomical adaptations of black and white colobus include a sacculated stomach and elongated intestines. In addition, their elongated hands, lack of a thumb, and the rather specialized locomotion pattern (for arboreal quadrupeds) allow for their remarkable leaping ability (Struhsaker and Leland 1987, Baranga 1982, 1986, Morbeck 1977, Freeland and Janzen 1974, Moreno-Black 1974). Guerezas generally live in drier habitats and have a more limited diet than other colobus species (Kingdon 1997, Baranga 1986, Clutton-Brock 1979, Struhsaker 1978).

Plate 2.1: Adult guereza female (*Colobus guereza*), member of the Natural Forest troop. Note broken ano-genital white 'ring'.

The guereza (*Colobus guereza*, Rüppell 1835) (= *abyssinicus*) is found across equatorial Africa. Guerezas are distinguished from the other black and white colobus species "in the teeth (e.g. small incisors, longer molars, large female canines) and face (e.g. broader nasal apertures)" (Oates et *al.* 1994:50). Guerezas have been described as unenergetic, quiet animals that can spend up to 80% of their day sitting (Altmann 1998, Stanford as referenced in Rowe 1996, Rose 1979, Morbeck 1977, Dunbar and Dunbar 1974, Moreno-Black 1974, Poirier 1974). Although the exact number is unknown, there are several subspecies of *Colobus guereza* distinguished by differences in pelage characteristics (Stanford 1998, Oates 1977a, 1994, Lehn, no date).

Guerezas are easily recognizable by the dramatic 'U' shaped mantle of white fur that runs across their back and shoulders, the shorter white hair that forms a mask around the dark face, and the white tail tip (Burton 1995, Oates and Trocco 1983, Oates 1977a, Marler 1972) (Plate 2.1). Guerezas express a 69% – 72% sexual dimorphism rate, with males weighing 9 to 14.5 kg, compared to a weight range of 6.5 to 10 kg for females (Rowe 1996, Oates, et *al.* 1994, Oates 1977a and c, Marler 1969).

Home Range and Population Density

Guerezas reside in colonizing, riparian, and upland forests, with some preference for water edges. They favor the main canopy levels in the forest and partially disturbed habitats, especially secondary forests (Fleagle 1999, Gillespie, et *al.* 1999, Thomas 1991, Oates 1977a, Kingston 1971). Home ranges are small (0.02 to 21.6 hectares), with animal density ranging between 0.2 - 5 individuals per hectare (Fashing and Cords 2000, Fleagle 1999, Krüger, et *al.* 1998, von Hippel 1998, Mitani and Rodman 1979, Strusaker and

Oates 1979, Suzuki 1979, Rose 1979, Oates 1977b and c, Dunbar and Dunbar 1974, Marler 1972, 1969, Schenkel and Schenkel-Hulliger 1967).

Guerezas are found at a higher density in disturbed habitats than in undisturbed, which is unusual for an arboreal species (Chapman and Lambert 2000, Oates 1996). For example, in a slightly disturbed forest compartment (in Kibale Forest, Uganda) where red colobus (*Procolobus badius*) populations had declined by one-third, the guerezas had increased their numbers by almost five times (from 22 to approximately 100 individuals/km^2) (Oates 1977c). Dunbar (1987) found a biomass three times higher in the species-poor gallery forests of Bole, Ethiopia than in the swamp forests of Kibale, Uganda. Guerezas can be found not only in secondary forest but also in "extremely degraded" small patches of residual forest (Gillespie, et *al.* 1999, Struhsaker 1997:188, Dunbar 1987, Oates 1977b). Oates (1996) and Davies (1994) suggest that one explanation for this ability to reside in disturbed habitats is that colonizing plants (plants that are short-lived and fast growing) provide fewer chemical defenses than climax species and would therefore contain fewer toxins than the mature climax leaves.

There is a relationship between group type and size with the habitat the group lives in (Struhsaker 1997, von Hippel 1996). Struhsaker (1997) found variation in group size to be related to habitat type with larger troops found in mature forests and smaller troops in disturbed areas. Von Hippel (1996) suggests that the number of adult males in a troop is also related to habitat type. Since habitat type affects group size and the size of the group determines the number of adult males, smaller uni-male troops will be more likely to reside in riparian habitats while larger multi-male troops will reside in continuous forests. A few studies have recorded fission between members of a troop (Bocian 1997, Dunbar 1987, Suzuki 1979, Dunbar and Dunbar 1974).

Day Range

The movements of troop members tend to be coordinated, with individuals rarely more than 15 minutes behind the lead animal (Oates 1977b, Dunbar and Dunbar 1976). Two movement patterns were recorded: either the animals would move in short bursts interspersed with scanning and feeding, or they would move to one site with a longer feeding stop, usually followed by a rest period (Dunbar and Dunbar 1974). Average day travel length, recorded over eight studies, was 447 meters (range: 0 - 1840 meters) with animals observed in the same hectare and even feeding in the same tree throughout the day (Fleagle 1999, Bocian 1997, Dunbar 1987, Struhsaker and Leland 1987, Oates 1977b and c, Dunbar and Dunbar 1974, Leskes and Acheson 1970). Struhsaker (1975) found that the reliance upon a continuously available food source as well as the small troop sizes allows for shorter day and monthly ranges.

Home Range Overlap

Guerezas have sections of defended, exclusive territories and sections of shared overlapping home ranges (von Hippel 1996, Suzuki 1979, Struhsaker 1975, Dunbar and Dunbar 1974, Poirier 1974, Marler 1969). Troop home ranges have been found to overlap 35% to 100% with one or more neighboring troops (Krüger, et *al.* 1998, von Hippel 1996, Oates 1977c). Studies that recognized the existence of a defended territory record sizes between 0.2 and 2.75 hectares (Krüger, et *al.* 1998, Oates 1977c).

<u>Social Structure</u>

The majority of recorded guerezas live in small social groups (2 to 19 animals) consisting of one to three adult males, three to five adult females, and their offspring (Bocian 1997, von Hippel 1996, Oates 1977a, Rose 1977, 1979, Oates 1977a and c, Struhsaker 1975, Groves 1973, Marler 1972) (Table 2.1). Guereza troops are either uni- or multi- male (Krüger, et *al.* 1998, von Hippel 1996, Suzuki 1979, Oates 1977a and c, Struhsaker 1975, Marler 1969, 1972). Of 118 studied troops, 32% were found to contain more than one adult male with no more than five males recorded in a single troop (Krüger, et *al.* 1998, von Hippel 1996, Dunbar 1987, Suzuki 1979, Oates 1977b and c, Dunbar and Dunbar 1974). Solitary males have also been observed (Marler 1969, 1972, Leskes and Acheson 1970).

Except for recognition of the alpha male, no clear hierarchy (among other group members) has been established in the majority of studies, in either uni- or multi- male troops. Males hold the alpha position for an average of three to four years and rarely interact socially with the other members of the troop. Males are the most active participants during inter-troop confrontations (Oates 1977c, Leskes and Acheson 1970, Marler 1969).

Table 2.1: Guereza Studies.

Study	**Study Site**	**# of Study Months**	**Total Number of Groups**	**Mean Group Size (range)**
Fashing & Cords, 2000	Kenya	4	5	?
Krüger, et *al.* 1998	Uganda	5	24	7.4 (3-13)
Bocian, 1997	Zaire	?	3	8
von Hippel, 1996	Kenya	3	18	12
Dunbar, 1987	Ethiopia	1	12	7 (3-10)
Struhsaker & Leland, 1987	Uganda	?	?	12
Rose, 1979	Kenya	12	1	19
Suzuki, 1979	Uganda	36	21	7 (2-13)
Oates, 1977b	Uganda	30	2	7
Oates, 1977c	Uganda	24	7	11
Clutton-Brock, 1975	Uganda	3	4	9
Struhsaker, 1975	Cameroon	?	1	8
Dunbar & Dunbar, 1974	Ethiopia	22	18	6
Morebeck, 1974	Kenya	3	1	11
Groves, 1973	Tanzania	2	5	8.3 (5-18)
Kingston, 1971	Kenya	?	110	4.95[1]
Leskes & Acheson, 1970	Uganda	1.25	1	12
Marler, 1969	Uganda	8	13	8 (2-13)
Schenkel, et *al.* 1967	Kenya	6	4	9.8 (6-15)
Ullrich, 1961[2]	Tanzania	6	1	13

Table partially adapted from von Hippel (1996).
[1] Based on survey data, possible underestimate.
[2] Ullrich data presented in Struhsaker (1975) and Marler (1972).

Guerezas seem to exibit a male dispersal pattern with the females residing in their natal troops. Although males are the emigrators they do not appear to be aggressively forced out of their natal troop (Dunbar and Dunbar 1976).

Reproduction and Mortality

Female guerezas mature, on average, two years prior to males, do not have a breeding season, and show no external signs of estrus (Struhsaker and Leland 1987, Clutton-Brock

1979, Dunbar and Dunbar 1976). Oates (1977c) and Dunbar and Dunbar (1976) found females to be the most common initiators of mating, with either single or multiple mountings.

Birth rates have been recorded between 0.5 and 0.6 births per female per year (Oates 1977a, Dunbar and Dunbar 1974). Infants are born white and change to the adult pelage gradually over their first 2.5 to 7 months of life (Oates 1977c, Horwich and Manski 1975, Struhsaker 1975, Marler 1972, Wooldridge 1971). During the first pelage stage, infants are attractive to other members of the troop and are regularly carried by females other than their mothers (Oates 1977c, Struhsaker 1975). Leskes and Acheson (1970) found 26% of the infant transfers to be unsuccessful, with one or more of the participants resisting the transfer. Studies found that all females have access to any infant, regardless of the female's position within the troop, with mothers spending less time carrying their infants than do the other combined female troop members (Horwich and Manski 1975, Poirier 1974). McKenna (1979) hypothesized that the leaf diet allows this high level of infant transfer. With the reduced need for both competition and a strong hierarchy dominance would not interfere with a female attempting to retrieve her offspring. Thus she will be more lenient when others show interest in carrying her infant.

Mortality occurs from disease, loss of habitat, falls, predation, and hunting (for meat, ceremonial costumes, and "genuine and suspected crop raiding") (Stanford 1998, Kingdon 1997, Teelan and Klingel 1994, Oates 1977a:421). Oates (1977a) states that he has not observed crop raiding but since guerezas travel and feed on the ground, it is possible that crop raiding occurs.

Feeding Behaviour

Both single and multiple peak daily feeding periods have been recorded (Rose 1979, Oates 1977b, Dunbar and Dunbar 1974). Studies in which more than one feeding peak takes place result in a daily pattern that includes: feeding, followed by inactivity, followed by movement, and then repeated. Individual feeding bouts last between one and two minutes (Oates 1977b). Generally very little food manipulation occurs during guereza feeding bouts. Bark is obtained by stripping off sections with the teeth. Leaves are obtained by either holding onto the branch and biting off the leaves directly or holding onto the branch with one hand while striping the leaves off with the other. This less adept method of food gathering is related to the reduced thumb and "lack of a precision hand-grip" (Davies, et *al.* 1999, Oates 1977b:288, Clutton-Brock 1975, Groves 1973).

Oates (1977b) found individual troop members were coordinated when starting to feed, even when animals were feeding from different species or plant parts, the majority of the troop would feed simultaneously. Feeding sites tended to be either a single large tree or several trees in a limited area (Oates 1977b). Throughout the day the guerezas changed feeding sites as well as the species being fed upon. Clutton-Brock (1975) found that a change in site and/or species was not linked to any visible decline in availability of the first species. It is unknown if these changes were made in order to add variety to the diet, to avoid accumulation of toxins, or for other reasons.

Diet

The major types of plant parts found in the guereza diet, in descending order of preference, include young leaves, fruit, and mature leaves, with all other food types (i.e., flowers, shoots, bark) making up less than 10% of the complete diet (Oates 1977b). Leaves make up 56% to 92% of the overall diet, with fruit and flowers making up 8% to 53% (see Table 5.2) (Fashing 1999, Bocian 1997, Plumptre et *al.* 1994, Dunbar 1987, Struhsaker and Leland 1987, Baranga 1986, Gautier-Hion 1983, Gautier-Hion et *al.* 1980, Rose 1979, Oates 1977b, Clutton-Brock 1975, Dunbar and Dunbar 1974, Oates 1974 as referenced in Dasilva 1994). Variation in the breakdown of plant parts in the guereza diet has been attributed to seasonal availability (Kirkpatrick 1999, Lowe and Sturrock 1998, Baranga 1986, Gautier-Hion 1983, Clutton-Brock 1975).

In addition to plant material, a few studies record guerezas feeding on animal material (including termite reproductives and ants) (Gautier-Hion 1983, Gautier-Hion et *al.* 1980, Suzuki 1979). Termite soil has also been reported in the guereza diet (Bocian 1997, von Hippel 1996, Gautier-Hion 1983, Oates 1978). Guerezas have never been recorded drinking water, although they do occasionally feed on aquatic plants (Struhsaker and Leland 1987, Oates 1978).

The guereza diet is generally "characterized by a lack of variety" (Moreno-Black 1974: 39). Although guerezas feed from 25 to 43 species of plants, the top species eaten makes up more than 50% of the overall diet (Fleagle 1999, Bocian 1997, Dunbar 1987, Oates 1977a). Oates (1977b) found that even during two long-term studies (of two years each), the animals only added a single species of tree to the existing feeding records. Both Clutton-Brock (1975) and Oates (1977b) found troop dietary differences to be minimal in a homogeneous habitat. Inter-troop differences most likely are the result of variations in resources available between the home ranges. No age-sex dietary differences were recorded between troop members (Oates 1977b).

Clutton-Brock (1975, 1979) found guerezas to be extremely particular when making food choices. For example, when fruit was unavailable from the guereza's two primary tree sources, rather than exploiting fruits from other species of trees they would increase the amount of leaves eaten. The guerezas would also increase the percentage of mature leaves eaten when there was a limited amount of new leaves and shoots available rather than change food species eaten (Clutton-Brock 1975). Along with choices of species and plant parts eaten, guerezas have also been found to prefer individual trees. They repeatedly fed from one or two individual trees in an area that may have many trees of the same species available (Clutton-Brock 1975). Studies have also shown plant part and individual tree selectivity in howlers (*Alouatta palliata*) (Glander 1998).

The three primary plant species used as food by the guerezas in the native habitats of East Africa are *Celtis durandii*, *Markhamia platycalyx*, and a *Ficus* species (Baranga, 1986, Clutton-Brock 1979, Oates 1975, 1977b, Struhsaker 1975, Dunbar and Dunbar 1974). Oates (1977b) found that not only do *Celtis durandii* and *Markhamia platycalyx* form the majority of the guerezas diet in his study, but they also were the most frequent species found in the animals' habitat.

Studies have found dietary differences between guerezas living in East Africa and those living in Central and West Africa (Davies, et *al.* 1999). Gautier-Hion (1983) found a heavier reliance on leaves in the East African guerezas (diet composed of 77% leaf matter) than with the West African (51% leaf matter). Gautier-Hion et *al.* (1980) described the guerezas residing in Central Africa (Gabon) as both folivorous and frugivorous. Dasilva (1994) found a similar pattern with all African colobine species, including 25% more seeds and fruit consumed by western colobines (Sierra Leone) than in the eastern species.

Inter-Troop Encounters

Inter-troop encounters can take the form of neutral proximity or the peaceful withdrawal of one of the troops upon visual contact. Aggression, however, is the most common type of encounter and usually takes the form of a ritualized display (von Hippel 1996, Suzuki 1979, Oates 1977b, Poirier 1974). Although the alpha male is the most active participant in inter-troop encounters, both sexes exhibit aggressive behaviour during the interactions (von Hippel 1996). When a male outsider is observed, Marler (1969) found the group alpha male's first reaction is to sit in a conspicuous position, glare at the intruder, and click his tongue. If this is unsuccessful in running off the outsider, the male will then start to display by jumping from tree to tree while branch shaking. Poirier (1974) stated that inter-troop interactions are not a means to increase territory size but to maintain existing boundaries. Recorded inter-troop encounters occur when two troops line up on territorial boundaries, usually in adjacent trees. They then proceed to glare and lunge at each other while performing high intensity tongue clicks (Marler 1969, 1972). Von Hippel (1996) found his subjects to be involved in inter-troop encounters 25% of the study time (out of 443 study hours).

Common inter-troop vocalizations include the male loud call or 'roar' (a croak-like vocalization) performed by the alpha male of the troop, 'squeaking and screaming' performed by the females and young during times of distress, and the tongue click, performed by all members either as an aggressive or affiliative gesture (Marler 1972). Roars have found to be contagious between the males of closely residing troops and can be heard from as far as a mile away. Rather than providing territorial defense (as males usually roar from their sleeping tree, out of sight of other troops), Marler (1969, 1972) found roaring to act as a spacing mechanism as it is accompanied by ritualized displays. Inter-troop aggressive tongue clicks are directed toward the outside troop, while the affiliative tongue click is performed between troop members as a form of reassurance. The difference between the two clicks is distinguished by context as well as the degree of mouth drop and whether the actual click can be heard (Struhsaker 1975, cited as personal communication from Leskes and Acheson in Marler 1972).

Intra-Troop Encounters

Generally guereza intra-troop aggression is low (Oates 1977b). Dunbar and Dunbar (1976:88) found male-male antagonistic interactions take an "approach-retreat" form and are more likely to occur in the presence of estrous female(s). When aggression does occur, it is usually in multi-male troops. Aggression is directed from the alpha male towards the subordinate male(s), with occasional displacements directed from males toward females (Marler 1972, Schenkel and Schenkel-Hullinger 1967). Additional observations of undirected, aggressive behaviour include yawning (which also occurred after sleeping bouts), stiff legs (as described by Oates 1977c), penis extensions (not the full erection as seen during copulation), and scratching (although not a direct aggressive act, it was expressed during times of tension). A complete summary of non-vocal behaviour can be found in Oates (1977c), and in Dunbar and Dunbar (1976).

Common intra-troop vocalizations include 'squeaking and screaming' and tongue clicks. Squeaks and screams were commonly heard from females and young during aggression between troop members. In addition, newborn neonates give this as a loud protest call when being carried by females other than their mothers, often the first indication of a troop's location. The low intensity tongue clicking was an affiliative or neutral gesture (Struhsaker 1975). It is commonly used before grooming, mating, or as a form of reassurance. A complete summary of vocalizations can be found in Marler (1972).

Most intra-troop social interaction, in the form of grooming, occurs between the adult females (Struhsaker and Leland 1987, Oates 1977c). Grooming is most commonly performed between the adult and juvenile females (Oates 1977c, Leskes and Acheson 1970). Adult females receive 76% more grooming bouts than they perform (Oates 1977c). Adult males receive fewer grooming bouts from the adult females than from other members of the troop (Leskes and Acheson 1970).

Juveniles and neonates spent large amounts of their social behaviour in play. Social play is first recorded at just over a month old (Oates 1977c, Struhsaker 1975). Play behaviour takes three forms (see Rose (1977) for a full description), including chasing, wrestling, and solitary branch shaking. Rose (1977) stated that play behaviour tends to be sporadic in nature with spurts of activity intermixed with short periods of rest while the animals observe each other. Oates (1977c) found no indication of fully adult animals being involved in play behaviour. Wooldridge (1969 as referenced in Oates 1977c), however, recorded adult female play behaviour in captive guerezas.

Inter-Species Encounters

Previous studies have found guerezas in inter-species encounters with other primates, including red colobus (*Procolobus badius*), blue monkeys (*Cercopithecus mitis*), vervets (*Cercopithecus aethiops*), grey-cheeked mangabeys (*Cercocebus albigena*), L'Hoest's monkeys (*Cercopithecus l'hoesti*), red-tail monkeys (*Cercopithecus ascanius*), olive baboons (*Papio anubis*), and gelada baboons (*Theropithecus gelada*) (Leland and Struhsaker 1998, Rowe 1996, Waser 1987, Suzuki 1979, Rose 1977, Struhsaker 1975, Dunbar and Dunbar 1974). Inter-species encounters include chance meetings, short or long term associations and can involve aggressive, affiliative, and neutral behaviour (Rose 1977, Dunbar and Dunbar 1974). Affilative interactions have been recorded lasting as long as 47 minutes (Rose 1977). Dunbar and Dunbar (1974) found guereza's displaying a preference for the company of vervets and would commonly follow the vervets to the edge of the guerezas' home range.

Höner, et *al.* (1997) and Waser (1987) found inter-species encounters could provide an increase in resource acquisition and predator defense. Species with small troop size (like the guerezas) have fewer animals to spot predators, and not as many animals to confuse the attacker, as opposed to species that live in large groups (like the vervets) (Leland and Struhsaker 1998). Nonhuman predators of guerezas include crowned eagles (*Stephanoaetus coronatus*), chimpanzees (*Pan troglodytes*), and leopards (*Panthera pardus*) (Leland and Struhsaker 1998, Skorupa referenced in Stanford 1998, Gautier-Hion, et *al.* 1997, Davies 1994, Cheney and Wrangham 1987, Oates 1977a and b).

<u>Comparisons with *Colobus angolensis*</u>

Similarities between feeding patterns, diet, and social behaviour have been found between guerezas and another black and white colobus, *C. angolensis*. A comparable feeding pattern (feeding, followed by inactivity, followed by movement, and then repeated) was both found in *C. angolensis* and guerezas (Dunbar and Dunbar 1974, Groves 1973). In addition, dietary similarities were reported, as both species will feed from *Celtis durandii* whenever it is available (Clutton-Brock 1979, Oates 1977b, Struhsaker 1975, Groves 1973). However, it should be noted that *C. angolensis* has a higher rate of seed eating than guerezas. Two social behavioural similarities include both colobus species having a low rate of intra-troop interactions and, in multi-male troops, only the alpha male performs all of the roars and displays (Groves 1973).

Adjustments To Exotic Foods and Human Altered Habitats

Exotics plant species have reportedly been used as dietary supplements, as sleeping trees, and as buffer zones between native forests and human populations (Rowe 1996, Bicca-Marques and Calegaro-Marques 1994, Ganzhorn 1987, Dunbar and Dunbar 1974). Exposure to exotic species can come from provisioning, crop raiding, alteration of the native environment, and the transport of animals to another location. Comparisons have been made between the animals in human altered habitats and those in native habitats.

Influence of Exotic Species on Diet, Demography, and Social Behaviour

Various primate species have been recorded feeding on exotic species (Koganezawa and Imaki 1999, Siex and Struhsaker 1998, 1999, Forthman Quick and Demment 1988, Iwamoto 1988, Winkler 1988, Struhsaker, et *al.* 1997, Rowe 1996, Wheatley, et *al.* 1996, Bicca-Marques and Calegaro-Marques 1994, Dunbar and Dunbar 1974, Chapman, personal communication). Exotic foods in the diet of guerezas, howler monkeys, and three species of red colobus are presented here.

The single recorded incident of guerezas feeding from unusual foods is found in Dunbar and Dunbar (1974); the guerezas were recorded feeding on coffee leaves (*Coffea* sp.). Although coffee originated in Africa, coffee plantations as well as individual plants have been propagated. Consequently, the trees found in Africa today most often are cultivated Arabian coffee plants (*Coffea arabica*) (Lötschert and Beese 1983). Howler monkey (*Alouatta caraya*) studies noted troops residing in marginal habitats supplemented their diet with *Citrus sinensis*, which can represent up to 25% of the monthly dry season diet (Bicca-Marques and Calegaro-Marques 1994).

Many studies have found exotic plant species in the diet of red colobus monkeys (Siex and Struhsaker 1998, 1999, Struhsaker, et *al*. 1997, Rowe 1996, Chapman, personal communication). Rowe (1996) notes the incorporation of eucalyptus species into pennant's red colobus (*Procolobus pennantii*) diet, and Chapman (personal communication) notes *Procolobus badius* feeding on pine, cypress, eucalyptus, guava, and avocado.

With the destruction of the native habitat in Zanzibar, more than half of the Zanzibar red colobus (*Procolobus kirkii*) have adjusted to an agricultural environment (Siex and Struhsaker 1998, 1999, Cooney and Struhsaker 1997, Struhsaker, et *al*. 1997). Native trees that have been cut down to make charcoal are being replaced with exotic tree species. As the native trees disappear the red colobus have incorporated exotic foods into their diet. The study found that animal density and charcoal consumption has increased in the area over the years (Struhsaker, et *al*. 1997).

Studies have shown individual troops to alter their diet and movement rates to match different habitats and available foods (see studies on red colobus - Siex and Struhsaker 1998, 1999, bonnet macaques - Schlotterhausen 1998, barbary macaques - Mènard and Vallet 1996, long-tail macaques - Wheatley, et *al*. 1996, white-faced capuchins - Chapman and Fedigan 1990, Hanuman langurs - Hrdy 1977).

Provisioning of exotic foods by humans can occur either through the direct offering of food or through animal crop raiding (Saj 1998, Asquith 1989, Fa 1988, Yoshiba 1968). Studies have found provisioning and crop raiding to influence demography and intra-troop social behaviour (Hill 1999). Provisioned groups have an increased rate of resting, aggression, and reproduction and a deceased rate of feeding, shorter day range, smaller home range size, and lower mortality than unprovisioned groups (Koganezawa and Imaki 1999, Saj, et *al.* 1999, Asquith 1989, Fa 1988, Forthman Quick and Demment 1988, Winkler 1984, Yoshiba 1968). Species of the subfamily Colobinae have been found utilizing provisioned foods. Groves (1973) records crop raiding, specifically on beans and new maize plants in the black and white colobus *C. angolensis*. Winkler (1984) and Hrdy (1977) stated that Hanuman langurs (*Presbytis entellus*) crop raid and are provisioned by local villagers. Winkler (1984) found that 33% of the feeding-time was spent feeding on provisioned foods (which included potatoes, carrots, cauliflower, banana, mango, and cooked foods).

Schlotterhausen (1998) found significant differences between the movement and feeding rates of troops of bonnet macaques (*Macaca radiata*) residing in native and human altered environments. The study found that the native groups had a higher rate of feeding and movement, with a decreased rate of social behaviour. This indicated that the native groups had less 'leisure' time than did the troops located in human altered environments. The study also found a decreased rate of variability in the diet of the groups that fed on human foods.

Long-tail macaques (*Macaca fascicularis*) residing in wild and food-enhanced habitats differed in regard to home range, day range, density, activities, and diet (Wheatley, et *al.* 1996). The animals studied in Kalimantan, located in the Kutai Nature Reserve, were largely undisturbed by humans. The animals in Bali were located on temple grounds that form a tourist site called Monkey Forest. The troops residing on the temple grounds had a more diverse diet, had a higher animal density, and spent more time resting than did the troops in the wild study site.

Exotic Habitat Uses

Studies on the non-dietary use of exotic trees include Australian eucalyptus plantations, which were located in Madagascar. These trees play an important role for lemurs, providing underbrush vegetation for feeding, resting trees, and arboreal traveling paths. In addition, the plantations provided a buffer between the human population and the natural reserve where the lemurs reside (Ganzhorn 1987).

Studies on groups of primates that had been moved from their indigenous habitat reveal ways of adjusting to exotic environments (i.e., the Arashiyama West Texas snow monkeys and the Cayo Santiago macaques). The Arashiyama West Texas Japanese macaques (*Macaca fuscata*) were relocated to Texas from Japan in 1972. The animals had to learn which foods were harmful and which were safe (Pavelka 1993). For example, the animals discovered the berry *Karwinskia humboldtiana* made them sick and then refrained from eating it even though there was a 50 day period before the onset of symptoms after ingestion (Bramblett 1994, Pavelka 1993). In addition to adjusting their feeding to the new flora, the animals also modified their time budget to adapt to the different climate. This modification did not alter their social structure (Fedigan 1976 as referenced in Bramblett 1994).

The Entebbe Botanical Gardens

The first curator, A. White, established the Entebbe Botanical Gardens in 1898. His intent was to use the area as an experimental garden to determine what crop species would survive in Uganda (D. Paterson 1992). Many of the cash crops from which Uganda has earned foreign exchange over the years were first introduced and tested in the Botanical Gardens. Originally the land was natural forest; currently only two small sections have been preserved in its natural state (covering 2.3 hectares). Many indigenous species were left when the garden was cleared. Four plant surveys have been conducted. The first, in 1969 revealed 2500 species of plants (Table 2.2). A second survey, conducted in 1992 by a Consultant from Royal Botanical Gardens, Edinburgh, revealed a significant drop in number of species due to neglect.

Table 2.2: Entebbe Botanical Garden Survey Results.

Date	Surveyor	Number of Species
1969	Unknown	2500
1992	Royal Botanical Gardens, Edinburgh	significant drop
1996	Byabafumu	240
1998	Katende	270

In 1996, the National Agriculture Research Organization (NARO) assumed management, a new curator was installed, funding was obtained to upgrade the Gardens, and a third survey was conducted. The 1996 survey listed 240 species of plants (Byabafumu 1996).

In 1998, Katende completed the fourth plant species inventory during the months January through May 1998. Plants were identified, collections were made and trees larger than 3cm in diameter at breast height (DBH) were measured, and numerical and/or alphabetical individual tree symbols (based on location) were updated. These alphabetical-numerical symbols formed a master list found in the Botanical Gardens Head Office. The list recorded 1625 trees and shrubs (greater than 3cm DBH) presently in the Botanical Gardens among which there are 270 species.

Uses of Entebbe Botanical Gardens

Both Ugandans and foreign tourists utilize the Entebbe Botanical Gardens. The Ugandans who reside in the capital city of Kampala (32 km from Entebbe) use the gardens as a weekend resort. Local Ugandans collect firewood, drinking water (from the natural spring), and fruit. As well, they fish, swim, wash laundry, and cars on the shore of Lake Victoria. Tourists come to the gardens to view the large number of plant and animal species. Both foreigners (expatriates residing in Uganda) and Ugandans also come into the gardens to purchase plants from the nursery.

Entebbe Botanical Gardens Staff

Entebbe Botanical Garden staff (employed by NARO) include landscapers, nursery staff (who grow seedlings for public sale), gate workers (who collect entrance fees from the public), road crew (temporary workers who fix roads and construct paths), guides (although not specifically employed by NARO - they are paid by their customers - these guides escort guests around the gardens pointing out specific plants and animals), and office staff (including the curator and secretaries, who implement changes and set up special functions).

CHAPTER THREE

METHODS

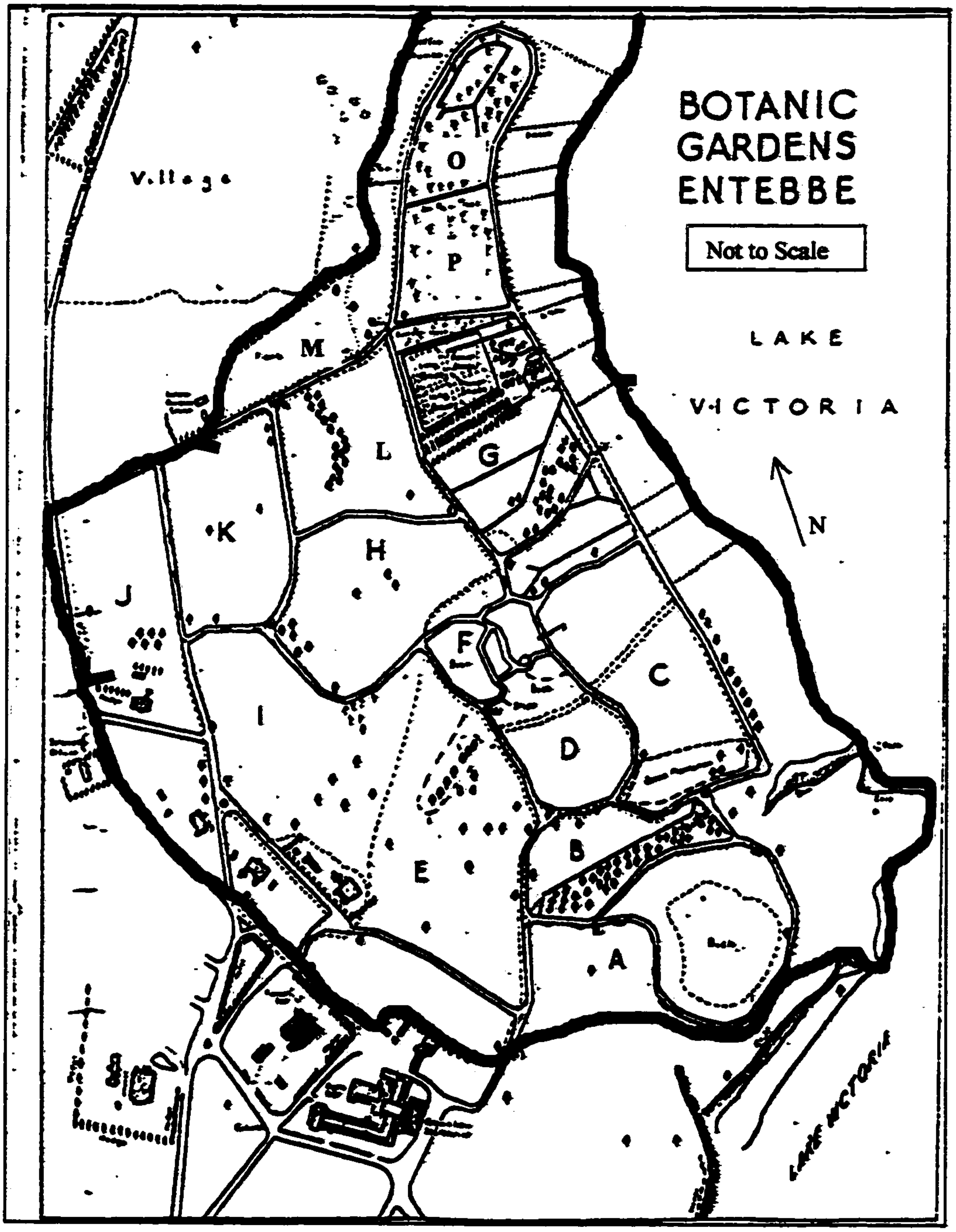
Study Site and Subjects

This study was conducted in the Entebbe Botanical Gardens. Previously the colonial administrative center of Uganda, Entebbe is a small city with a population of less than 50,000 (Map 3.1). It is located in southeastern Uganda, with the Botanical Gardens situated on the north shore of Lake Victoria (00°04'N, 35°29'E; 1134 meters above sea level) and is surrounded by houses and small farms (D. Paterson 1992). Annual monthly precipitation of Entebbe is approximately 114 mm. There are two peak rainy seasons that occur in May and October. In the Lake Victoria region, temperatures range between 15 and 29°C (Byabafumu 1996, Byrnes, 1990).

The Botanical Garden covers 35 hectares and consists of mostly open parkland with a south-facing slope that drains into Lake Victoria. There are fourteen distinct areas in the gardens (Map 3.2) including tropical fruit, palm, rubber, and cocoa collections, as well as two sections of natural forest that are largely undisturbed (Plate 3.1 and 3.2). The sections of natural forest cover 2.3 hectares and include the main natural forest in Section F and Bush Area A. There is some discrepancy over the number of recorded tree and shrub species found in the Entebbe Botanical Gardens. However, based on a Plant Species Inventory published in 1998, there are 270 identified species plus 16 unknown species (see Appendix D for the complete list of trees, shrubs and vines growing in the Gardens). In addition, the staff at the Makerere University Herbarium identified nine more species

Figure 3.1: Map of Entebbe, showing the Entebbe Botanical Gardens (shaded area in upper right corner). Scanned from Entebbe Map 1:12,000, Series U.S.D. 2, Edition 2, Department of Lands and Surveys, Uganda, 1965.

Figure 3.2: Botanical Gardens with distinctive sections (external border in bold).



Section Legend (n = total number of trees in section)

A- economic trees (n=62)	E and I- open park (n=184)	L- palm trees (n=78)
B- rubber trees (n=66)[1]	F- natural forest (n=215)[4]	M- medicinal plants[5]
C- cocoa plants (n=112)[2]	G- bamboo/nursery (n=57)	O and P- crops[5]
D, H, K- open park[3]	J- tropical fruit trees[3]	Bush A- natural forest (n=288)[6]

[1] dates to 1912 [2] dates to 1903 [3] collectively contains 118 trees [4] includes natural spring
[5] originally contained 445 trees, but O and P cleared for crops [6] no public access

Plate 3.1: Open parkland area, Entebbe Botanical Gardens, Section D.

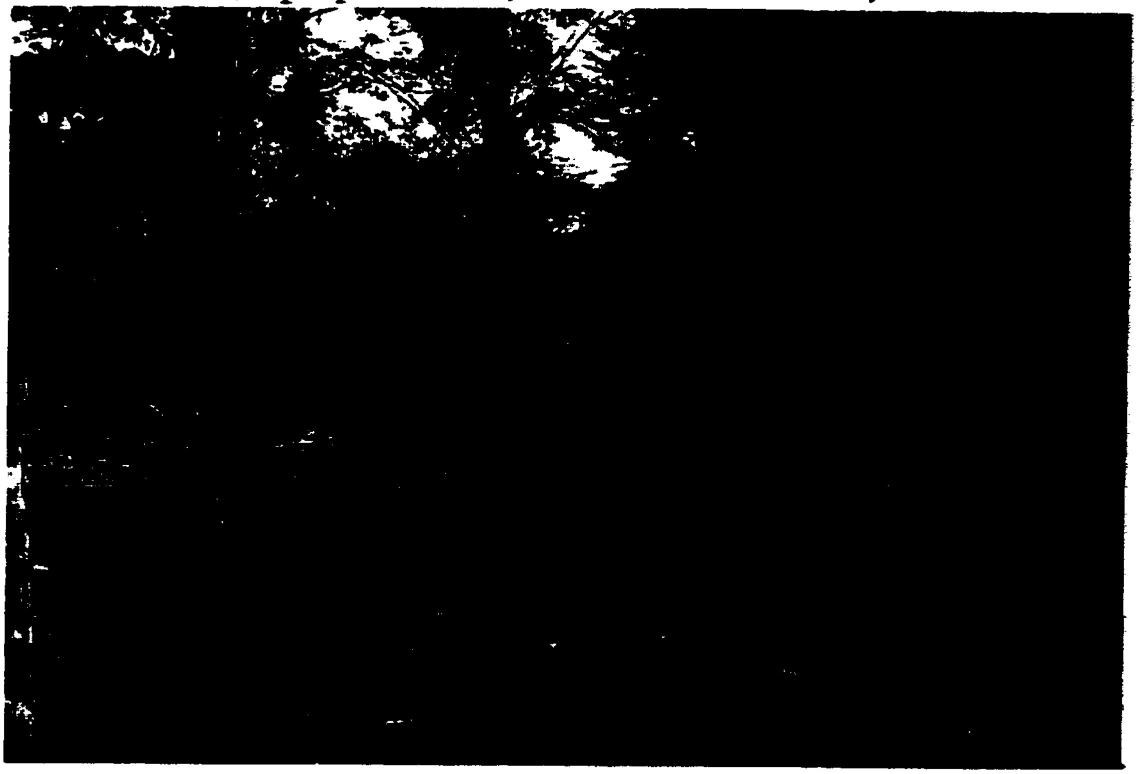


Plate 3.2: Edge of Natural Forest, Entebbe Botanical Gardens, Section F.

of trees and shrubs. Of these 279 identified species, 45% are exotics originating from outside Africa, with 14% of unknown origin (Table 3.1). The inventory lists 21 species of climbers and vines (also eaten by the guerezas); Makerere University Herbarium identified one additional vine. Many of the vine origins are unknown (n = 12); however, of the identified vines four are from Africa, three from Tropical America, and two from India.

Table 3.1: Origin of Trees and Shrubs found in Entebbe Botanical Gardens

Africa	41%	(114 species)
Tropical America	15%	(42 species)
Unidentified origin	14%	(40 species)
Asia	10%	(27 species)
Pacific Islands[1]	6%	(17 species)
Australia	5%	(14 species)
North America	4.3%	(12 species)
India	2.5%	(7 species)
Caribbean Islands[2]	1.8%	(5 species)
Europe	0.4%	(1 species)

[1] Pacific Islands includes Philippines, Indonesia, Malaysia, and Polynesia.
[2] Caribbean Islands includes Bermuda, Trinidad, and West Indies.

The Botanical Gardens contain 25 guerezas in three groups, a mean of 8.3 individuals per group (range: 4 - 14). Besides guereza monkeys, other resident primate species include a troop of vervet monkeys (*Cercopithecus aethiops*) and a lone red-tail monkey (*Cercopithecus ascanius*). Additional identified animals include Nile monitor lizards (*Varanus niloticus*), various squirrel species (*Paraxerus* sp.), and a vast array of birds species.

The three guereza troops (the Para, Natural Forest, and Hill troops) were observed for comparative purposes and to supplement existing data. All members of the three troops were assigned to an age-sex class (adult, large or small juvenile, black and white infant, and white neonate) on the basis of body size and sexual characteristics (Table 3.2). Troop identification was determined by location in the gardens, troop size, and composition. Individual identification was generally unreliable beyond age-sex categories. However, the Para troop alpha male was recognizable due to an injury on his right ankle (which he favored during movement). Although, guerezas have been present in this area for at least thirty years, life histories were unavailable, as they have not been previously studied.

Table 3.2: Description of Age-Sex Categories. Adapted from Oates (1977c) and Marler (1972).

Black and White Infant or White Neonate	Infants and neonates under one year of age, may have changed to adult pelage but are fully dependent on mother for major troop movements.
Small Juvenile	1 to 2 years, approximately half the size of an adult female, movement completely independent, pelage is fluffy, and spends much time in play behaviour, occasionally nurses.
Large Juvenile	2 to 6 years, more than half the size of an adult, males have full canines but a small penis, female nipples are visible but not distended, some involvement in play behaviour. Labeled as sub-adults in some literature.
Adult Male	9 - 14.5 kg, muscular, with full sized canines and penis, pelage is sleek, crown of head has two distinctive humps, complete circle of white ano-genital fur, sexually mature.
Adult Female	6.5 - 10 kg, visible distended nipples, pelage is sleek, broken circle of white ano-genital fur, sexually mature (Plate 2.1).

Observational Methods

Observations were completed on three troops of guerezas during the dry season months of May through October 1998. The first month (May 1998) was allocated to gaining permission from the National Council for Science and Technology, the Mipigi Regional District Commissioner, and from the Curator of the Botanical Gardens to complete the study. In addition, identification, census and habituation of the troops, and a description of individual troop home range location and size were made on an *ad lib* basis. Data sheet evaluation and ethogram preparation were also completed during this initial period.

As previous studies have shown guerezas to be inactive at night (Clutton-Brock 1975), observations were made throughout the daylight hours. Troops were usually located between the hours of 06:45 to 07:30 and followed until 19:00. Due to poor visibility in the evenings, data sampling was stopped at 18:45 and *ad lib* data was collected for the remaining fifteen minutes or until age-sex classification became unreliable. A midday break was taken between 12:00 and 13:00. During periods of heavy rain, data collection was suspended (although it was noted that the majority of members would band together and remain stationary for the length of the shower) (as found by von Hippel 1996 and Oates 1977a). The groups moved to the evening's sleeping tree on or before 19:00 and thus could be located the next day (as in the study of von Hippel 1998). Initial census data was collected whenever the troop being observed moved to open sections of the Gardens or onto the ground. All activities were recorded on data collection sheets with the aid of a stopwatch.

Dependent offspring (including white neonates and newly changed black and white infants, n = 4) were excluded from both instantaneous sample and focal data collection.

Instantaneous Samples

I collected instantaneous samples (also called 'scan sampling' Altmann 1974) on all three troops. Over 20 minute sessions, instantaneous sample activities were recorded every two minutes on each age-sex category. To avoid observer fatigue, rest periods were taken between the 20 minute sessions. This technique allowed comparable frequency data to be collected while taking into account the three different home range habitats and troop sizes. The following mutually exclusive categories were recorded: scanning, sleeping, movement, feeding, social activity, out of sight, and other activities (see below for a more detailed list). This method made it possible to record all visible activity within a short period while providing frequencies of each activity (Altmann 1974). A total of 5790 instantaneous samples were recorded for the three troops over 11,580 minutes (193 hours) of sample observation time (Table 3.3). Due to the midday break (between 12:00 – 13:00) activities performed during this time were unrecorded, and may provide a data collection bias.

Table 3.3: Troop Session Breakdown of Instantaneous Samples. n = number of individuals, excluding infants and neonates.

Troop	Number of Sessions
Para (n = 10)	1950
Natural Forest (n = 5)	1940
Hill (n = 3)	1900
Total	**5790**

Focal Samples

The Natural Forest troop was selected for focal animal sampling (Altmann 1974). Focal observations provided in-depth data on a single troop. Individual rates, frequencies, and durations of behaviour and feeding were collected during focal samples. This entailed

Table 3.4: Individual Session Breakdown of Focal Samples.

Individual	**# of Sessions**	**Total Minutes**
Adult Male	45	900
Lg. Adult Female	43	860
Sm. Adult Female	48	960
Lg. Juvenile Female	42	840
Sm. Juvenile Female	42	840
Total	**220**	**4400**

following an individual animal for a set amount of time (20 minutes) and recording the action being performed by the subject, including time spent in that action (Altmann 1974). Rest periods were taken between samples. If the animal being followed was out of sight for more than 10 minutes of focal observation, the sample was terminated and a new one was started. Individuals were observed in a repetitive, continuous order to prevent a skewed data set. Two hundred and twenty focal sessions (73.3 hours) were collected, for a mean of 14.7 hours of focal samples per animal (range: 14 - 16 hours) (Table 3.4). Social activity was regarded as a 'single bout' if it was uninterrupted. However, if there was a change of one or both of the actors or change of behaviour between two episodes of the same behaviour, or if more than one minute passed without a repeat of the behaviour, they were considered to be separate bouts. As in the instantaneous samples, social activity categories included all involved individuals as well as the direction of the behaviour.

Habituation

I attempted to establish and maintain neutrality with the animals and did not feed or otherwise intentionally interact with them. However, despite the levels of habituation differing between the troops, all the guerezas in this study were habituated to some extent and by moving quietly and slowly during observations, that level increased over the course of the study. Of the three troops, the Para troop habituated to my presence the fastest and demonstrated the highest level of habituation. The Para troop was approachable within approximately 5 - 10 meters. The Natural Forest troop showed no signs of unease within approximately eight meters, but due to the height of the natural forest (a main portion of their home range), they were commonly found at a height of 15 - 20 meters. The Hill troop maintained a distance of approximately 15 - 20 meters and showed signs of anxiety when I approached within 15 meters.

Plant Identification

Many of the trees in the Entebbe Botanical Gardens had existing tree identification signs and/or alphabetical-numerical symbols that could be matched up with the master list found in the Botanical Gardens Head Office. Trees without existing labels were given one by the observer as a future reference. Plant species were identified either by the existing tree labels or onsite by the staff at the Makerere University Herbarium. All feeding plants that were unlabeled or unidentified onsite were collected and preserved. The leaves, flowers (if present), and fruit (if in season), were dried and taken to the Makerere University Herbarium, Kampala, Uganda for identification. They are stored at the University of Calgary, Physical Anthropology Laboratory.

Data Collection

The following activity categories were collected to create an activity budget: scan, sleep, movement, feed, social, out of sight, and other activities (Appendix A).

Scan

When recorded as scanning, the animal was inactive but alert with its eyes open. Scanning also included distinct head movement, possibly from a prominent position (e.g., from the top or edges of trees). Body movement included shifting of position rather than locomotion. The comparison of scanning data between this and previous studies will help reveal differences, if any, in physical activity and vigilance levels.

Sleep

Sleep was recorded when the individual was inactive, eyes closed, usually huddled up with other troop members. The collection of sleep data provides comparative information on activity levels with previous studies. A relationship has been found between diet and activity levels, both in energy received from food type as well as digestion time (Oates 1977b, Moreno-Black 1974, Poirier 1974). Comparisons between sleeping rates will help reveal differences in consumed nutrients, and therefore available energy. The 20 minute sessions did not always encompass the sleeping bouts.

Movement

Movement was recorded when an animal traveled at least one-body length. Movement included leaping, walking, climbing, and running and was recorded regardless of arboreal or terrestrial locomotion. The collection of movement data allowed for a continuous daily record to be made of the troops' day range, as well as the level of energy expended. Troops were not followed for an hour during the afternoon so day range length may be conservative. However, the troops generally moved little during this time so errors should be slight (similar to von Hippel 1996). Animals were relatively inactive when feeding. When they were masticating while moving, the activity was recorded as moving (Clutton-Brock 1974, 1975).

Feed

An animal was recorded as feeding when masticating or ingesting a food source. Included were species eaten (if known), individual tree identification, and part of plant eaten (comparable to Oates 1977b). The following categories were used:

Mature Leaves	Fruit
New Leaves	Vines
Shoots	Epiphytes
Bark	Termite Soil
Flowers	Unidentified
Seeds (including seed pods)	

In certain areas of the Botanical Gardens, especially areas with a large number of vines, feeding often occurred out of sight of the observer. Consequently, it was seldom evident which part of the plant or species of vine was being eaten. Vines were recorded as 'vine' unless the animal was feeding on flowers that were easily distinguishable. As with other studies, the guerezas did not eat continuously, but made either a few short feeding stops or moved to a single site where feeding continued for a period of time (Oates 1977b).

Foraging was included in feeding data. The total number of feeding records per troop and per age-sex category was summed for each food species and recorded as percentages to be analyzed (Clutton-Brock 1975).

The collection of feeding data allows comparisons to be made with studies of guerezas living in a natural environment. In addition, inter-troop comparisons show how each troop alters its diet, thus exposing dietary options available to guerezas presented with novel foods. Dietary differences may be a result of monthly differences, especially between the Para and Hill troops as the Para troop data was collected in June and July while the Hill troop data was collected in October.

Social

Behaviour recorded as social included mutual grooming (actively grooming or being groomed by another animal), play (wrestling and play chases), aggression (chases, lunges, displacement), vocalizations (male roaring, clicking, female and juvenile squeaks and screams, infant and neonatal protests), mounting (both sexual and non-sexual mounting), presents (of any body part, including sexual presents and presenting to be groomed), clinging (infant and neonatal clinging and ventral clinging between females), and neonatal transfer (both successful and unsuccessful transfers). Social activity categories included all involved individuals as well as the direction of the behaviour.

Social behaviour was noted as being affiliative, aggressive, or neutral in context (if apparent). Neutral contact was recorded when two or more animals came into proximity with each other without overt affilative or aggressive social contact. For example, the red-tail monkey would occasionally spend a portion of the day following the Natural Forest troop as they moved around their home range. There were no open interactions between them as compared to the incidents when the Natural Forest male chased the red-tail away from the troop, which was recorded as an aggressive interaction.

Inter- and intra-species encounters were also recorded. Start and end times were recorded on an *ad lib* basis for both inter-troop and inter-species interactions during both instantaneous sample and *ad lib* data collection. This allowed for comparisons to be made between the lengths of time the troops spent interacting with each other and with other species.

The collection of social instantaneous samples may bias the amount of individual recorded behaviours due to the differing lengths of activities. For example, behaviours that occur for longer periods (i.e., grooming) will be recorded more often than those that are instantaneous (i.e., tongue clicking).

<u>Out of Sight</u>

The animal was recorded as out of sight when no longer visible to the observer. This allowed for continuous data to be collected.

Other Activities

Included any activity (i.e., masturbation) that did not fall into the above categories. This allowed for continuous data to be collected regardless of the activity.

Additional Data

In addition to the above, records were made of the presence of rain, public use of the Botanical Gardens (including school trips, tour groups, and parties), and the appearance of fruit or flowers on individual feeding trees. Guereza vocalizations and interactions with other species (including vervets, the red-tail monkey, birds, squirrels, and humans) were collected on an *ad lib* basis. Social observations that were not included in the data being collected were described immediately after they occurred (*ad lib*, Altmann 1974).

Ad lib neonatal data was included if the neonate was not being carried by an adult female. Occasionally the neonate's behaviour (i.e., protesting and attempting to reach its mother) indicated it was on a female other than its mother. However, due to the inability to differentiate adult females (specifically between the Para troop females) and for consistency the neonate was recorded as being off its dam if it was alone or being carried by a juvenile. Infant and neonate play behaviour was also recorded when observable, as well as what state the animal was in while being carried (i.e., awake or asleep). Neonate transfers were recorded on an *ad lib* basis.

Ranging data was also collected. Similar to Oates' (1977c) findings, home range size included the entire area within which the group was recorded during the length of the study and could overlap with other troop home ranges. The individual troop territories were comprised of a smaller section within the home range that was defended from other troops. Day range included the area in which the troop moved throughout the day.

Landmark and vegetation sections made it easy to plot the location of a troop in the Botanical Gardens. During observations the movement of the groups was recorded to plot their daily and home range. A record was kept of in which section (including in which part of the section) in the Botanical Gardens the troop was found, as well as any movements outside that section. For example, if the Natural Forest troop was in the natural forest (which is divided by a road) in the section by Lake Victoria, then the animals were recorded as being in LNF (lake-side natural forest). In addition, the labeled individual trees allowed each member of the troop to be recorded in which specific tree they were found. For example, the Para Rubber trees (*Hevea brasiliensis*) in Section B were labeled AW1 to AW40. The existing labels also allowed for a continuous record of individual ranging behaviour throughout the day.

Collections were made of the recorded diameter at breast heights (DBH) of all feeding trees in the individual home ranges. DBH is commonly used as an "index of food availability" (Chapman and Chapman 1999:219) and is used to compare available food resources between the three troops.

Data Analysis

Instantaneous Samples

Data analysis was completed by age-sex categories for all three troops in the instantaneous samples. Scores for all categories were totaled daily with a final sum of overall troop age-sex totals. By summing the frequency of each behaviour and dividing the sum by the total frequency of all behaviours, mean percentages were derived. This produced a mean proportion of instantaneous samples of each of the three troops in scanning, sleeping, movement, interacting with other guerezas, out of sight, and other activities. The median and range of the instantaneous samples are also provided on each of the three troops in the above categories. Comparisons were made between both age-sex categories and between the three troops.

Focal Samples

Data analysis was completed on an individual basis. Focal sample activity breakdowns were determined by dividing the overall activity category totals by the individual daily activity totals for the duration of the study. This provided a mean percentage for each activity category. Comparisons were made between the age-sex categories.

Statistical Analysis

Data analysis included Kruskall-Wallis one-way Analysis of Variance (Siegel and Castellen 1988). When the test was found to be significant a multiple comparison was then performed between the significant categories in order to locate the differences. The degrees of freedom (df), H, and p-value are noted for all tests. Data analysis was performed using SSPS 8.0 version for Windows 95. The significance level was set at 0.05.

Four animals were included in the data collection but excluded from the statistical analysis. Older, more independent black and white infants (n = 2) were excluded as they spent a portion of their time clinging and nursing on their mothers. In addition, the two adult males (one immigrating into the Para troop and one emigrating out of the Natural Forest troop) were also excluded, as a complete data set was unobtainable.

CHAPTER FOUR

RESULTS

Introduction

This chapter is divided into five sections. The first section presents the diet of the subjects, including what food parts as well what species of foods are being eaten. Individual troop as well as age-sex comparisons will be made. The use of exotic species and medicinal plants will be explored. The second section will reveal home range size, investigating the use of troop daily ranges, home ranges, and areas of inter-troop conflict. The third section presents the subjects' activity budget, examining troop as well as age-sex differences. Group size and composition will be presented in the fourth section, including changes during the course of the study. Additional information in the fifth section includes intra-troop, inter-troop, and inter-species interactions.

1. DIET COMPOSITION

Of the instantaneous sample data, the subjects spent a mean 15.1% (range: 5.8 - 24.2%) feeding. They were observed feeding on leaves (including freshly budded out shoots, new and mature leaves), bark, flowers, seeds, fruit, vines, epiphytes, and unidentified food parts. The guerezas were also occasionally seen eating termite soil. The majority of the diet consisted of new leaves (64.7%), with all leaf types (including mature and new leaves, and shoots) making up 83% of the overall recorded diet. Bark represented 7.1%, while vines composed 4.9% of the diet. The other food categories that constituted more than 1% of the diet included fruit, flowers, and seeds. Epiphytes, termite soil, and unidentified foods made up less that one percent, collectively, of the diet. Although there was one recorded termite swarm during the collection of Hill troop instantaneous sample data, there were no observations of any of the Hill troop members attempting to catch or eat termite reproductives.

Dietary Composition Differences Between the Troops

The Para troop had the highest level of feeding on leaves (of all ages); a mean 87.6% of their diet was composed of leaf matter. The Natural Forest troop fed on leaves 76.7% of the feeding instantaneous sample data, while bark made up 17.2%. Similar to the other troops, new leaves were the most commonly eaten food type, making up 78.3% of the Hill troop feeding instantaneous samples (Figure 4.1).

<u>Natural Forest Troop - Focal Data</u>

The Natural Forest troop spent 16.6% (14.3 hours) of the focal data feeding. Of that, leaves (of all ages) made up 36% of the diet, with 22% (3.13 hours) of the diet composed of new leaves. Bark made up 29.4% (4.2 hours) of the focal diet. Although bark made up a smaller portion of the diet than did the consumption of new leaves (17.2% versus 70% of the instantaneous feeding sample data), bark was consumed over a greater time period than were new leaves (4.2 versus 3.13 hours of the focal feeding data). None of the food types were found to be significantly different between the age-sex categories of the members of the Natural Forest troop.

Mature Leaves (ML)

Significant differences were found between the three troops' feeding on mature leaves (H = 13.684, n = 18, df = 2, p = 0.001). A multiple comparison was performed between the three troops and confirmed that the significant difference occurred between the Para troop and the other two troops (critical differences 7.0, 8.38, 9.3, z = 2.394). The Para troop spent a mean 17.7% of the instantaneous samples feeding on mature leaves, compared to the Natural Forest and Hill troops that fed on mature leaves 5.8% and 0.3%, respectively.

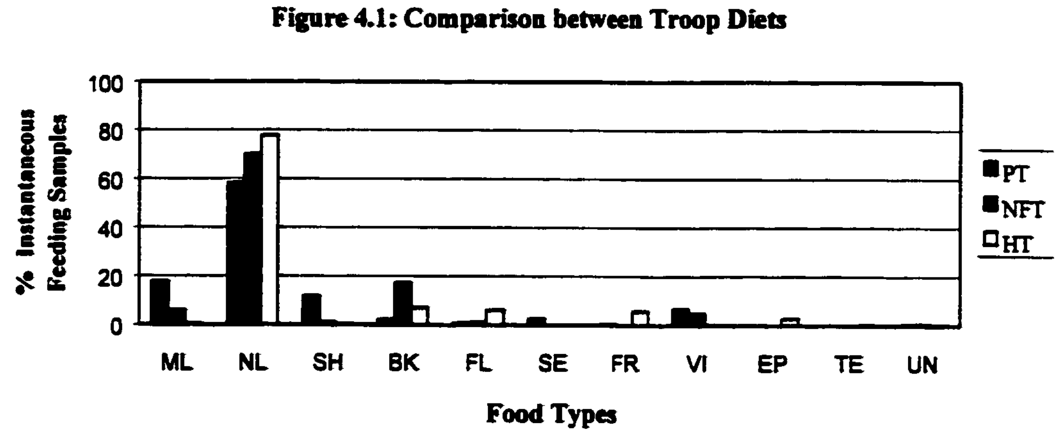
New Leaves (NL)

The rate of instantaneous samples on the feeding of new leaves was found to be significantly different between the three troops (H = 10.905, n = 18, df = 2, p = 0.004). Multiple comparisons between the troops were performed in order to locate the differences (critical differences 7.0, 8.38, 9.3, z = 2.394). This test confirmed the significant difference occurred between the Para troop and the other troops. The Para troop fed on new leaves a mean 58.2 % as compared to the Natural Forest troop (70%) and the Hill troop (77.7%).

Shoots (SH)

The differences in the instantaneous samples of feeding on shoots were found to be significant (H = 13.422, n = 18, df = 2, p = 0.001). Multiple comparisons showed that the differences occurred between the Para troop and the other two troops (critical differences 7.0, 8.38, 9.3, z = 2.394). The Natural Forest and Hill troops spent a mean 1% and 0.3%, respectively, of the instantaneous samples feeding on shoots. The Para troop, however, fed on shoots a mean 11.7%.

Figure 4.1: Comparison between Troop Diets. Based on mean instantaneous sample feeding data. It shows that the greatest proportion of instantaneous feeding samples was devoted to feeding on new leaves, with significant differences in mature leaves, new leaves, shoots, bark, flowers, seeds, fruit, vines, epiphytes, and termite soil. PT= Para troop, NFT= Natural Forest troop, HT= Hill troop, ML= mature leaves, NL= new leaves, SH= shoots, BK= bark, FL= flowers, SE= seeds, FR= fruit, VI= vines, EP= epiphytes, TE= termite soil, UN= unidentified.



Bark (BK)

Significant differences were found between the three troops' rate of feeding on bark ($H = 12.833$, $n = 18$, $df = 2$, $p = 0.002$). Multiple comparison tests revealed the significant differences occurred between the Natural Forest troop and the other two troops (critical differences 7.0, 8.38, 9.3, $z = 2.394$). The Natural Forest troop fed on bark a mean 17.2% of the instantaneous feeding samples. The Para troop spent 2.1% and the Hill troop spent 6.9% of the instantaneous samples feeding on bark.

<u>Flowers (FL)</u>

Feeding on flowers was found to differ significantly among the three troops ($H = 7.588$, $n = 18$, $df = 2$, $p = 0.023$). A multiple comparison was performed between the three troops but the differences were found to be insignificant (critical differences 7.0, 8.38, 9.3, $z = 2.394$). The Hill troop spent a mean 6% of the instantaneous sample data feeding on flowers, as compared to the flowers in the samples of the Para troop (0.8%) and Natural Forest troop (1%).

<u>Seeds (SE)</u>

Feeding on seeds was found to differ significantly in the instantaneous feeding sample data ($H = 11.678$, $n = 18$, $df = 2$, $p = 0.003$). Seeds were eaten solely by the Para troop, and made up a mean 2.4% of the diet.

<u>Fruit (FR)</u>

Feeding on fruit was found to differ significantly between the three troops ($H = 10.546$, $n = 18$, $df = 2$ $p = 0.005$). A multiple comparison performed between the three troops found the differences to be insignificant (critical differences 7.0, 8.38, 9.3, $z = 2.394$). Fruit composed 5.6% of the Hill troop diet and 0.4% of the Para troop diet. Fruit was not recorded in the instantaneous sample diet of the Natural Forest troop. Fruit was composed of unripe whole fruit and ripe and unripe fruit exocarp. No whole ripe fruit was recorded being eaten.

Vines (VI)

Feeding on vines was found to be significantly different between the three troops (H = 8.388, n = 18, df = 2, p = 0.015). A multiple comparison performed between the three troops found the differences to be insignificant (critical differences 7.0, 8.38, 9.3, z = 2.394). The Hill troop spent a mean 0.1% of the instantaneous sample data feeding on vines, as compared to vines eaten by the Para troop, which made up 6.5%, and the 4.7% vines eaten by the Natural Forest troop.

Epiphytes (EP)

Epiphytes were found solely in the diet of the Hill troop, and were significantly different between the three troops. Epiphytes made up a mean 2.7% of the Hill troop diet (H = 16.834, n = 18, df = 2, p = 0.000).

Termite Soil (TE)

Feeding on termite soil differed significantly between the three troops. (H = 10.588, n = 18, df = 2, p = 0.005). Soil was eaten solely by the Hill troop during the instantaneous sample data collection and made up a mean 0.3% of the feeding instantaneous samples.

The Natural Forest troop was also recorded feeding on termite soil. During the collection of focal data, termite soil made up 0.7% (6.3 minutes) of the Natural Forest troop feeding focal data.

Unidentified Foods (UN)

Unidentified foods were not found to differ significantly between the three troops (H = 1.817, n = 18, df = 2, p = 0.403). Unidentified foods made up a mean 0.25% of the Para troop diet, 0.47% of the Natural Forest troop diet, and 0.23% of the Hill troop diet.

Dietary Composition Between Age-Sex Classes

I found no significant differences in the diet of the different age-sex categories with regard to food types eaten, including: mature leaves, new leaves, shoots, bark, flowers, seeds, fruit, vines, epiphytes, termite soil, and unidentified food parts (Figure 4.2, Table 4.1).

Figure 4.2: Comparison between Age-Sex Diets. Based on mean instantaneous sample feeding data. Showing a very similar breakdown of food types eaten by the age-sex categories with new leaves making up the majority of the samples. ML= mature leaves, NL= new leaves, SH= shoots, BK= bark, FL= flowers, SE= seeds, FR= fruit, VI= vines, EP= epiphytes, TE= termite soil, UN= unidentified.

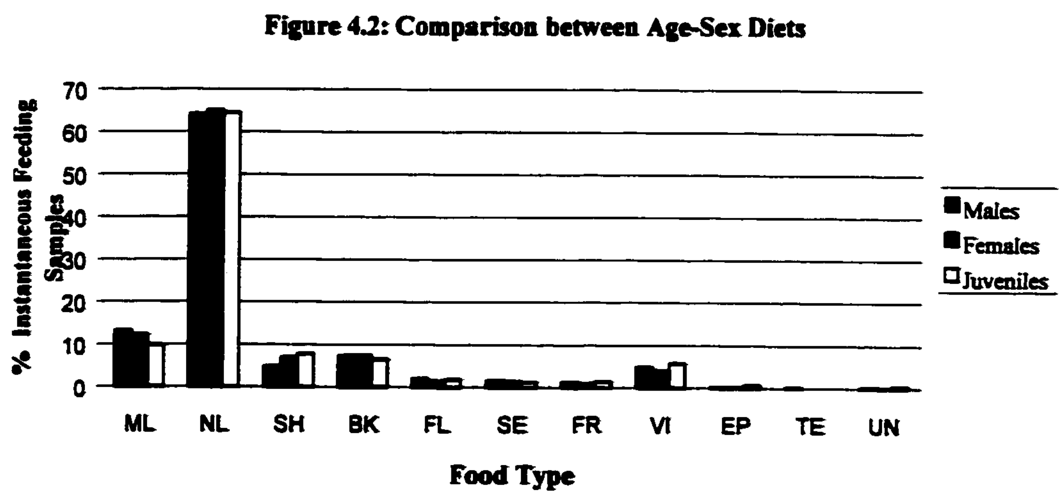


Table 4.1: Kruskall-Wallis one-way Analysis of Variance results for food parts eaten between the age-sex categories. Based on instantaneous feeding samples, showing no significant differences.

	H	n	df	p
mature leaves	0.364	18	2	0.834
new leaves	0.08	18	2	0.961
shoots	1.928	18	2	0.381
bark	0.244	18	2	0.885
flowers	2.319	18	2	0.314
seeds	0.278	18	2	0.87
fruit	2.463	18	2	0.292
vines	1.336	18	2	0.513
epiphytes	0.045	18	2	0.978
termite soil	1.22	18	2	0.543
unidentified	1.333	18	2	0.514

Species of Foods Eaten

The guerezas fed from thirty-one different plant families (Appendix C). The most widely eaten families included: *Moraceae* (9 species eaten), *Euphorbiaceae* (7 species), and *Meliaceae* (5 species). The guerezas fed from eighty-one species of trees, shrubs, and vines, of which 52 are indigenous to East Africa, 21 are exotic, six of unidentified species, and two of unknown origin (Table 4.2). No insect material was observed being eaten, however while feeding on plant matter some insects were likely ingested. All three troops fed on the following nine species: *Antiaris toxicaria, Canthium vulgare, Ficus natalensis, Hevea brasiliensis, Maesopsis eminii, Musanga cecropioides, Piptadeniastrum africanum, Pseudospondias microcarpa,* and *Trichilia prieuriana.* Although this section contrasts the diet and tree density between the troops it does not present comparable nutrition available in the three home ranges (Siex and Struhsaker 1999).

Table 4.2: Origin Breakdown of Species. Including feeding trees, shrubs and vines eaten by the individual troops and collective overall species origin totals. 'Troop Breakdown' chart numbers do not match above text numbers (and 'Overall Breakdown' numbers) as there is an overlap in species eaten, therefore some species will be counted once overall but may be counted two or three times when broken down by troop. Unk. = Unknown.

	Indigenous	**Exotic**	**Unidentified**	**Unk. Origin**	**Total**
Troop Breakdown -					
Para	25	7	1	0	**33**
Natural Forest	33	15	3	1	**52**
Hill	21	7	3	1	**32**
Total	**79**	**29**	**7**	**2**	**117**
Overall Breakdown -	**52**	**21**	**6**	**2**	**81**

Para Troop

The Para troop fed on 32 identified species of trees, shrubs, and vines (and one unidentified species) of which 25 were indigenous, seven exotic, and one of unknown origin (Table 4.3). Out of the 32 identified species, 13 (39.4%) were eaten solely by the Para troop. Exotic species made up 21.2% of the diet. The top five species in the Para troops' diet made up 82.5% of the overall recorded diet (Table 4.4).

Natural Forest Troop

The Natural Forest troop ate 49 identified species of plants (and three unidentified species), 33 of those were indigenous, 15 exotic, and one of unknown origin. Of the 52 species, 26 (50%) were eaten solely by the Natural Forest troop animals. Exotic species made up 28.8% of the diet. The top five species in the Natural Forest troops' diet made up 73.5% of the overall recorded diet.

Table 4.3: List of Foods Eaten

Latin Name	Common Name	Troop	ML	NL	SH	BK	FL	SE	FR	VI	EP	UN	Other
Indigenous Species													
Albizia coriaria	Mugavu	HT		X			X						
Albizia grandibracteata	Lg. Leaved Albizia	HT		X	X	X							
Albizia gummifera	Peacock Flower	NFT		X		X							
Albizia zygia	Red Nongo	HT		X	X	X							
Antiaris toxicaria	Black Cloth Tree	ALL	X	X					X			X	
Antiaris toxicaria var. *africana*	Antiaris	HT	X										
Azanza garckeana ***		HT					X						
Blighia unijugata		PT		X									
Canthium vulgare		ALL		X								X	
Cola acuminata	Cola Nut Tree	NFT	X			X							
Cordia abyssinica	Lg. Leaved Cordia	PT				X							
Cordia millenii	Drum Tree	NFT, PT		X									
Craibia rawraufi		NFT, PT		X									
Croton megalocarpus	Croton	HT		X		X							
Croton sylvaticus (C. oxypetalus)	Forest Croton	PT			X	X							
Entandrophragma sp. (utile?)	Budongo Mahogany	HT		X									
Erythrina excelsa		NFT		X	X	X							
Fagaropsis angolensis		PT	X	X									
Ficus artocarpoides		PT		X									
Ficus exasperata		NFT		X									
Ficus natalensis	Bark-Cloth Fig	ALL		X									

SYMBOLS - PT=Para troop, NFT=Natural Forest troop, HT=Hill troop, ML=mature leaves, NL=new leaves, SH=shoots, BK=bark, FL=flowers, SE=seeds, FR=fruit, VI=vines, EP=epiphytes, UN=unidentified parts.

Table 4.3: Continued,

Latin Name	Common Name	Troop	ML	NL	SH	BK	FL	SE	FR	VI	EP	UN	Other
Indigenous Species continued,													
Ficus sur (F. capensis)	Cape Fig	NFT		X									
Ficus thonningii (F. stipilata)		PT	X	X									
Funtumia africana	Bush Rubber	NFT	X	X									
Lovoa trichilioides	Uganda Walnut	NFT, PT				X							
Maesopsis eminii	Musizi	ALL	X	X				X	X				
Markhamia lutea		HT		X									
Michelia champaca	Champak	NFT		X									
Momordica foetida		NFT								X			
Morinda lucida	Brimstone Tree	NFT, PT	X	X	X								
Musanga cecropioides	Umbrella Tree	ALL	X	X			X						
Myrianthus holstii	Giant Yellow Mulberry	NFT, PT	X?										
Nauclea diderrichii	Opepe	HT		X									
Piptadeniastrum africanum	Mpewere/Dahoma	ALL		X	X	X		X					
Podocarpus latifolius	E. Africa Yellow Wood	PT	X	X	X	X							
Polyscias fulva	Parsol Tree	ALL	X	X		X	X					X	
Polysias zuwa		NFT, HT	X										
Premna sp.		HT		X									
Pseudospondias microcarpa		ALL		X		X							
Pseudospondias sp.		NFT											Sap?
Rauvolfia vomitoria		NFT		X		X							
Sapium ellipticum	Musasa	NFT, PT	X	X		X							Termite Soil
Spathodea campanulata	Flame of the Forest	NFT, HT	X	X									Cut down 8/98

Table 4.3: Continued,

Latin Name	Common Name	Troop	ML	NL	SH	BK	FL	SE	FR	VI	EP	UN	Other
Indigenous Species continued,													
Sterculia dawei		NFT, PT				X							
Syzigium sp.		PT		X								X	
Teclea nobilis	Nzo	PT	X	X		X							
Teroi cocoa		NFT	X										
Tetrorchidium didymostemon		NFT										X	
Trichilia africana **	African Breadfruit	NFT		X									
Trichilia dregeana	Sekoba	NFT		X									
Trichilia prieuriana		ALL		X									
Trilepisium madagascariense		NFT	X	X								X	
Exotic Species													
Aleurites moluccana (Malaya)	Candle-Nut Tree	NFT		X									
Arenga pinnata (spedis) (Malaya)	Sugar Palm	NFT, HT	X	X		X							
Aristolochia elegans (T. America)	Calico-Flower	NFT, PT								X			
Bougainvillea glabra (T. America)	Bougainvillea	HT					X			X			
Caryota urens (T. Asia)	Fishtail Palm	NFT, HT	X										
Ceiba pentandra (T. America)	Kapok Silk Cotton	PT		X									
Eucalyptus citriodora (Australia)	Lemon-Scented Gum	PT	X			X							
Eucalyptus sp. (Australia)		NFT, HT				X							
Eugenia uniflora (T. America)	Brazil Cherry	NFT, PT		X									
Ficus benjamina (Asia)	Java Fig	NFT										X	
Gmelina arborea (Asia)*		PT				X							

Table 4.3: Continued,

Latin Name	Common Name	Troop	ML	NL	SH	BK	FL	SE	FR	VI	EP	UN	Other
Exotic Species continued,													
Grevillea banksii (Australia)		NFT					X						
Haematoxylon campechianum	(T. America) Logwood	NFT		X?									
Hevea brasiliensis (T. America)	Para Rubber Tree	ALL	X	X	X				X				AW2 fell 10/98
Manihot esculenta (America)*	Cassava	HT	X										
Melia dubia (Asia)	Flowering Ash	NFT	X										
Philodendron sp. (T. America)	Philodendron	NFT								X			
Sapindus saponaria (T. America)	Soap Berry Tree	NFT, HT		X	X				X			X	
Spondias lutea (Pacific Islands)	Hog-Plum	PT	X	X									
Tabebuia pentaphylla (T. America)	Rosy Trumpet	NFT	X	X									
Thunberga grandiflora (India)	Blue Trumpet Vine	NFT					X			X			
Unknown Origin													
Aedzia zygia *		HT				X						X	
Alafia grandis		NFT								X			
Unidentified Species	**Symbol**												
Unidentified Species 1	204/205	PT, NFT	X			X							
Unidentified Species 2	P48	HT		X									
Unidentified Species 3	P49	HT									X		
Unidentified Species 4	Lng. epi.	HT							X		X		
Unidentified Species 5	P14	NFT								X			
Unidentified Species 6	P23	NFT								X			

* Represents eaten outside the scope of instantaneous sample or focal data collection   ** Not a positive identification   ***Possibly introduced to E. Africa

Table 4.4: Top Five Species Eaten. Top five plant species eaten by each guereza troop. Based on percentage of instantaneous feeding samples.

	Troop		
Species	**Para**	**Natural Forest**	**Hill**
Albizia grandibracteata	-	-	34
Albizia gummifera	-	21.5	-
Antiaris toxicaria	-	-	7.6
Craibia rawraufi	-	11	-
Ficus thonningii	9	-	-
Hevea brasiliensis	37.1	-	-
Maesopsis eminii	6.1	6.1	-
Markhamia lutea	-	-	6.5
Piptadeniastrum africanum	23.5	-	5.5
Premna sp.	-	-	19.8
Pseudospondias microcarpa	-	24.8	-
Trichilia africana	-	10.1	-
Vines[1]	6.8	-	-
Total	**82.5%**	**73.5%**	**73.4%**

[1] Vine species consists of *Alafia grandis*, *Aristolochia elegans*, *Thunberga grandiflora*, *Philodendron* sp., *Momordica foetida*, and unidentified.

Hill Troop

The Hill troop ate 29 identified species of plants (plus three unidentified), 21 of those were indigenous, seven exotic, and one of unknown origin. Of the 31 identified species, 15 (48.4%) were eaten solely by the Hill Troop animals. The diet was composed of 21.9% exotic species. The top five species in the Hill troops' diet made up 73.4% of the overall recorded diet.

Available Feeding Trees

There were 710 feeding trees (greater than 3cm DBH) available in the Entebbe Botanical Gardens, of which 22% were exotics (156 trees). The guerezas fed from 149 individual measured trees (Table 4.5). In addition, there were nine species of trees and four species of vines that were unmeasured (see Appendix D for breakdown number of feeding trees by section). The Para and Natural Forest troop feeding tree numbers are an underestimate due to the decreased visibility in the residual sections of natural forest.

Para Troop

The Para troop ate from the highest number of individual trees (n = 65), possibly due to the large number of available trees as well as the troops high reliance upon *Hevea brasiliensis*. They ate from 30 of the 46 available trees. There were 253 feeding trees available (of which 51 trees were exotic species) in the Para troop home range making up a cumulative DBH of 11,507 cm and a total density of 39.5 trees per hectare (Table 4.6). Density of the top five recorded feeding trees was 8.59 trees per hectare (with one tree unmeasured). The tree most frequently fed upon by the Para troop had a density of 6.88 trees per hectare.

Natural Forest troop

The Natural Forest troop fed from 68 individual trees. There were 311 feeding trees (of which 121 trees were exotic species) available in the Natural Forest troop home range making up a cumulative DBH of 18,686 cm and a total density of 45.7 trees per hectare. Density of the top five recorded feeding trees was 5.88 trees per hectare (with one tree unmeasured). The tree most frequently fed upon by the Natural Forest troop had a density of 2.79 trees per hectare.

Table 4.5: Top Five Available Feeding Species. Top five species of feeding trees available in each individual troop home range.

Species	Troop Para	Troop Natural Forest	Troop Hill
Antiaris toxicaria	16[5]	11	18[1]
Arenga pinnata	1	60[1]	4
Canthium vulgare	14	12[5]	9[5]
Entandropragma sp.	-	-	11[4]
Hevea brasiliensis	44[1]	1	1
Maesopsis eminii	3	17[4]	15[3]
Musanga cecropioides	8	10	9[5]
Pseudospondias microcarpa	25[4]	19[3]	18[1]
Sapium ellipticum	31[2]	21[2]	15[3]
Spathodea campanulata	-	2	16[2]
Trichilia prieuriana	26[3]	-	1
Total	**168**	**153**	**117***

The superscripts indicate the availability ranking of the five most commonly eaten species.
* Ties were found for the first, third, and fifth positions.

Table 4.6: Total Density and Cumulative DBH. Broken down by individual home range. See also Appendix D.

Troop	Total tree[1] density no/ha	Total feeding[2] tree density no/ha	Cumulative feeding tree DBH	Top 5 feeding tree density no/ha	Top 1 feeding tree density no/ha
Para	69.4	39.5	11,507	8.59[3]	6.88
Natural Forest	83.8	45.7	18,686	5.88[3]	2.79
Hill	82.8	21.7	13,868	3.66	0.22

1 All trees in each individual home range.
2 All recorded feeding trees in each individual home range.
3 One of the Top 5 feeding trees unmeasured.

Hill troop

The Hill troop ate from 32 individual trees. There were 202 available feeding trees (of which 69 trees were exotic species) in the Hill troop home range making up a cumulative DBH of 13,868 cm and a total density of 21.7 trees per hectare. Density of the top five recorded feeding trees was 3.66 trees per hectare. The tree most frequently fed upon by the Hill troop had a density of 0.22 trees per hectare.

Foods of Special Interest

There were a few species of plants that played an important role and/or are of special interest in this study. These plants are presented below.

Hevea brasiliensis – Important Exotic Food

Hevea brasiliensis (Para Rubber tree) played an important role in the diet of the Para troop. There were 46 Para trees of which 44 were found in the Rubber plantation (Section B) of the Botanical Gardens, a 33 x 202 meter section of rowed, planted trees. The trees made up a large portion of the Para troop's home range, and formed 37.1% of the Para troop's diet. This Brazilian tree produces a milky sap that can be turned into rubber (Lötschert and Beese 1983). The *Hevea brasiliensis* found in the Gardens average eight to 20 meters in height. Leaves are shed during the dry season and when the three-celled ovary ripens it "explodes noisily into 6 pieces, flinging seeds a distance of about 15m" (Lötschert and Beese 1983:244).

The animals fed on a wide array of *Hevea brasiliensis* plant parts, including shoots, new and mature leaves, and the exocarp of the unripe fruit. There was a single small *Hevea brasiliensis* tree in Section F (Natural Forest troop home range) and the animals had it stripped of leaves whenever it budded out. Aside from that single tree, both the Hill and

Natural forest troops had to move into the Para troops' defended territory to obtain food from *Hevea brasiliensis*.

Albizia gummifera - Feeding on Bark

As found in the previous section, the Natural Forest troop had a significantly higher rate of feeding on bark than was found in the diet of the other two troops. *Albizia gummifera* (Peacock Flower, a 15 meter tree indigenous to East Africa) made up 21.5% of the total Natural Forest troop instantaneous feeding samples, with an observed dietary composition of 63.1% bark and 36.9% new leaves. *Albizia gummifera* bark made up 85.1% of all bark eaten by the Natural Forest troop. The Natural Forest troop fed from the only two available *Albizia gummifera* trees. Although the animals were obtaining bark by peeling it off of the branches, as this species of tree exudes sap, the animals may have been ingesting the sap while feeding on bark. Ugandans use *Albizia gummifera* bark for medicinal purposes (Katende, et *al.* 1995).

Piptadeniastrum africanum - Individual Tree Preference

There were 20 available *Piptadeniastrum africanum* trees (Mpewere tree) located in the Botanical Gardens. All three troops fed on the new leaves, shoots, bark and seedpods of this tree. *Piptadeniastrum africanum* made up 5.5% of the Hill troop diet. The Hill troop fed on two trees located in the Botanical Gardens and one outside the Gardens. Similar to other studies, the Hill troop guerezas showed an individual tree preference (Clutton-Brock 1975). Although there were 11 trees of this species located in the Botanical Gardens portion of the Hill troops' home range, the animals fed from a *Piptadeniastrum* *africanum* tree located outside the Botanical Gardens. To get to the tree they had to cross through the private property of a Ugandan home, thereby increasing their visibility. The animals were observed outside the Gardens on more than one occasion: however, they only left the Gardens once during the collection of instantaneous sample data. On that day, they spent almost five hours outside the Gardens resting and feeding in the *Piptadeniastrum africanum* tree. When attempting to return to the Gardens, they received aggression from local children (see Inter-Species Interactions, Section 5).

Manihot esculenta - Crop Raiding

Although *Manihot esculenta* was only recorded once as a food item, it represents the single recorded incident of crop raiding. While moving outside the Botanical Gardens, the adult male of the Hill troop fed off the mature leaves of a cassava plant (*Manihot esculenta*) located in a garden plot on private property.

Medicinal Plants

Humans have medicinal uses for some of the food species eaten by the guerezas (Abbiw 1990, Lötschert and Beese 1983, Hall and Swaine 1981, Ayensu 1978, Lind and Morrison 1974, Dale and Greenway 1961, Williams 1949). Species used as purgatives and laxatives, to treat dysentery and intestinal worms include: *Croton megalocarpus*, *Ficus natalensis*, *Funtumia africana*, *Maesopsis eminii*, and *Morinda lucida*. Plant species used to increase milk flow, to treat sexually transmitted diseases, urethral problems, and amenorrhorea include: *Ficus sur*, *Musanga cecropioides*, *Spathodea campanulata*, and *Tabebuia pentaphylla*. Species used for general medicinal purposes include: *Albizia* *coriaria, Albizia gummifera, Antiaris toxicaria, Ceiba pentandra, Eucalyptus citriodora, Markhamia lutea, Piptadeniastrum africanum, Pseudospondias microcarpa, Sapium ellipticum*, and *Teclea nobilis*. In addition, *Cola acuminata* is a source of caffeine and *Albizia zygia* is used as an aphrodisiac.

A medicinal plant of particular interest is *Rauvolfia vomitoria*, which made up 2.9% of the Natural Forest troop's instantaneous feeding samples. Of the six available trees one was recorded being fed on by the Natural Forest troop. *Rauvolfia vomitoria* is native to Africa and has been found to have a high level of alkaloid-rich leaves (Waterman and Kool 1994). Although they have a high toxin level, McKey, et *al.* (1981), in a study examining food selection in the diet of *Colobus satanas*, found *Rauvolfia vomitoria* to have the greatest concentration of nitrogen, potassium, and ash, and lowest concentration of digestion-inhibitors of all plants in the subjects' diet. The bark is used by humans as a compress for swellings and sprains, to induce vomiting, decoction for measles, parasitic skin disease, yaws, head lice, and used as an aphrodisiac and sedative. In addition, it is used to control hypertension, indigestion, colic, diarrhea, and scabies (Ayensu 1978).

Summary

Leaves (of all ages) made up the majority of the three troops cumulative diet, with the Para troop having the greatest amount of leaves recorded during the instantaneous sample data collection. Significant differences between the feeding rates of shoots, mature and new leaves were found between the Para troop and the other two troops. The Para troop fed more on mature leaves and shoots and less on new leaves than the other troops.

Significant differences were found in bark feeding rates, with the Natural Forest troop having a higher feeding rate than the other two troops. Flowers, fruit, and vines were found to be significantly different, however when multiple comparisons were preformed they were unable to confirm the differences. Epiphytes, and termite soil were recorded solely in the Hill troop diet, with seeds found only in the Para troop diet. The instantaneous feeding samples spent on unidentified foods were similar between troops. The breakdown of plant parts was similar between the age-sex categories.

The guerezas in this study fed from 31 plant families and 81 species, of which 25.9% are exotic to East Africa. The Natural Forest troop fed on the highest number of overall species and the highest number of exotic species. In addition, the Natural Forest troop had the least amount of dietary overlap with the other two troops. Only nine species were fed on by all three troops. The monkeys fed from 149 individual trees, of which the Para troop fed from the highest number of individual trees. The Natural Forest troop had the highest cumulative overall DBH and the greatest density of feeding trees in their home range. The Para troop had the highest feeding tree density of the most frequently fed upon tree species.

A few tree species played an important role in the diet of the Botanical Garden guerezas. *Hevea brasiliensis* made up 37.1% of the Para troop diet and was a source of territorial dispute between the three troops. *Albizia gummifera* bark made up a large portion of the Natural Forest troop diet. The amount of bark found in the Natural Forest troop diet was significantly different from the other two troops and was at a much higher rate than found in any other guereza study. The Hill troop left the Botanical Gardens to selectively feed on an individual tree that was commonly available in their home range. In addition, some of the plants used by the human population for medicinal purposes were fed on by the guerezas.

2. RANGING PATTERNS AND SITES OF INTER-TROOP CONFLICT

This section will present the daily individual troop ranges, as well as the total troop home range sizes observed during the course of this study. In addition, density of the individual troop home ranges and areas of inter-troop conflict will be presented.

Day Range

The major movements during the day occurred during two travel periods, one in the midmorning (09:00 - 11:00) and one in the late afternoon while moving toward the sleeping tree. Once the travel direction toward a new feeding or sleeping site was chosen the troop seldom diverged. However, the animal to start and lead the progression altered during the day. The Entebbe Botanical Garden guerezas had an observed daily range from 62 to 1036 meters. During the instantaneous sample data collection, the Para troop had an approximate mean day range of 252 meters, the Natural Forest troop had a approximate mean day range of 378 meters, while the Hill troop had an approximate mean day range of 529 meters (Table 4.7).

Home Range, Density, and Overlap

Home range included all observed areas used by the individual troop and was reconstructed from the day range data. Each of the troops resided in a somewhat distinctive area compared to the other two. All three of the troops ventured out of the territory that they actively defended.

Table 4.7: Home Range, Density and Overlap

Troop	Day Range	Home Range	Density[1]	% Home Range Overlap[2]		
				PT	NFT	HT
Para (PT)	252 m	6.4 ha	2.2	-	54.8%	22.5%
Natural Forest (NFT)	378 m	6.8 ha	1	51.5%	-	18.2%
Hill (HT)	529 m	9.3 ha	0.4	15.3%	13.2%	-

[1] Density = number of individuals / hectare.
[2] Percent of total home range overlapped with the other troop(s).

The Para troop's observed home range (approximately 6.4 hectares) fell completely within the boundaries of the Botanical Gardens and had the highest density of individuals per area used (2.2 individuals per hectare). They were primarily found in Sections A, B, E, and Bush Area A. They were also occasionally seen in Sections C and D. The Para troop spent 20% (13 hours of instantaneous sample time) inside the small, impenetrable, residual natural forest (Bush Area A). Their home range overlapped 54.8% with the Natural Forest troop and 22.5% with the Hill troop (Table 4.7).

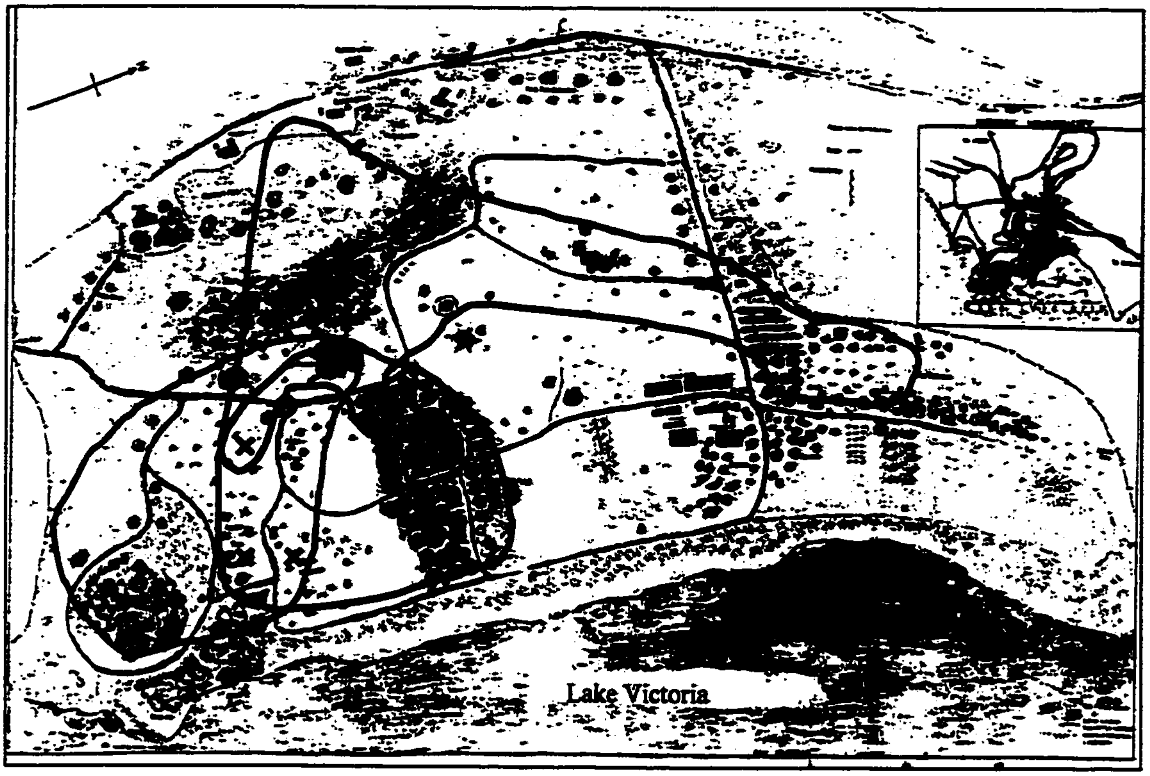
The Natural Forest troop's observed home range (approximately 6.8 hectares) occurred exclusively in the Botanical Gardens, and was found in Sections B, C, D, E, and F. The Natural Forest troop spent the majority of their time inside the residual natural forest with only 700 minutes (11.7 hours - 18% of the instantaneous sample data) outside of the natural forest (Section F). They had a density of 1.0 individual per hectare. Their home range overlapped 51.5% with the Para troop and 18.2% with the Hill troop.

The Hill troop had the largest home range (approximately 9.3 hectares) and the only home range with no residual natural forest. They were the only troop to leave the fenced area of the Botanical Gardens during the course of the study. The troop was found in Sections E, H, I, K, L, and M. In addition, on one day they were observed in Sections B and F. The Hill troop had the lowest density at 0.4 individuals per hectare. Their home range overlapped 15.3% with the Para troop and 13.2% with the Natural Forest troop.

Sites of Inter-Troop Conflict

All three troops had sites of inter-troop conflict (Figure 4.3). Recorded Para troop conflict sites were recorded in the planted Para Rubber trees (*Hevea brasiliensis*), in Section B, with both the Natural Forest (four interactions were recorded) and Hill troops (two interactions). The Natural Forest troop interacted with the Para troop (three recorded interactions) in Section C and in the preserved natural forest (Section F) from the Hill troop (one interaction). The Hill troop interacted with both the Para (one interaction) and

Figure 4.3: Home Ranges with Sites of Inter-troop Conflict. Map and home ranges not to scale, copied with permission from Entebbe Botanical Gardens.



<u>**Legend**</u>

External border of the Para troop home range.

External border of the Natural Forest troop home range.

External border of the Hill troop home range.

X's - sites of inter-troop encounters
Red x's - Para troop defense sites against the Natural Forest or Hill troops.
Blue x's - Natural Forest troop defense sites against the Para or Hill troops.
Green x's - Hill troop defense site against both the Para and Natural Forest troops.

Natural Forest troops (one interaction) in a small-planted garden in Section E. Section 5 presents a description of inter-troop interactions.

Summary

All three troops actively defended sections of their home range. Of the three troops the Para troop had the smallest observed day and home ranges, with the highest population density level, and greatest percentage of home range overlap with the other troops. The Hill troop had the largest observed day and home ranges of the three troops, the lowest population density, and the least amount of home range overlap. In addition, the Hill troop was the only troop observed outside the Entebbe Botanical Gardens during the course of the study. During the course of this study there were no shifts in home ranges, however the entire study was completed during the dry season.

3. ACTIVITY BUDGET

In this section I examine the proportion of time the animals spent scanning, sleeping, moving, feeding, involved in social behaviour, out of the observer's sight, as well as other activities. I will look at differences between the three troops (Figure 4.4) and between the age-sex categories (Figure 4.5).

Scan

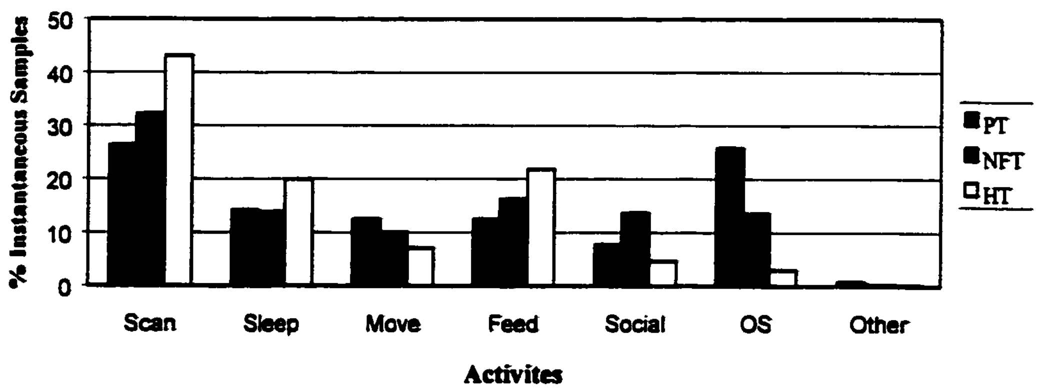
The recorded instantaneous sampling of guereza activity indicated that scanning was the main activity throughout the samples making up a mean of 30.7% and median 30.5% (range: 11.1 - 50.8%).

Inter-troop Differences

The Para troop (n = 10) spent a mean 26.3% of the instantaneous samples scanning, while the Natural Forest troop (n = 5) spent 32.2%, and the Hill troop (n = 3) spent 43.1% scanning. Scanning was not found to be significantly different between the individual troops (Kruskall Wallis one-way Analysis of Variance, H = 5.337, n = 18, df = 2, p = 0.069).

Figure 4.4: Comparison between Troop Activity Budgets. Based on mean percentages of instantaneous sample data. Showing a significant difference between the troops with regards to feeding and the number of instantaneous 'out of sight' samples. PT= Para troop, NFT= Natural Forest troop, HT= Hill troop, OS= out of sight.

Figure 4.4: Comparison between Troop Activity Budgets



Age-sex differences

Significant scanning differences were found between the age-sex categories (H = 9.732, n = 18, df = 2, p = 0.008). A multiple comparison between the age-sex groups (critical values 6.46 and 7.58, z = 2.394) confirmed that scanning was significantly different between all three categories. Males (n = 4) spent a mean 46.5% of the data in scanning behaviour, as compared to females (n = 7) and juveniles (n = 7) who spent 31.6% and 20.8%, respectively, of the data scanning.

Focal Data

Focal scans lasted an average of 67.9 seconds (range: 1 - 1200 seconds). There was no significant difference between the Natural Forest troop age-sex categories in scanning (Kruskall Wallis one-way Analysis of Variance, H = 3.600, n = 5, df = 2, p = 0.368).

Sleep

Sleeping made up a mean of 15.1%, median 15% of the instantaneous sample data (range: 8.6 - 22%).

Inter-troop Differences

Although the probability was close to the alpha level, sleeping was not significantly different between the three troops (H = 5.927, n = 18, df = 2, p = 0.052). The Para troop spent a mean 14.2% of the instantaneous sample data sleeping, while the Natural Forest and Hill troops spent 13.9% and 20%, respectively.

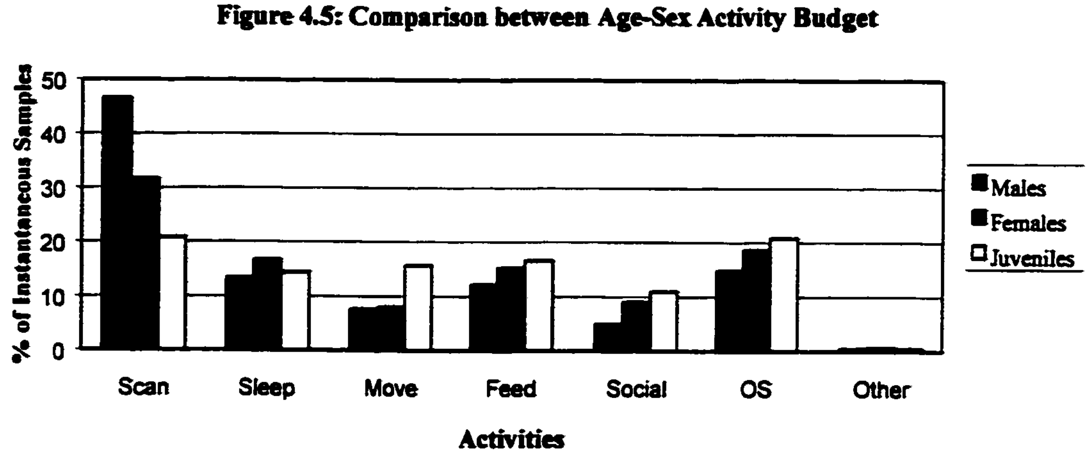
Age-sex Differences

Sleeping was not significantly different between the age-sex categories (H = 3.350, n = 18, df = 2, p = 0.187). The males slept a mean 13.4% of the instantaneous samples, while the females slept 16.7% and the juveniles slept 14.5%.

Focal Data

Sleeping lasted a mean of 414.7 seconds (focal range: 16 - 1200 seconds). Focal data found no significant differences between the Natural Forest age-sex categories (H = 1.400, n = 5, df = 2, p = 0.497).

Figure 4.5: Comparison between Age-Sex Activity Budgets. Based on mean percentages of instantaneous sample data. Showing the proportion of instantaneous samples devoted to scanning to be significantly different between the age-sex categories and movement to be significantly different between the juveniles and adults of both sexes. OS= out of sight.



Movement

Movement made up a mean of 11% and median 9.6% of the instantaneous sample data (range: 3.7 - 18.9%). In addition to the inter-troop and age-sex tests, a comparison between the age-sex categories of the Para troop showed a significant difference in regards to movement ($H = 6.545$, $n = 10$, $df = 2$, $p = 0.038$). A multiple comparison test (critical values 6.28 and 5.13, $z = 2.394$) confirmed that the significant differences occurred between the juveniles and the adult members of the troop. The Para troop juveniles ($n = 4$) spent a mean 17.5% of the instantaneous sample data moving, as compared to the adult males ($n = 2$) who spent 9.4% and adult females ($n = 4$) who spent 9.2% moving.

Inter-troop Differences

There were no significant differences found between of the troops ($H = 3.832$, $n = 18$, $df = 2$, $p = 0.147$). The Para troop spent 12.5% moving, while the Natural Forest troop moved 10.1% and the Hill troop moved 7.1% of the instantaneous samples.

Age-sex Differences

Significant differences were found between the categories of individuals and the relative proportion of time spent in movement ($H = 12.158$, $n = 18$, $df = 2$, $p = 0.002$). A multiple comparison between the age-sex groups (critical values 7.58 and 6.46, $z = 2.394$) confirmed that the differences occurred between the adults and the juveniles. The juveniles spent a mean 15.7% of the instantaneous sample data moving, as compared to the movement of the adult males (7.7%) and adult females (8%).

Focal Data

Movement lasted a mean of 6.6 seconds (focal range: 1 - 54 seconds). Focal data showed no significant differences between the age-sex categories ($H = 3.600$, $n = 5$, $df = 2$, $p = 0.165$).

Feed

Feeding averaged a mean of 15.1% and median 15.5% of the instantaneous sample data (range: 5.8 - 24.2%).

Inter-troop Differences

Feeding was found to be significantly different between the three troops ($H = 8.454$, $n = 18$, $df = 2$, $p = 0.015$). A multiple comparison between the troops (critical value 7.0, 8.38, 9.3, $z = 2.394$) revealed that the significant difference occurred between the Para and Hill troops (sample sizes: n = 10 and n = 3) with regards to feeding. The Para troop spent a mean 12.5% of the instantaneous samples feeding while the Hill troop spent 21.8%. The Natural Forest troop fed for 16.3% of the instantaneous samples.

Age-sex Differences

There were no significant feeding differences between the age-sex categories (H = 1.927, n = 18, df = 2, p = 0.381). The males spent 12.2% of the instantaneous samples feeding, while the females spent 15.3% and the juveniles spent 16.7% feeding.

Focal Data

Feeding bouts lasted a mean of 64.9 seconds (focal range: 1 - 650 seconds). Focal data showed no significant difference between feeding age-sex categories (H = 0.600, n = 5, df = 2, p = 0.741).

Social

Social interactions made up a mean of 8.9% and median 9% of the total instantaneous sample data (range: 2 - 18.7%). Similar to other studies, the majority (99.2%) of interactions were neutral or affiliative in nature (Oates 1977c, Dunbar and Dunbar 1976).

Inter-troop Differences

Social interactions were found to be significantly different between the three troops (H = 8.163, n = 18, df = 2, p = 0.017). A multiple comparison between the troops (critical values 7.0, 8.38, and 9.3, z = 2.394), however, showed that there were no significant differences between pairs of troops. The Para troop, Natural Forest troop, and Hill troop were involved in social activities - 7.8%, 13.7%, and 4.7% of instantaneous samples, respectively.

Age-sex Differences

Although significant differences were found between the categories of individuals and the proportion of time spent in social behaviour, this probability is very close to the alpha level ($H = 6.023$, $n = 18$, $df = 2$, $p = 0.049$) and was not found to be significant when a multiple comparison was performed on the age-sex categories. The males were involved in social behaviour 4.9% of the instantaneous samples, while the females and juveniles were involved 9.1% and 11.1%, respectively.

Focal Data

There were 291 social interactions recorded in the focal data (3.9 per focal observational hour). Social bouts lasted a mean of 34.1 seconds (focal range: 1 - 390 seconds). Focal data showed no significant difference between age-sex categories in social behaviour ($H = 2.000$, $n = 5$, $df = 2$, $p = 0.368$).

Out of Sight (OS)

The animals were out of the observers' sight a mean 18.6% and median 20.3% of the instantaneous sampling data (range: 2.1 - 37.3%).

Inter-troop Differences

Significant differences were found between the three troops for the 'out of sight' condition ($H = 13.168$, $n = 18$, $df = 2$, $p = 0.001$). A multiple comparison performed between the troops (critical values 7.0, 8.38, and 9.3, $z = 2.394$) revealed each troop was significantly different from the other two. The Para troop was found to have a mean 'out of sight' rate of 25.8%, while the Natural Forest troop and the Hill troop were at 13.5% and 3.1% respectively.

Age-sex Differences

Age-sex comparisons with regard to individuals being out of sight revealed no significant differences (H = 1.044, n = 18, df = 2, p = 0.593). The males were out of sight a mean 14.8% of the instantaneous sample data. The females and juveniles were out of sight 18.6% and 20.8%, respectively.

Focal Data

The Natural Forest troop was out of site a mean 58.6 seconds (range: 1 – 309 seconds). Focal data revealed no significant differences between the age-sex categories of the Natural Forest troop (H = 3.600, n = 5, df = 2, p = 0.165).

Other

The animals were involved in the 'other' activity category a mean 0.6% and median 0.6% of the instantaneous samples (range: 0.1 - 1.4%).

Inter-troop Differences

Significant differences were found between the troops and the proportion of time spent in 'other' activities (H = 8.822, n = 18, df = 2, p = 0.012). A multiple comparison test between the troops (critical values 7.0, 8.38, and 9.3, z = 2.394) confirmed the differences occurred between the Para troop and the other two troops. The Para troop spent a mean 0.8% of the instantaneous sample data in 'other' activities as compared to the 'other' activities of the Natural Forest troop (0.4%) and Hill troop (0.2%).

Age-sex Differences

'Other' activities were not found to be significantly different between the age-sex categories (H = 0.692, n = 18, df = 2, p = 0.708). The males were involved in 'other' activities a mean 0.5% of the instantaneous sample data, while the females and juveniles were involved 0.7% and 0.5%, respectively.

Focal Data

Other activities lasted a mean 20.3 seconds (range: 4 – 33 seconds) of the focal data. Focal data revealed no significant differences between the age-sex categories ($H = 1.400$, $n = 5$, $df = 2$, $p = 0.497$).

Summary

Overall, the guerezas in the Entebbe Botanical Gardens spent the greatest proportion of time scanning. Feeding was found to be different between the Para and Hill troops, with the Hill troop spending more time feeding than the Para troop. Significant differences between all three troops were found in the amount of recorded 'out of sight' instantaneous samples, with the Para troop recorded out of sight the most often. Social behaviour was found to be significant in both the inter-troop and age-sex comparisons, however no significance was found when the multiple comparisons were preformed. Significant differences were found between the Para troop and the other two troops in the time spent in 'other' categories. Instantaneous samples spent sleeping, scanning, and moving were similar between troops.

Scanning rates were significantly different between the age-sex categories, with males spending the most amount of time scanning. Significant differences in movement rates were found between the juvenile and the adults of both sexes, with the juveniles spending more time moving than the adult members of the troop. Instantaneous samples spent sleeping, feeding, out of sight, and other activities were similar between the age-sex categories.

4. GROUP COMPOSITION

In May, when the study began, the largest of the three troops (the Para troop) consisted of twelve animals (two adult males, four adult females, two large juvenile females, two small juvenile females, a female black and white infant, and one white male neonate) (Table 4.8). On July 1 an additional male immigrated into the troop (from an unknown location) and on September 1 a neonate (sex unknown) was born.

Table 4.8: Group Composition and Size on May 23, 1998. Numbers in brackets include changes in-group size and indicate composition at the end of the study (October 21, 1998).

Troop	TOTAL	AM	AF	LG. JF	SM. JF	B&W F	B&W -M	WHT. M	WHT. ?
Para (PT)	**12(14)**	2(3)	4	2	2	1	-	1[1]	(1)[3]
Natural Forest (NFT)	**7(7)**	2(1)	2	1	1	-	1	-	(1)[4]
Hill (HT)	**3(4)**	1	1	-	1	-	(1)[2]	-	-

AM= adult male, AF= adult female, LG.JF= large juvenile female, SM.JF= small juvenile female, B&W F= black and white female infant, B&W M= black and white male infant, WHT.M= white male neonate, WHT.?= white neonate of unknown sex.

[1] DOB - ?/05/98 [2] DOB - 28/05/98 [3] DOB - 01/09/98 [4] DOB - 14/09/98

The Natural Forest troop originally consisted of seven animals (two adult males, two adult females, one large juvenile female, one small juvenile female, and a male black and white infant). This troop also had a change in male membership during the study. On July 22, the smaller of the two males emigrated out of the troop (it is unknown if the male emigrated to another location or died). In addition, on September 14 a white neonate (sex unknown) was born.

The smallest of the three troops (Hill troop) consisted of one adult male, an adult female, and a small juvenile female. Observations of the juvenile suckling on the adult female may indicate she was the daughter of the adult female. On May 28, a neonate (male) was born.

Summary

Over the course of the study the population of all three troops increased due to births. Other recorded demographic changes included changes in male membership in both the Para and Natural Forest troop.

5. ANECDOTAL SOCIAL BEHAVIOUR

Social interactions were relatively infrequent and in some cases difficult to observe due to dense vegetation. This section presents anecdotal behavioural observations that were collected during instantaneous and focal samples, as well those noted on an *ad lib* basis. Inter-troop, intra-troop, and inter-species interactions are presented here.

A. Inter-troop Interactions

Most of the inter-troop interactions occurred when two troops moved into adjoining sections of their own home range and had visual observation of the other troop. When this occurred, the two troops would vocalize toward each other and individual troop members would affiliate within the troop (usually taking the form of ventral-ventral clinging or grooming). Occasionally the male(s) would display and/or lunge at the other troop. There were no observations of contact aggression or chases during these encounters. There was no record, in this study, of males roaring during any inter-troop interactions. In addition, all three troops spent time in inter-troop conflict in another troops' actively defended territory. The troop that most commonly used the area would vocalize, approach, and chase the outside troop back to the outside troop's home range.

Para troop

The Para troop had two sites of inter-troop conflict in Section B, one with the Natural Forest troop and one with the Hill troop (Figure 4.3). When either the Natural Forest or the Hill troop entered the Para troop's home range they fed from the Para Rubber trees. The Natural Forest troop spent 417 minutes and the Hill troop spent 110 minutes in the Para troops' territory.

Below are examples of two of interactions (involving the Para and Natural Forest troops) that do not fit the above pattern of the outside troop entering another troops defended territory and being chased out. During the first interaction the Natural Forest troop moved into the Para Rubber trees and the Para troop approached them. The Para troop chased the Natural Forest troop out of the Para Rubber trees, however, the Natural Forest troop re-entered the Para Rubber trees (18 minutes later) at which time the four males (two Natural Forest and two original Para troop males) fought, lunging at each other with possible contact aggression (clear observations were unreliable due to the dense foliage). The result of the aggression was the withdrawal of the Para troop leaving the Natural Forest troop feeding in the Para Rubber trees.

The second interaction (approximately a month later) involved the Para troop animals approaching the Natural Forest troop animals (who had returned to the same area as in the above incident). The Para troop vocalized and lunged but never entered the trees that contained the Natural Forest troop animals. The Natural Forest troop responded by returning the lunges until the Para troop moved away. The interaction ended with the Natural Forest troop spending the morning in the Para Rubber trees.

Natural Forest troop

The Natural Forest troop had two sites of inter-troop conflict in their home range. Section C was sites defended from the Para troop, who spent 36 minutes in the Natural Forest troop's territory and Section F from the Hill troop who spent 10 minutes in one interaction. During the Hill troop – Natural Forest troop interaction the Hill troop moved into a tree in the Natural Forest troops' defended territory 13 minutes after the end of a Hill troop - Para troop interaction. The Natural Forest troop male entered the same tree and threatened the Hill troop. The Hill troop male chased the Natural Forest troop male out of the tree. The Natural Forest troop male retreated but only a short distance. He immediately returned and was again chased away. The Hill troop then returned to their territory in Section E.

Hill troop

The Hill troop had a single site of inter-troop conflict (with both the Para and the Natural Forest troops) in the newly planted garden of Section E. During the collection of instantaneous samples the Para troop spent 198 minutes, and during the collection of the focal data the Natural Forest troop spent 553 minutes (9.12 hours) in Section E.

Inter-troop Vocalizations

Inter-troop vocalizations included squeak and screams emitted by all three troops. There were a total of 20 recorded squeaks and screams during the collection of the instantaneous sample data (four performed by the Para troop, five performed by the Natural Forest troop, and 11 by the Hill troop). During the collection of the focal data the Natural Forest troop squeaked and screamed 14 times toward the Para troop, and 18 times toward the Hill troop (lasting a mean 3.9 seconds, range: 1 – 24 seconds). In addition, one unidentified grunt-like male vocalization (lasting 49 seconds) was directed toward the Para troop by the Natural Forest troop's alpha male.

Male roars were sometimes contagious between the Natural Forest and Hill troop males. The Natural Forest troop responded to a Hill troop male roar once and received three responding roars from the Hill troop male. The Natural Forest troop male roared 10 times without receiving a response from the other males, while the Hill troop male roared twice with no response. The Para troop male was never noted as responding to roars performed by the other troop males.

Para troop Male Immigration

During the collection of instantaneous sample data on the Para troop, an unknown, outside male immigrated into the troop. The male came from an unidentified location outside of the Botanical Gardens. The first day the male was observed, he was in the Para troops' home range but not within visual range of the troop. Over the next few days, the male attempted to approach and follow the troop as they moved around their home range. The Para troop, as a group, would move away from this outside male. This reaction was different from when the Para troop observed either the Natural Forest troop or Hill troop in or close to their home range. In that case, the Para troop members moved toward rather than away from the outsiders. Individual Para troop members chased the outside male away (usually the alpha male, although occasionally the other adult male or one of the adult females would join in). The initial chases ranged 100 meters or more, which moved them out of visual observation. The females met the outside male's approaches with squeaks and screams, the males met the approaches with high intensity tongue clicking, and mutual intra-troop grooming was performed by all of the Para troop animals. The outside male slowly moved closer and closer to the Para troop until the Para troop male lunged and/or chased him away. The Para male then returned to the troop and the outside male resumed slowly moving closer and closer to the troop. This occurred continuously for the nine days of data collection. However, within four days of actively approaching the troop, the outside male was able to spend greater amounts of time in the same tree as the troop. Aggression was reduced to the outside male receiving lunges and short chases of five or ten meters.

On day five of the immigration, the Natural Forest troop male joined the outside male in directing aggression toward the Para troop. The Para troops' reaction was stronger toward the Natural Forest troop male than to the outside male. The Natural Forest troop male joined the outside male in threatening and lunging at the Para troop. It is unknown whether they had a previous relationship, whether the Natural Forest troop male was using this male opportunistically to move in on the Para troops' territory, or for other reasons. The two males pushed the Para troop into the far southern edge of their home range and then retreated back toward the Para – Natural Forest troop border.

By days six and seven, chases from the Para troop directed toward the outside male were more commonly being initiated and led by the beta male, while the alpha male stayed with the females.

By day eight, the outside male spent most of the day in close proximity to the Para troop with occasional chases being initiated by females. By the end of the data collection (10 days after the initial immigration), the outside male was continuously traveling with the Para troop as well as spending the majority of the day in the same tree as the troop. He was receiving fewer and shorter chases and had started to receive affiliative signals from some of the members of the Para troop (especially from the juvenile females). During and after the immigration, the outside male adapted his eating behaviour to the Para troop, feeding on the same plant species. Over the 10 days of observations there were 25 recorded chases during the instantaneous sample data (and 17 additional *ad lib* chases) directed toward the outside male and two chases from the outside male toward Para troop males. In addition, there was one recorded incident where the outside male lunged at the alpha Para troop male who then redirected and chased one of the Para troop adult females. Vocalizations directed toward the outside male included the females and juveniles squeaking and screaming 61 times during the instantaneous sample data (over 10 episodes).

B. Intra-troop Interactions

Intra-troop interactions took the form of grooming, play, sexual behaviour, neonatal transfers, aggression, and vocalizations.

Grooming

The guerezas in this study spent the greatest portion of their social activity grooming. Occasionally when a female solicited a second female, the two females would ventral-ventral cling for a few seconds prior to the grooming bout.

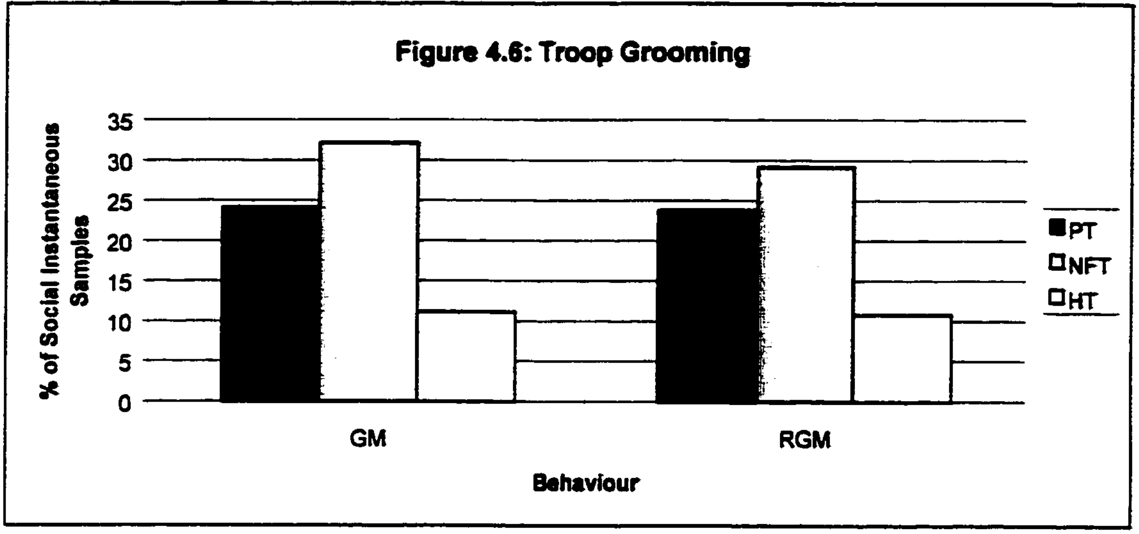
Inter-troop Differences

Neither grooming (GM), nor receiving grooming (RGM) was found to be significantly different amongst the three troops in the instantaneous sample data ($n = 18$, $df = 2$; GM: $H = 3.375$, $p = 0.185$; RGM: $H = 1.931$, $p = 0.381$) (Figure 4.6).

Age-sex Differences

The frequency of grooming was found to differ significantly when comparing the age-sex categories ($H = 9.343$, $n = 18$, $df = 2$, $p = 0.009$) (Figure 4.7). Multiple comparisons were run on the age-sex categories to determine where the grooming differences occurred. It

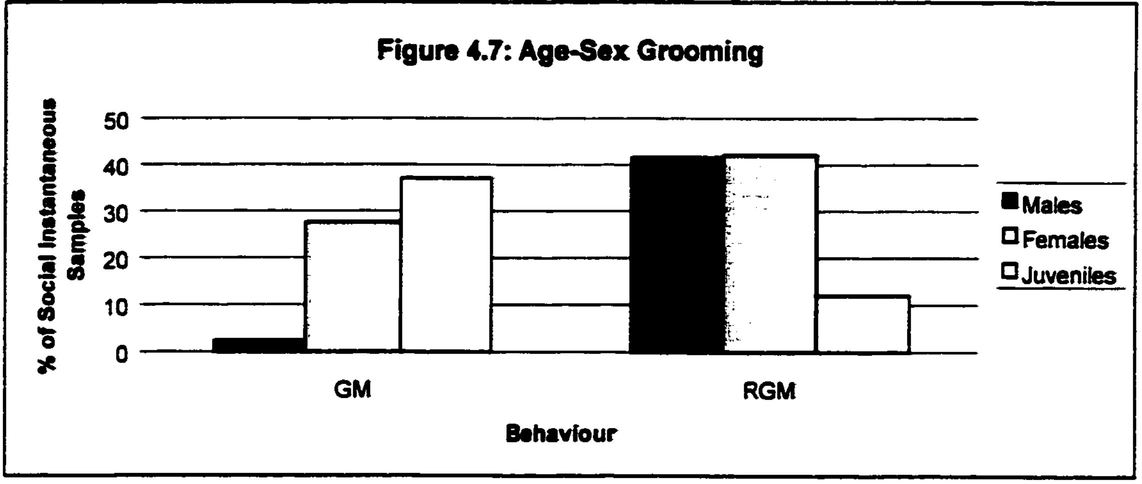
Figure 4.6: Comparison of Troop Grooming Rates. Based on mean percentages of social instantaneous sample data. Showing no significant difference between the three troops. PT= Para troop, NFT= Natural Forest troop, HT= Hill troop, GM= grooming, RGM= receive grooming.



was confirmed that the differences occurred between all three age-sex categories (critical values 7.98 and 6.76, $z = 2.394$). The males spent 2.4% of the social instantaneous sample data grooming (most commonly the adult females) as compared to the grooming performed by the females (27.6%), who groomed other adult females the most often, and by the juveniles (37.1%), whom also most commonly groomed adult females.

The act of receiving grooming was also found to be significant between the age-sex categories ($H = 9.575$, $n = 18$, $df = 2$, $p = 0.008$). Multiple comparisons (critical values 7.98 and 6.76, $z = 2.394$) were run on the age-sex categories and confirmed the differences occurred between the juveniles and the adults of both sexes. The juveniles spent a mean 12% of the social instantaneous sample data receiving grooming bouts (most commonly from other juveniles), as compared to the receiving of grooming by the males (41.6%), who received grooming most often from adult females, and females (42.2%) who received grooming most often from juveniles.

Figure 4.7: Comparison of Age-Sex Grooming Rates. Based on mean percentages of social instantaneous sample data. Showing significant differences between the grooming rates of all three age-sex categories and between the juvenile and adults receiving grooming rates. GM= grooming, RGM= receive grooming.



Focal Data

Focal observations found social activity to compose 12% (10.3 hours) in the Natural Forest troop. Similar to the instantaneous sample data, grooming was the most commonly performed social activity making up 76% of the social activities (3.13 hours). Grooming made up 83.5% of the male focal social behaviour, 76.7% of the females', and 71.6% of the juveniles'. There were 177 recorded grooming bouts in the Natural Forest troop focal data (Table 4.9). The average number of grooming bouts per individual was 29.5 (range: 1 - 57), with the majority of the grooming performed by adult and juvenile females. Adult females received grooming in 48.5% of the bouts. The juveniles performed the grooming in 60.5% of the bouts. Grooming bouts lasted an average of 62.7 seconds (range: 2 - 388 seconds). Grooming was not found to vary significantly between the age-sex categories of the members of the Natural Forest troop (H = 3.600, n = 5, df = 2, p = 0.165).

Table 4.9: Natural Forest troop Focal Grooming Breakdown. Grooming bout breakdown by actor (including neonatal grooming bouts).

		Performer				
		Male (n=1)	Females (n=2)	Juveniles (n=2)	B&W Neo. (n=1)	**Total**
	Male	-	12	16	0	**28**
	Females	1	27	57	1	**86**
Receiver	Juveniles	0	18	21	7	**46**
	B&W Neo.	0	4	13	-	**17**
	Total	**1**	**61**	**107**	**8**	**177**

Plants were sporadically incorporated into the grooming session. The animal performing the activity would usually sit and lean over the animal being groomed. The groomer would reach over and pull a piece of foliage down and over the body of the receiver then, while continuing to groom with one hand, would hold the plant with the other. I have found no record of this happening in any previous guereza study (nor has Oates, personal communication). The use of plants during a grooming bout occurred 22 times out of 98 focal grooming bouts (or in 22% of the grooming bouts).

Play Behaviour

Observed play behaviour between two or more individuals included chasing and wrestling. Juveniles and neonates were the most common participants in play behaviour (Table 4.10). Play would mainly occur during adult rest periods.

Table 4.10: Play Rates, indicating play to be more common the younger the individual (including neonatal play rates).

	Age	n	Mean %	Range
Adults	6 + yr.	11	0.54	0 - 3.3
Large Juveniles	2 - 6 yr.	3	10.2	2 - 16.6
Small Juveniles	1 - 2 yr.	4	44.4	22.7 - 69.5
Infants and Neonates	under 1 yr.	2	66.5	63.1 - 69.9

Focal Data

Playing made up 8.9% of the Natural Forest troop social focal data. There were 54 recorded play bouts over 23.9 focal minutes (an average of 24 seconds per bout), breaking down to 10.8 bouts per individual (range: 0 - 49). Wrestling was the most common form of play and occurred in 36 out of the 54 bouts. Juveniles and neonates were the most likely participants in play behaviour (involved 49 and 51 times, respectively). Adult females joined in play behaviour five times during the collection of focal data, while there was no record of adult males involved in play.

Sexual Behaviour

Sexual mounting was recorded during the collection of instantaneous sample data on the Para troop and in both instantaneous and focal sample data on the Natural Forest troop. Two mounts over two consecutive instantaneous sample days were recorded in both the Para and Natural Forest troops.

Focal data on the Natural Forest troop recorded three mounts during a single day of observations. The first copulation was recorded as *ad lib* data and occurred approximately two hours prior to the second and third mountings. The last two mountings occurred 3.5 minutes apart and lasted three and 10 seconds, respectively.

In all seven incidents, it was the alpha male who performed the mount. The male approached the female and gave the same low intensity mouth clicking as seen in grooming behaviour. All mounts recorded as 'sexual' included male thrusts. Only single mounts were observed in this study. As there is no external sign of estrous in guereza females, it is assumed that the females involved in the sexual mounting were, in fact, in estrous (Struhsaker and Leland 1987, Clutton-Brock 1979). Recorded non-sexual mounts included female-female mounts.

Neonatal Transfers

Neonatal transfers occurred when the neonate was taken from its mother. Horwich and Manski (1975) stated failed transfers occurred when the mother was unwilling to give up the neonate, when the receiver was not fully motivated to take the neonate, and/or when an older infant would cling stubbornly to its mother. None of the guereza males were observed attempting to or actually holding any of the neonates.

The high number of Para troop members and thus a high number of neonatal transfers meant *ad lib* data collection on the neonates were unreliable. I could not accurately follow the neonate and collect data on the other animals without changing the focus of the study. Collection of neonatal data on the Hill troop was also unobtainable as data collection was focused on the Para troop at the time of the Hill troop birth.

Due to the birth of a neonate during the collection of focal data on the Natural Forest troop, six days of neonatal observation are included in the data collection. Data revealed 50 successful neonatal transfers and 11 unsuccessful transfers occurring over the six days, breaking down to 0.23 neonatal transfers per minute of data collection (0.05 unsuccessful neonatal transfers per minute). Transfers lasted a mean 9.9 seconds (range: 2 - 28 seconds).

Aggression and Dominance

Aggression between individuals within the troops was a rare occurrence. Aggression took the form of spatial supplantations that included chases, lunges, and displays. Occasionally the alpha male would displace other members from feeding sites.

Para troop

There were two recorded intra-troop aggressive acts during the Para troop instantaneous sample data. One involved an unsuccessful neonatal transfer when the dam bit and slapped the female attempting to take her neonate. There was also one recorded *ad lib* lunge from an adult female toward the small adult male.

Natural Forest troop

Two intra-troop chases were recorded during the Natural Forest troop instantaneous sample data, one occurring between the juveniles and one between the adult females. Focal data revealed the adult male spent four incidents directing chases, lunges, and displays toward the females and juveniles. The females directed three incidents of displays and a single lunge toward each other and toward the juveniles. The black and white infant received aggression during three attempts to dorsal cling on his mother.

Hill troop

The Hill troop male lunged once toward the adult Hill troop female during the instantaneous sample data.

Vocalizations

Intra-troop vocalizations included mouth clicking and squeaks and screams. The low intensity mouth click is an affiliative or neutral gesture performed between members of the same group. It was commonly used prior to social interactions. For example, occasionally when a female approached another female of the same troop, she gave a low intensity mouth click prior to grooming. Squeaks and screams occurred between members of the individual guereza troops during aggressive interactions. Dependent infants and neonates gave this vocalization when left alone or occasionally when an animal other than their mother was carrying them.

Para troop

Intra-troop squeaks and screams were recorded four times during the instantaneous sample data. Three of the vocalizations occurred for unknown reasons. The other vocalization was directed toward the adult male by a juvenile female while attempting to play with him.

Natural Forest troop

Two intra-troop squeaks and screams occurred prior to a grooming bout and eight for undetermined reasons during the Natural Forest troop instantaneous sample data. Two squeaks and screams were recorded in response to the male roaring. Focal data revealed 11 intra-troop squeaks and screams lasting a mean 7.4 seconds (range: 1 - 24 seconds). These occurred during neonate transfers, ventral-ventral clinging, and prior to grooming.

Hill troop

There were no recorded vocalizations between the Hill troop members.

C. Inter-Species Interactions

Interactions periodically took place between the guerezas and other animal species. Although encounters between the three non-human primate species were the most common, interactions also occurred involving birds, squirrels, and humans. Human interactions included the humans chasing, yelling and/or throwing things at the monkeys (all three troops received human attention). There were no observations of physical contact between humans and guerezas. This study site contained three species of non-human primates (the guerezas, a single red-tail monkey, and a vervet troop) residing in overlapping home ranges. The orphan red-tail (*Cercopithecus ascanius*) was brought to the Uganda Wildlife Education Center before 1996 (no prior data available). The monkey resided in and around the Education Center grounds until approximately April 5, 1998, when he voluntarily migrated to the Botanical Gardens (Cox, personal communication).

The Botanical Garden troop of vervet monkeys (*Cercopithecus aethiops*) consisted of approximately 35 animals (see Saj 1998 for a more detailed description). Vervet - guereza interactions tended to be more active than with other species with both play and aggressive encounters recorded. Since the vervet home range included a large portion of the Botanical Gardens, this may account for the frequency of vervet - guereza interactions. Every morning the vervet troop moved through the length of the Botanical Gardens from south to north (and reverse in the evening). This path cut through all three of the guereza troops' home ranges.

Para troop

The Para troop interacted the least with other species. They spent 21 minutes (over two incidents, lasting four and 17 minutes respectively) in neutral interactions with the vervet troop, with both groups usually feeding or resting in the same tree. There was one recorded chase by the vervets directed toward the Para troop and there were three recorded squeaks and screams by the Para troop directed toward the vervet troop. Humans chased the troop twice and a young boy spent two minutes sitting in the same tree as the troop.

The Para troop male was recorded roaring a total of six times. Occasionally he roared in response to dogs barking (if the dogs were visible), or to vervet alarm calls. Although the presence of dogs and/or vervet alarm barks would not always result in a roar.

Natural Forest troop

The Natural forest troop interacted with other primate species eight out of nine instantaneous sample days, over a total of 6.02 hours during nine incidents. Incidents lasted an average of 40.1 minutes (range 10 - 140 minutes). Interactions occurred with birds, a squirrel, the red-tail monkey and the vervets. Non-primate encounters included the Natural Forest troop juvenile playfully chasing a squirrel (*Paraxerus* sp.) and a Black Kite (*Milvus migrans*) spent four minutes swooping at the guereza male. The male's response was to swipe at the bird with his hand, however he never vocalized nor shifted his position. Human children threatened the troop once during the instantaneous sample data collection.

The majority of the Natural Forest troop's inter-species interactions occurred with the single resident red-tail monkey (lasting a total of 5.17 hours). Incidents involving the red-tailed monkey were usually neutral, with the red-tail following the guerezas for a period of time during the day (usually in the morning or evening). There was one recorded chase by the adult male and one of the adult females toward the red-tail monkey (lasting 22 seconds) during the focal data, and one chase by the male toward the red-tail monkey during the instantaneous sample data.

Two affiliative incidents were recorded between vervets and Natural Forest troop guerezas during the instantaneous sample data. This included one recorded incident of play between a juvenile vervet and juvenile guereza, and one occurrence of the adult female guereza presenting to receive grooming from a vervet. Focal data recorded four *ad* *lib* incidents of vervet - guereza play bouts and a single 120 second non-contact aggressive bout between the vervets and guerezas, with the vervets threatening and chasing the Natural Forest troop.

Inter-species vocalizations included two squeaks and screams that were directed toward the vervets. In addition, five male roars were performed in response to a vervet alarm bark, a dog chasing a vervet, humans whistling (this happened twice), and in response to workers felling trees with a chain saw.

Hill troop

The Hill troop male also experienced swooping from a large bird, in this case it was a single incident from a Palm Nut Vulture (*Gypohierax angolensis*). The male did not respond to the vulture other than to duck his head slightly. The Hill troop juvenile female chased Hornbills (*Ceratogymna subcylindricus*) eleven times and once chased a squirrel (*Paraxerus* sp). All of the juvenile's chases were playful in nature.

Most Hill troop - human interactions were neutral with the humans calling to the guerezas. In response to an approaching human the animals would move farther up in the canopy were they would observe the humans until they left the area. On one occasion, humans came to feed the vervets (a regular occurrence in the Botanical Gardens) when the vervets and guerezas were in the same tree. The vervets moved to the ground while the guerezas stayed in the canopy. The animals had one aggressive human interaction. The Hill troop had been feeding outside of the Botanical Gardens for most of the day. In order to return to the Gardens, they had to pass through the trees and shrubs located on private property. The adult male returned to the Gardens unnoticed but when the adult female and juvenile attempted the move, local children pursued them. The children chased and threw sticks at the guerezas whenever they tried to move toward the Gardens. The female guerezas were unable to follow the male safely until the children left the area, after more than an hour. The reunion between the male and females included vocalizations, touching and grooming.

Hill troop animals interacted with vervets spending 214 minutes of instantaneous sample time (range: 4 - 168 minutes) on six days (over seven incidents). Two aggressive encounters were recorded. The first was a lunge at a vervet by the adult female guereza. There was no response by the vervet. The second encounter involved lunges, vocal threats, and chases between the adult Hill troop male and an adult male vervet. The episode lasted six *ad lib* minutes and there were no injuries.

Summary

Inter-troop interactions were common and took the form of ritualized displays with very little contact aggression and a high level of troop vocalizations. All three troops had areas of their home range that they actively defended. Inter-troop encounters occurred either along troop boundaries or when one troop entered the defended territory of another troop.

Most intra-troop social behaviour was affiliative and consisted of grooming between troop members. Significant differences were found between all three age-sex categories, with the juveniles being the most common performer of the grooming bout and the adult males being the least common. Significant differences were found between the juveniles and the adult members of both sexes with regards to receiving grooming bouts, with the juveniles the least likely to receive grooming. The other common affiliative intra-troop interaction included play behaviour. Similar to other studies, the younger the individual the more likely they were to play. Intra-troop aggression tended to be short lived and rare, taking the form of chases and lunges. Neonatal transfers were common and usually successful (similar to other studies).

All three troops interacted with other species of animals found in the Entebbe Botanical Gardens. Interactions were aggressive, affiliative, and neutral in context, with most interactions occurring between the guerezas and the other two primate species.

CHAPTER FIVE

DISCUSSION AND CONCLUSION

The main objective of this study was to describe the behaviour and diet of three troops of *Colobus guereza* living in a human modified habitat. Several studies suggested that exotic foods could supplement native diets, especially during the dry season, and provide habitat substrate such as sleeping trees or serve as a buffer between the native forest and human populations.

More and more primates are becoming threatened due to increased habitat disturbance, the encroachment of humans, and the introduction of exotic species into national parks and wildlife preserves. Understanding dietary and behavioural plasticity is important if we are to understand a primates' ability to adapt to their environment and if we are to successfully manage these groups (Chapman and Lambert 2000, Siex and Struhsaker 1999, Lowe and Sturrock 1998, Saj 1998, Altmann and Muruthi 1988).

In order to discern whether the human altered habitat and exposure to exotic foods affected the guerezas, descriptions were made of the three troops in this study and compared to existing data on troops residing in native habitats. The results of this preliminary study provide behavioural and dietary data on previously unstudied guerezas when exposed to new foods and habitats. This study suggests that guerezas are more adaptive than previously shown.

Diet

Significant individual troop dietary differences were recorded in this study. The Para troop had the highest reliance upon leaves, while the Hill troop had the least reliance upon leaves and expressed the most diverse diet of the three troops. The Natural Forest troop ate a significantly greater amount of bark than found in any other recorded study. The breakdown of plant parts was similar between the age-sex categories in agreement with existing data. Habitat differences as well as the different months of data collection on each troop may account, at least partially, for these dietary differences.

Most common food parts recorded being eaten in other studies included, in order of importance, new leaves, fruit, and mature leaves. Existing studies on guerezas show a mean 66.7% (range: 55.8 – 92.1%) of the diet to consist of leaves (of all ages), with fruit making up 1.1 – 53% of the diet, and all other food types making up less than 10% (Table 5.1). This study finds a higher mean leaf consumption rate (including vines) of 87.9% (range: 78.4 – 94.1%). Fruit is rarely eaten by the Para troop and only recorded in the focal diet of the Natural forest troop (making up 1% of the cumulative focal diet). Fruit made up 5.6% of the Hill troops' diet. The Clutton-Brock (1975) study was the only other that found a low rate of fruit in diet.

Troop diets have traditionally been found to be similar in homogeneous habitats. Recent studies by Chapman and Chapman (1999) and Chapman and Fedigan (1990), however, are finding variation in behaviour and diet among groups of the same species. These dietary differences seem to be independent of available foods, although in some cases it may be a result of availability differences. Differences between the plant parts found in the individual troop diets may also account, at least in part, by seasonal differences. Clutton-Brock (1975) found considerable differences between the various plant parts on different months, regardless of species. This may account, at least partially, for the vast plant part dietary differences found in this study, especially between the Para and Hill troops.

Table 5.1: Dietary Comparisons. Comparing existing guerezas dietary breakdowns with this study. Data in percentage form. L = leaves (including vine leaves, shoots, new and mature leaves), FL = flowers, FR = fruit, BK = bark, AQ = aquatic plants, LE = lichens and epiphytes, TE = termite soil, UN = unidentified.

Study	L	FL	FR	BK	AQ	LE	TE	UN	TOTAL
Bocian, 1997	57.9	2.9	24.6[1]	-	-	0.2	0.5	13.8	**99.9**
Clutton-Brock, 1975 -									
Site A	67.4	17.1	-	-	-	-	-	15.5[2]	**100**
Site B	92.1	6.7	1.1	-	-	-	-	-	**99.9**
Dunbar, 1987	70.6	1.3	28	-	-	-	-	-	**99.9**
Dunbar & Dunbar, 1974	46.8	-	53.3	-	-	-	-	-	**100.1**
Oates, 1977b	76.6	2.1	13.6	1.1	0.6	0.6	-	5.3	**99.9**
Oates, 1977c	55.8	-	12.1	-	-	-	-	32.1[3]	**100**
This Study, 1998 -									
Para troop	94	0.8	2.9[4]	2.1	-	-	-	0.2	**100**
Natural Forest troop	81.4	1	-	17.1	-	-	-	0.5	**100**
Hill troop	78.4	6	5.6	6.9	-	2.7	0.2	0.2	**100**

[1] includes seeds and fruit.
[2] listed as shoots or flowers.
[3] sum of other food items, each less than 2%.
[4] includes seed pods.

Previous studies have found guerezas to feed on from 25 to 43 individual species, with the most common making up more than 50% of the overall diet. The Natural forest troop was the least similar to this pattern as they fed from 52 species, with the most common species making up 24.8% of the diet. During the course of this study, the Natural Forest troop fed from the highest number of individual species (including the highest number of exotic species), had the largest dietary overlap with the other two troops, and fed from the most individual trees. In addition, the home range of the Natural Forest troop had the greatest amount of feeding trees available (including the greatest cumulative DBH and highest tree density). Species density of feeding trees tended to be higher in the Para troop home range than in the other two. Exotic species made up 25.9% of the overall diet in this study. Dietary species overlap was low with only nine species fed on by all three troops.

A few tree species play an important role in the diet of the Botanical Garden guerezas. *Hevea brasiliensis* (native to Brazil) made up 37.1% of the Para troop diet. During 80% of the inter-troop encounters occurring in the Para troop home range, the outside troop fed on *Hevea brasiliensis* trees. *Albizia gummifera* bark made up a large portion of the Natural Forest troop diet. The amount of bark found in the Natural Forest troop diet was significantly different from the other two troops and was at a much higher rate than found in any other guereza study. Davies, et *al.* (1999), however, recorded bark to make up 3.6% of the diet of *C. polykomos*. The Hill troop animals risked increased visibility by leaving the Botanical Gardens to preferentially feed from an individual *Piptadeniastrum africanum* tree. Preferential feeding on individual trees has also been found in other studies.

Home Range

Day range length, home range size, density, and territorial defense are all connected to the distribution of resources (Fleagle 1999). Differences between the guerezas in this and other studies may indicate differences in available resources. The Para troop and Hill troop were the most diverse in relation to ranging behaviour. Of the three troops, the Para troop had the smallest observed day and home ranges, the largest troop size, the highest population density level, and the greatest percentage of home range overlap. The Hill troop had the largest observed day and home ranges of the three troops, the smallest troop size, lowest population density, the least amount of home range overlap, and was the only troop with no residual natural forest in its' home range. In addition, during the course of the study the Hill troop was the only troop observed outside the Entebbe Botanical Gardens.

There is a relationship between guereza habitat type, troop size (including the number of adult males), and mean home range size with smaller troops tending to having smaller home ranges and tending to live in more disturbed habitats (Struhsaker 1997, von Hippel 1996). In this study, the troop with the fewest members and found in the most disturbed habitat resided in the largest home range (the Hill troop). This may be related to the decreased available density of feeding trees found in the Hill troops' home range (21.7 trees per hectare vs. 39.5 and 45.7 in the home ranges of the Para and Natural Forest troops, respectively). Thus, the Hill troop may have had to cover greater distances to obtain sufficient foods.

Table 5.2: Density, Day, and Home Range Comparisons. Partially adapted from von Hippel (1996).

Study	Mean Group Size	Density (ha)	Mean Day Range (m)	Mean Home Range (ha)	Habitat Type
Bocian, 1997	8	1	609		
Clutton-Brock, 1975	9			31.5[1]	
Dunbar, 1987	7		260	2.03 (1.4-3.6)	riverine
Dunbar, et *al.* 1974	6	3.7	260	2	riparian
Kingston, 1971	5[2]	2			
Krüger, et *al.* 1998	7.4	3.5		3.7 (1.7-6.2)	
Leskes, et *al.* 1970	12		97	1.5	riverine
Marler, 1969	8	0.5		15.3 (9.3-21.6)	primary
Oates, 1977b	7		535	1.1	riverine
Oates, 1977c	11	1	703	15.1	primary
Rose, 1979	19	3.9		4.8	riverine
Schenkel, et *al.* 1967	9.8	5		2.02 (1-3.5)	primary
Struhsaker, et *al.* 1987	12	1.5	540		
Suzuki, 1979	7	0.5		14.3 (7.3-21.3)	primary
Ullrich, 1961[3]	13			15	primary
von Hippel, 1996	12	2.5	574	12.5	riparian
This Study, 1998 -					
Para troop	14	2.2	252	6.4	garden
Natural Forest troop	7	1	378	6.8	garden
Hill troop	4	0.4	529	9.3	garden

[1] Clutton-Brock states that this is an overestimate of home range size.
[2] based on survey data, possible underestimate.
[3] Ullrich data presented in Struhsaker (1975) and in Marler (1972).

Although individual troop size tends to be smaller in disturbed habitats, the overall animal density in the area tends to be larger. When comparing the Para and Natural Forest troops, a similar pattern is found with a density of 2.2 individuals per hectare found in the Para troop home range, vs. the one individual per hectare found in the Natural Forest troop home range (the troop with the largest section of residual natural forest). However, this tendency was not found in the Hill troop as they had a density of 0.4 individuals per hectare. In Table 5.2 a comparison between density, day and home range is shown. A comparison between this study (1.2 individuals per hectare) and published overall density data of 2.3 individuals per hectare reveals a lower combined population density and higher disturbance rate in this study.

Comparisons between existing home range data (7.4 ha, range: 1.1 – 15.3 ha) and the home ranges found in this study (7.5 ha) show similar mean home range size. With the inclusion of the Clutton-Brock (1975) study, existing mean home ranges are larger (8.3 ha). Comparisons between the mean day ranges found in existing data (447 meters, range: 97 – 609 meters) and this study (386 meters) reveals a lower day range of daily movement by the Garden guerezas, but still well within the existing range.

Activity Budget

There is a relationship between diet and activity levels, thus the examination of diet and the proportion of time spent in different activities (both between the individual troops as well as within age-sex categories) may indicate differences in energy received from the consumed foods. Changes in diet to include exotic or provisioned foods have been related to increased time spent resting and involved in social behaviour with decreased feeding and movement rates. Decreased day range length has also been reported.

Inter-troop comparisons found a differential use of feeding time. The Hill troop spent significantly more time feeding than did the Para troop (21.8% vs. 12.5% of the instantaneous sample data). Another distinction occurred in the amount of time spent 'out of sight' with all three troops significantly different (Para troop 25.8% vs. Natural Forest troop 13.5% vs. Hill troop 3.1%). This is a result of the habitat differences found in the three home ranges. The Hill troop was clearly visible during the majority of the study due to the lack of any forest plots in their home range. The Para troop, however, spent 20% of their time in a section of impenetrable natural forest that provided poor visibility.

Table 5.3: Comparison of Activity Budgets. This study compared to the activity budgets completed on other guerezas and on other black and white colobus species. Data is expressed in percentage form. OS= out of sight.

	Rest [1]	**Move**	**Feed**	**Social**	**OS**	**Other**	**Total**
This Study, 1998 -							
Para troop	41	12	12	8	26	1	**100**
Natural Forest troop	47	10	16	14	13	-	**100**
Hill troop	63	7	22	5	3	-	**100**
Guereza Studies -							
Dunbar, et *al.* 1974	60-80[2]	-	-	-	-	-	
Oates, 1977a	57	5	20	6	-	1	**89**
von Hippel, 1996	55	9	36	-	-	-	**100**
Other Colobus Studies -							
C. angolensis (Lowe et *al.* 1998)	72	10	12	6	-	-	**100**
C. polykomos (Dasilva, 1994)	55	12	31	-	-	2[3]	**100**
C. satanas (McKey, et *al.* 1982)	54	4	23	13	-	6	**100**

[1] rest includes sleeping, resting, and scanning activities.
[3] includes social behaviour.
[2] based on 10 minute sweep intervals.

Age-sex comparisons detected dissimilar uses of time. Similar to other studies, as animals got older they became significantly less active. The sexes also used their time differently. Male guerezas spent significantly more time scanning than did the females. This is a reflection of the male role in the guereza social group, i.e. their higher level of vigilance while being the most active during inter-troop encounters.

In order to determine whether or not modifications in the activity budget are linked with exotic foods, intraspecific comparisons were made between the troops in this study and with troops in native areas. In Table 5.3, a comparison of the activity budgets between groups in native and exotic habitats is shown. When comparing existing guereza studies, and when combining the three categories of sleep, rest, and scan, the range of rest is 55% to 80%. The combined totals found in this study are slightly lower, ranging between 41% and 63%. Comparisons between studies indicate the Hill troop having the most similar activity budget to other studies, and the least similar to the other two Botanical Garden troops. The Para and Natural Forest troops have decreased resting and feeding rates. This, however, may be a result of the number of instantaneous samples when the animals were 'out of site'.

Troop Composition

Over the course of the study demographic changes included the birth of neonates in all three troops and the adjustments in male membership in both the Para and Natural Forest troop. This pattern of births and male migration is similar to published studies: of Dunbar and Dunbar (1974) and Oates (1977c), who recorded births as well as the emigration and immigration of their study males.

Anecdotal Social Behaviour

This study found very few differences between the social behaviour of the Botanical Garden guerezas and existing data on guerezas in native habitats. Similar to other studies, all three troops were involved in inter-troop encounters. The non-contact, highly vocal encounters were common and located along troop boundaries. Existing studies have found the adult male roar to be contagious between troops. This pattern was found between the Natural Forest and Hill troops. However, the Para troop alpha male was never heard responding to the roar of any other male during the course of this study.

Similar to existing studies, common intra-troop social behaviour included grooming. Significant grooming differences were found between each age-sex category. The males were the least common performers of grooming bouts. The juveniles were the most common performers of grooming and the least likely to receive grooming, with the adult males and females approximately equal in the receiving rates of grooming bouts. Plants were incorporated into 22% of the grooming bouts during the collection of Natural Forest troop focal data. The use of plants has not been noted in previous studies.

Another common affilative intra-troop interaction included play behaviour. Similar to other studies, the younger the individual the more likely they were to be involved in play. Intra-troop aggression tended to be short lived and rare, taking the form of chases and lunges. Aggression has been found to be more common in multi-male troops. In this study the Para troop (the only consistently multi-male troop) had the highest rate of overall aggression and a higher rate of male aggression than either of the other two troops. Neonatal transfers were common and usually successful (similar to other studies).

All three troops interacted with the other animal species found in the Entebbe Botanical Gardens. An increased rate of predator avoidance had been found during inter-species associations. Similar to other studies, interactions were found to be aggressive, affilative, and neutral in context, with the Botanical Garden guerezas seeming to have a preference for the company of vervets. A limiting factor to the interactions between the vervets and the three troops of guerezas was the much larger home range and higher level of mobility of the vervets (also found in Dunbar and Dunbar 1974). The vervets would pass through the territory of one of the troops and the guerezas would follow the vervets (usually on the ground) until the latter moved outside the guerezas home range. The increased amount of time spent on the ground when in the presence of the vervets may be an indication the guerezas lower vigilance levels while in association with the vervets. This may be due to the vervet tendency to have several 'look-outs' (Dunbar and Dunbar 1974).

Guereza Dietary Modifications

Traditionally, rather than studying variations occurring in differing troops and neighboring habitats, Suzuki (1975) found many researchers have taken the data from a few troops and generalized it to the species as a whole. However, there is an increasing amount of primate field studies that indicates a variation in the diet and social behaviour of different troops of the same species (Chapman and Fedigan 1990, Oates 1977b). Although many species share dietary adaptations and restrictions, Oates (1987) states it may be detrimental to 'clump' animals in relation to diet without recognizing that there are troop as well as individual ways to acquire the necessary foods and nutrients. The labels of 'folivore' or 'frugivore' suggest the animals' diets are solely comprised of leaves or fruit. When in fact the majority of primates actually incorporate fruit, leaves, flowers, bark, gums, and insects into their diet, rather than having a total reliance upon one food type.

Although there are limits to dietary variations, a growing number of studies are showing species that were originally considered to be specialists to have a broader range dietary flexibility than originally observed. Other species adapted to leaf eating also have been shown to reduce the leaves in their diet at certain times of the year (Horwich 1972, Altmann 1959). Chapman and Chapman (1990:126) state that since this flexibility in diet is "difficult to incorporate into many of the existing views of how feeding strategies develop and are maintained" it has usually been dismissed.

Dasilva (1994:656) states that although colobines are described as folivores and specialists, there is increasing evidence that they are "not obligate leaf-eaters". It may be the colobine dietary specialization that provides more flexibility when confronted with change in food availability. Quiatt and Reynolds (1993) and Milton (1980) found they seem to be able to switch back and forth between foods of greater and lower nutrition and toxicity (including mature leaves and bark).

The ability to increase diversity in a primates' diet may be linked to its survival. One of the results of forest disturbance is change in the plant composition. Johns and Skorupa (1987) found an indication of survival ability may be related to the degree of folivory/frugivory expressed in a species. Thus, Bauchop (1978) states the ability of colobines to adapt to new plant species may be due to their complex digestive system's ability to adapt rapidly to new plant products.

Oates (1977a:459) stated that guerezas seem to be "an ecologically flexible species" with the ability to exploit a wide variety of habitats by crossing open ground to inhabit new areas. Although there are few records of guerezas feeding on exotic foods, they do seem to prefer disturbed habitats (including secondary forests and deteriorated patches of residual forests). So it may not be that surprising to find guerezas residing in a human altered habitat. However, even though guerezas express this preference they may have conservation problems and may not be as successful in the long-term as native guereza populations (Altmann and Muruthi 1988).

LIMITATIONS OF THIS STUDY

There are a few aspects of this study I would like to have followed more thoroughly. For comparative purposes, an increase in data collection to include the other guereza troop in the Entebbe area would have provided stronger evidence for the effects of both exotic foods and the Entebbe Botanical Garden habitat on the guerezas. In addition, a complete year long data set would have provided more conclusive evidence that the differences recorded between the three troops were not just in response to seasonal changes or habitat differences.

A more in-depth look at the dietary aspects of the study would have provided additional data on available foods, towards this a complete phenology and nutritional study would have provided increased evidence of available foods. The overall knowledge of guereza nutritional needs and dietary availability is unknown. Due to seasonal variation and toxin digestibility, actual food availability is difficult to measure. While the guerezas' main native diet species (*Celtis durandii*) have been subject to nutritional analysis, the digestibility and toxins found in the majority of the diet are generally unknown, and in many cases (especially with vines and climbers) have yet to be identified. Although a comparison was made between the abundance of diet foods in this study, the site is new and not all dietary plants were identified. Consequently, it is unknown if the abundance of potential food may have been greater than recorded (Clutton-Brock 1975).

The collection of instantaneous sample data may introduce biases in the activity budget, with a decrease in recorded social data and an increase in scanning data. For example, activities that are subtle and/or instantaneous, like tongue clicking, may be missed and the animal would be recorded scanning. Consequently the collection of comparable focal data on the three troops would have been preferable. However, due to the limited amount of time available for this study a comparable amount of focal data from the three troops was not feasible. The comparison between various troops required limiting the data collected on an individual troop. As a result, in addition to the above biases, overall patterns may be suggested but there is not enough data to confirm the existence of these patterns. For example, although the Hill troop was seen outside of the Botanical Gardens on three occasions, this data is insufficient to state that they regularly leave the gardens year-round.

Although the goal of this study was to document variability the number of troops examined was small; thus conclusions found in this study may be uncharacteristic of guereza adjustments to new environments (Clutton-Brock 1975).

DIRECTIONS FOR FUTURE RESEARCH

The Entebbe Botanical Garden troops' condition is a reflection of what is occurring to other primate groups. Monitoring changes in groups like those residing in the Entebbe Botanical Gardens will help increase our understanding of the incorporation of exotic foods and the use of human altered habitats, which in turn will help manage troops residing in human altered habitats (Saj 1998).

An element for future research is the accumulation of nutritional data on the foods found in native primate populations. A long-term comprehensive nutritional study would allow a clear comparison between the guerezas from this study and troops residing in other areas of Uganda. In addition, due to the ongoing planting and removal of new tree species this study site provides a unique opportunity to study guereza food choice. For example, would either of the other troops feed from a plant species that is being utilized but only available to one of the troops, if that species were available in their home range? Or if *Celtis durandii* and/or *Markhamia platycalyx* were planted in the Gardens would the troops feed from these trees? And if they do what species, if any, would they give up?

Due to the high level of habituation a detailed study could be completed on the social behaviour of the animals to be compared to the ongoing data being collected in native habitats.

CONCLUSIONS

1. With the increasing encroachment of humans into the native habitats of Africa, the incorporation of exotic foods into the diet of nonhuman primates can play an important role in the survival of these animals.

2. Diet was associated with the individual troop habitats. Exotic species made up 25.9% of the diet, and significant amounts of bark was found in the diet of the Natural Forest troop. The animals in this study had decreased fruit consumption in their diet and there was a low recorded dietary overlap between the troops. Although differences were found between the diets of the three troops of guerezas in this study and in existing data from previous studies the results were inconclusive to determine of the differences were the result of habitat differences and/or study season.

3. The guerezas in this study were able to exploit different habitats and diets. Although troop composition was found to remain consistent with other studies, differences in home range, day range, and density were found between the three Garden troops.

4. Activity budget data was consistent with existing studies. Age-sex differences found a decreased activity level with increase in age. Feeding time differences between the Para and Hill troops were found to be significant.

5. Behavioural patterns recorded in this study were similar to existing guereza behavioural data. Inter-troop encounters, the rates of grooming, play, and neonatal transfers, and the inter-species interactions were all similar to other studies.

6. Management recommendations designed at maintaining viable guereza populations were made (Appendix D). Recommendations for the Entebbe Botanical Gardens include: the incorporation of native dietary tree species, tree plantings to be made with the arboreal movement of the animals in mind, monitoring demographic changes, and incorporating public education into the managerial plan for the Gardens.

REFERENCES

Abbiw, D. 1990. *Useful Plants of Ghana: West African Uses of Wild and Cultivated Plants*. London: Intermediate Technology Publications and The Royal Botanic Gardens, Kew.

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

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

Altmann, S.A. 1998. *Foraging for Survival: Yearling Baboons in Africa*. Chicago: University of Chicago Press.

Altmann, S.A. 1959. Field observations on a howling monkey society. *Journal of Mammalogy*, 40: 317-330.

Asquith, P.J. 1989. Provisioning and the study of free-ranging primates: history, effects and prospects. *Yearbook of Physical Anthropology*, 32: 129-158.

Ayensu, E.S. 1978. *Medicinal Plants of West Africa*. Michigan: Reference Publications, Incorporated.

Baranga, D. 1986. Phenological observation on two food tree-species of colobus monkeys. *African Journal of Ecology*, 24: 209-214.

Baranga, D. 1983. Changes in chemical composition of food parts in the diet of colobus monkeys. *Ecology*, 64(4): 668-673.

Baranga, D. 1982. Nutrient composition and food preferences of colobus monkeys in Kibale Forest, Uganda. *African Journal of Ecology*, 20: 113-121.

Bauchop, T. 1978. Digestion of leaves in vertebrate arboreal folivores. In: *The Ecology of Arboreal Folivores*. G.G. Montgomery (ed.). Washington: Smithsonian Institute Press, pp. 193-204.

Bicca-Marques, J.C. and C. Calegaro-Marques 1994. Exotic plant species can serve as staple food sources for wild howler populations. *Folia Primatologica*, 63: 209-211.

Bocian, C.M. 1997. *Niche Separation of Black-and-White Colobus Monkeys (Colobus angolensis and C. guereza) in the Ituri Forest*. The City University of New York: Unpublished Ph.D. thesis.

Bourliere, F. 1985. Primate communities: their structure and role in tropical ecosystems. *International Journal of Primatology*, 6(1): 1-26.

Bramblett, C.A. 1994. *Patterns of Primate Behaviour, Second Edition*. Illinois: Waveland Press, Incorporated.

Brown, A.D. and G.E. Zunino 1990. Dietary variability on *Cebus apella* in extreme habitats: evidence for adaptability. *Folia Primatologica*, 54: 187-195.

Burton, F. 1995. *The Multimedia Guide to the Non-Human Primates*. Ontario: Prentice Hall Canada, Incorporated.

Byabafumu, D.G. 1996. *A Guide to Entebbe Municipality*. Kampala: Lakeside Publishers.

Byrnes, R.M. (ed). 1990. *Uganda: A Country Study*. Internet web resource located at - http://www.1cweb2.loc.gov/frd/cs/ugtoc.html.

Cant, J.G.H. 1980. What limits primates? *Primates*, 21(4): 538-544.

Chapman, C.A. 1987. Flexibility in diets of three species of Costa Rican primates. *Folia Primatologica*, 49: 90-105.

Chapman, C.A. 1985. The influence of habitat on behavior in a group of St. Kitts green monkeys. *Journal of Zoology, Proceeds of the Zoological Society of London*, 206: 311-320.

Chapman, C.A. and L.J. Chapman 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates*, 40(1): 215-231.

Chapman, C.A. and L.J. Chapman 1996. Mixed-species primate groups in the Kibale Forest: ecological constrains on association. *International Journal of Primatology*, 17(1): 31-50.

Chapman, C.A. and L.J. Chapman 1990. Dietary variability in primate populations. *Primates*, 31(1): 121-128.

Chapman, C.A. and L.M. Fedigan 1990. Dietary differences between neighboring *Cebus capucinus* groups: local traditions, food availability or responses to food profitability? *Folia Primatologica*, 54: 177-186.

Chapman, C.A. and J.E. Lambert 2000. Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. *American Journal of Primatology*, 50(3): 169 – 185.

Cheney, D.L. and R.W. Wrangham 1987. Predation. In: *Primate Societies*. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker (eds.). Chicago: University of Chicago Press. pp. 227-239.

Clutton-Brock, T.H. 1979. Primate social organization and ecology. In: *Primate Ecology: Problem-oriented Field Studies*. R.W. Sussman (ed.). New York: John Wiley and Sons, pp. 503-567.

Clutton-Brock, T.H. 1975. Feeding behaviour of red colobus and black and white colobus in East Africa. *Folia Primatologica*, 23: 165-207.

Clutton-Brock, T.H. 1974. Activity patterns of red colobus (*Colobus badius tephrosceles*). *Folia Primatologica*, 21: 161-187.

Coelho Jr., A.M., C.A. Bramblett, and L.B. Quick 1977. Social organization and food resource availability in primates: a socio-bioenergetic analysis of diet and disease hypothesis. *American Journal of Physical Anthropology*, 46: 253-264.

Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusions in some marine animals and in rain forests. In: *Dynamics of Populations*. P.J. den Boer, and G.R. Gradwell (eds.). PODOC, Wageningen, pp. 298-312.

Conney, A.H. and J.J. Burns 1972. Metabolic interactions among environmental chemicals and drugs. *Science*, 178: 576-586.

Cooney, D.O. and T.T. Struhsaker 1997. Absorptive capacity of charcoals eaten by Zanzibar red colobus monkeys: implications for reducing dietary toxins. *International Journal of Primatology*, 18(2): 235-246.

Cork, S.J. 1996. Optimal digestive strategies for arboreal herbivorous mammals in contrasting forest types: why Koalas and Colobines are different. *Australia Journal of Biology*, 21: 10-20.

Corner, E.J.H. 1966. *The Natural History of Palms*. London: Weidenfeld and Nicolson.

Curtin, S.H. 1976. *Niche differentiation and social organization in sympatric Malaysian Colobines*. University of California: Unpublished Ph.D. thesis.

Dale, I.R. and P.J. Greenway 1961. *Kenya Trees and Shrubs*. London: Buchanan's Kenya Estates Limited.

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.

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

Davies, A.G. 1994. Colobine Populations. In: *Colobine Monkeys: Their Ecology, Behaviour and Evolution.* Davies and Oates (eds.). Cambridge: Cambridge University Press, pp. 285-310.

Davies, A.G. and J.F. Oates 1994. *Colobine Monkeys: Their Ecology, Behaviour and Evolution.* Cambridge: Cambridge University Press.

Davies, A.G., J.F. Oates, and G.L. Davies 1999. Patterns of frugivory in three West African colobine monkeys. *International Journal of Primatology*, 20(3): 327-357.

Dunbar, R.I.M. 1987. Habitat quality, population dynamics, and group composition in colobus monkeys (*Colobus guereza*). *International Journal of Primatology*, 8(4): 299-329.

Dunbar, R.I.M. and E.P. Dunbar 1976. Contrasts in social structure among black-and-white colobus monkey groups. *Animal Behaviour*, 24: 84-92.

Dunbar, R.I.M. and E.P. Dunbar 1974. Ecology and population dynamics of *Colobus guereza* in Ethiopia. *Folia Primatologica*, 21: 188-208.

Fa, J.E. 1988. Supplemental food as an extranormal stimulus in Barbary macaques (*Macaca sylvanus*) at Gibraltar - its impact on activity budgets. In: *Ecology and Behaviour of Food-Enhanced Primate Groups*. J.E. Fa and C.H. Southwick (eds.). New York: Alan R. Liss, Incorporated, pp. 53-78.

Fairgrieve, C. 1994. *The comparative ecology of blue monkeys (C. mitis stuhlmanni) in logged and unlogged forest. Budongo Forest Reserve, Uganda.* Edinburgh University: Unpublished Ph.D. thesis.

Fashing, P. 1999. Diet and food choice in Eastern black and white colobus monkeys in the Kakamega Forest. *American Journal of Primatology*, 49(1): 50. Abstract.

Fashing, P.J. and M. Cords 2000. Diurnal primate densities and biomass in the Kakamega Forest: an evaluation of census methods and a comparison with other forests. *American Journal of Primatology*, 50(2): 139-152.

Fleagle, J.G. 1999. *Primate Adaptation and Evolution: Second Edition.* New York: Academic Press.

Fleagle, J.G. 1984. Primate locomotion and diet. In: *Food Acquisition and Processing in Primates.* D.J. Chivers, B.A. Wood and A. Bilsborough (eds.). New York: Plenum Press, pp. 105-117.

Forthman Quick, D.L. and M.W. Demment 1988. Dynamics of exploitation: differential energetic adaptations of two troops of baboons to recent human contact. In: *Ecology and Behaviour of Food-Enhanced Primate Groups.* J.E. Fa and C.H. Southwick (eds.). New York: Alan R. Liss, Incorporated, pp. 25-51.

Freeland, W.J. and D.H. Janzen 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist,* 108(961): 269 - 285.

Ganzhorn, J.U. 1987. A possible role of plantations for primate conservation in Madagascar. *American Journal of Primatology,* 12: 205-215.

Gautier-Hion, A. 1983. Leaf consumption by monkeys in western and eastern Africa: a comparison. *African Journal of Ecology,* 21: 107-113.

Gautier-Hion. A., L.H. Emmons, and G. Dubost 1980. A comparison of the diets of three major groups of primary consumers of Gabon (primates, squirrels and ruminants). *Oecologia,* 45: 182-189.

Gautier-Hion, A., J. Gautier, and A. Moungazi 1997. Do black colobus in mixed-species groups benefit from increased foraging efficiency? *Ecology,* 320: 67-71.

Gillespie, T.R., S.R. Balcomb, C.A. Chapman, J.R. Skorupa, and T.T. Struhsaker 1999. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *American Journal of Primatology,* 49(1): 57. Abstract.

Glander, K.E. 1998. Poison in a monkey's garden of eden. In: *The Primate Anthology: Essays on Primate Behaviour, Ecology, and Conservation from Natural History.* R.L. Ciochon and R.A. Nisbett (eds.). New Jersey: Prentice Hall, pp. 146-152.

Glander, K.E. 1982. The impact of plant secondary compounds on primate feeding behaviour. *Yearbook of Physical Anthropology,* 25: 1-18.

Groves, C.P. 1973. Notes on the ecology and behavior of the Angola colobus (*Colobus angolensis* P.L. Sclater 1860) in N.E. Tanzania. *Folia Primatologica,* 20: 12-26.

Hall, J.B. and M.D. Swaine 1981. *Distribution and Ecology of Vascular Plants in a Tropical Rain Forest: Forest Vegetation in Ghana.* Boston: Dr. W. Junk Publishers, The Hague.

Healey, J.F. 1996. *Statistics: A Tool for Social Research, Fourth Edition.* New York: Wadsworth Publishing Company.

Herklots, G. 1976. *Flowering Tropical Climbers.* England: Dawson, Science History Publications.

Heywood, V.H. (ed.) 1985. *Flowering Plants of the World.* England: Croom Helm Publishers Limited.

Hill, D.A. 1999. Effects of provisioning on the social behaviour of Japanese and rhesus macaques: implications for socioecology. *Primates*, 40(1): 187-198.

Höner, O.P., L. Leumann, and R. Noë 1997. Dyadic associations of red colobus and diana monkey groups in the Taï Natural Park, Ivory Coast. *Primates*, 38(3): 281-291.

Horwich, R.H. 1972. Home range and food habits of the Nilgiri langur *Presbytis johnii. Journal of Bombay Natural History Society*, London 69: 255-267.

Horwich, R.H. and D. Manski 1975. Maternal care and infant transfer in two species of *Colobus* monkeys. *Primates*, 16(1): 49-73.

Hrdy, S.B. 1977. *The Langurs of Abu: Female and Male Strategies of Reproduction.* Cambridge: Harvard University Press.

Iwamoto, T. 1988. Food and energetics of provisioned wild Japanese macaques (*Macaca fuscata*). In: *Ecology and Behaviour of Food-Enhanced Primate Groups.* J.E. Fa and C.H. Southwick (eds.). New York: Alan R. Liss, Incorporated, pp. 79-94.

Johns, A.D. and J.P. Skorupa 1987. Responses of rain-forest primates to habitat disturbance: a review. *International Journal of Primatology*, 82(2): 157-191.

Katende, A.B. 1998. *Entebbe Botanic Gardens: A Report on its Plant Species Inventory.* Kampala: Botany Department, Makerere University.

Katende, A.B., A. Birnie, and B. Tengnas 1995. *Useful Trees and Shrubs for Uganda: Identification, Propagation and Management for Agricultural and Pastoral Communities.* Kenya: Regional Soil Conservation Unit (RSCU),Technical Handbook #10.

Kay, R.N.B. and A.G. Davies 1994. Digestive physiology. In: *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge: Cambridge University Press, pp. 229-249.

Keay, R.W.J. 1989. *Trees of Nigeria*. Oxford: Clarendon Press.

Keng, H. 1969. *Orders and Families of Malayan Seed Plants: Synopsis of Orders and Families of Malayan Gymnosperms, Dicotyledons, and Monocotyledons*. Singapore: University of Malaya Press.

Kingdon, J. 1997. *The Kingdon Field Guide to African Mammals*. London: Academic Press.

Kingston, T.J. 1971. Notes on the black and white colobus monkey in Kenya. *East African Wildlife Journal*, 9: 172-175.

Kirkpatrick, R.C. 1999. Colobine diet and social organization. In: *The Nonhuman Primates*. P. Dolhinow and A. Fuentes (eds.). California: Mayfield Publishing Company, pp. 93-105.

Koganezawa, M. and H. Imaki 1999. The effects of food sources on Japanese monkey home range size and location, and population dynamics. *Primates*, 40(1): 177-185.

Kool, K.M. and D.B. Croft 1992. Estimators for home range areas of arboreal colobine monkeys. *Folia Primatologica*, 58: 210-214.

Krüger, O., E. Affeltt, M. Brackmann, and K. Milhahn 1998. Group size and composition of *Colobus guereza* in Kyambura Gorge, southwest Uganda, in relation to chimpanzee activity. *International Journal of Primatology*, 19(2): 287-297.

Kunkel, G. 1984. *Plants for Human Consumption: An Annotated Checklist of the Edible Phanerogams and Ferns*. Germany: Koeltz Scientific Books.

Lehn, C. (n.d.). *The Captive Population of the Black-and-White Colobus Monkey, Colobus guereza*. New Orleans: Audubon Zoo.

Leland, L. and T.T. Struhsaker 1998. Teamwork tactics. In: *The Primate Anthology: Essays on Primate Behaviour, Ecology, and Conservation from Natural History*. Ciochon and Nisbett (eds.). New Jersey: Prentice Hall, pp. 119-123.

Leskes, A. and N.H. Acheson 1970. Social organization of a free-ranging troop of black and white colobus monkeys (*Colobus abyssinicus*). *Proceedings from the Third International Congress of Primatology*, Vol. 3, pp. 22-31.

Lind, E.M. and M.E.S. Morrison 1974. *East African Vegetation*. Great Britain: Longman Group Limited.

Little, Jr. E.L. and R.G. Skolmen 1989. *Common Forest Trees of Hawaii (Native and Introduced)*. Washington: United States Department of Agriculture, Handbook No. 679.

Lötschert, W. and G. Beese 1983. *Collins Photo Guide: Tropical Plants*. United Kingdom: Harper Collins Publishing.

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

The Macdonald Encyclopedia of Trees: A Field Guide to Conifers, Palms, Broadleafs, Fruit, Flowering Trees, and Trees of Economic Importance. 1982. London: Macdonald and Company.

Maisels, F., A. Gautier-Hion, and J.P. Gautier 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soil. *International Journal of Primatology*, 15(5): 681-701.

Marler, P. 1972. Vocalizations of East African monkeys II: black and white colobus. *Behaviour*, 42: 175-197.

Marler, P. 1969. *Colobus guereza*: territoriality and group composition. *Science*, 163(3862): 93-96.

McKenna, J.J. 1979. The evolution of allomothering behavior among Colobine monkeys: function and opportunism in evolution. *American Anthropologist*, 81: 818-840.

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

McKey, D.B. and P.G. Waterman 1982. Ranging behaviour of a group of black colobus (*Colobus satanas*) in the Dovala-Edea Reserve, Cameroon. *Folia Primatologica*, 39: 264-304.

McNab, B.K. 1978. Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply. In: *The Ecology of Arboreal Folivores*. G.G. Montgomery (ed.). Washington: Smithsonian Institution Press, pp. 153-162.

Mènard, N. and D. Vallet 1996. Demography and ecology of barbary macaques (*Macaca sylvanus*) in two different habitats. In: *Evolution and Ecology of Macaque Societies*. J.E. Fa and D.G. Lindburg (eds.). Cambridge: Cambridge University Press, pp. 106-131.

Menninger, E.A. and 50 Collaborators 1970. *Flowering Vines of the World: An Encyclopedia of Climbing Plants*. New York: Hearthside Press Incorporated.

Milton, K. 1984. The role of food-procession factors in primate food choice. In: *Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismal Biology of Prosimians, Monkeys, and Apes*. P.S. Rodman and J.G.H. Cant (eds.). New York: Columbia University Press, pp. 249-279.

Milton, K. 1980. *The Foraging Strategy of Howler Monkeys: A Study in Primate Economics*. New York: Columbia University Press.

Mitani, J.C., J. Gros-Louis, and J.H. Manson 1996. Number of males in primate groups: comparative tests of competing hypothesis. *American Journal of Primatology*, 38: 315-332.

Mitani, J.C. and P.S. Rodman 1979. Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behavioural Ecology and Sociobiology*, 5: 241-251.

Morbeck, M.E. 1979. Forelimb use and positional adaptation in *Colobus guereza*: integration of behavioural, ecological, and anatomical data. In: *Environment, Behaviour, and Morphology: Dynamic Interactions in Primates*. M.E. Morbeck, H. Preuschoft, and N. Gomberg (eds.). New York: Gustav Fisher, pp. 95-118.

Morbeck, M.E. 1977. Positional behaviour, selective use of habitat substrate and associated non-positional behaviour in free-ranging *Colobus guereza* (Rüppell, 1835). *Primates*, 18: 35-58.

Morbeck, M.E. 1974. Positional behaviour in *Colobus guereza*: a preliminary quantitative analysis. In: *Proceedings for the Symposia of the Fifth Congress of the International Primatological Society*. S. Kindo, M. Kawai, A. Ehara, S. Kawamura (eds.). Tokyo: Japan Science Press, pp. 331-343.

Moreno-Black, G.S. 1974. *Differential habitat utilization of four African Cercopithecidae*. University of Florida: Unpublished Ph.D. thesis.

Moreno-Black, G.S. and E.F. Bent 1982. Secondary compounds in the diet of *Colobus angolensis*. *African Journal of Ecology*, 20: 29-36.

Nagy, K.A. and K. Milton 1994. Energy metabolism and food consumption by wild howler monkeys (*Alouatta palliata*). *Ecology*, 60: 475-480.

Newton, P.N. and R.I.M. Dunbar 1994. Colobine monkey society. In: *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge: Cambridge University Press, pp. 311-346.

Norusis, M.J. 1998. *SPSS 8.0: Guide to Data Analysis*. New Jersey: Prentice Hall.

Oates, J.F. 1996. Habitat alteration, hunting and the conservation of folivorous primates in African forests. *Australian Journal of Ecology*, 21: 1-9.

Oates, J.F. 1994. The natural history of African colobines. In: *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge: Cambridge University Press, pp. 75-128.

Oates, J.F. 1987. Food distribution and foraging behaviour. In: *Primate Societies*. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker (eds.). Chicago: University of Chicago Press. pp. 197-209.

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. 1977a. The guereza and man: how man has affected the distribution and abundance of *Colobus guereza* and other black colobus monkeys. In: *Primate Conservation*. H.S.H. Prince Rainer and G.H. Bourne (eds.). New York: Academic Press, pp. 420-467.

Oates, J.F. 1977b. The guereza and its food. In: *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes*. T.H. Clutton-Brock (ed.). New York: Academic Press. pp. 275-321.

Oates, J.F. 1977c. The social life of a black-and-white colobus monkey, *Colobus guereza*. *Zeitschrift fur Tierpsychologie*, 45: 1-60.

Oates, J.F. and A.G. Davies 1994. What are the colobines? In: *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge: Cambridge University Press, pp. 1-9.

Oates, J.F., A.G. Davies, and E. Delson 1994. The diversity of living colobines - the natural history of African colobines. In: *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge: Cambridge University Press, pp. 45-75.

Oates, J.F. and T.F. Trocco 1983. Taxonomy and phylogeny of black and white colobus monkeys; inferences from an analysis of loud call variation. *Folia Primatologica*, 40: 83-113.

Olson, D.K. 1986. Determining range size for arboreal monkeys: methods, assumption and accuracy. In: *Current Perspectives in Primate Social Dynamics*. D.M. Taub, and F.A. King (eds.). New York: Van Nostrand Reinhold Company, pp. 212-227.

Paterson, D. 1992. *Entebbe Botanical Garden, Uganda: Rehabilitation Proposal.* Edinburgh: Royal Botanical Gardens.

Paterson, J. D. 1992. *Primate Behaviour: An Exercise Workbook.* Illinois: Waveland Press Incorporated.

Pavelka, M.S.M. 1993. *Monkeys of the Mesquite: The Social Life of the South Texas Snow Monkey.* Iowa: Kendall/Hunt Publishing Company.

Perry, F. and R. Hay 1982. *A Field Guide to Tropical and Subtropical Plants.* New York: Van Nostrand Reinhold Company.

Plumptre, A.J., V. Reynolds, and C. Bakunteea 1997. *The Effects of Selective Logging in Monodominant Tropical Forests on Biodiversity. Final Report of ODA Project #R6057.* Oxford: Budongo Forest Project, Institute of Biological Anthropology.

Plumptre, A.J., V. Reynolds, and C. Bakunteea 1994. *The Contribution of Fruit Eating Primates to Seed Dispersal and Natural Regeneration After Selective Logging. Final Report of ODA Project #R4738.* Oxford: Budongo Forest Project, Institute of Biological Anthropology.

Poirier, F.E. 1974. Colobine aggression: a review. In: *Primate Aggression, Territoriality and Xenophobia.* R.L. Holloway (ed.). New York: Academic Press, pp. 123-157.

Poirier, F.E. 1970. The nilgiri langur (*Presbytis johnii*) of South India. In: *Primate Behaviour: Developments in Field and Laboratory Research.* L.A. Rosenblum (ed.) New York: Academic Press, pp. 251-383.

Quiatt, D. and V. Reynolds 1993. *Primate Behaviour: Information, Social Knowledge, and the Evolution of Culture.* Cambridge: Cambridge University Press.

Rham, V.H. 1970. Ecology, zoogeography and systematics of some African forest monkeys. In: *Old World Monkeys: Evolution, Systematics and Behaviour.* J.R. Napier and P.H. Napier (eds.). New York: Academic Press, pp. 589-628.

Ridely, M. 1986. The number of males in a primate troop. *Animal Behaviour*, 34: 1848-1858.

Riley, H.P. 1963. *Families of Flowering Plants of Southern Africa*. Kentucky: University of Kentucky Press.

Rose, M.D. 1979. Positional behaviour of natural populations: some quantitative results of a field study of *Colobus guereza* and *Cercopithecus aethiops*. In: *Environment, Behaviour, and Morphology: Dynamic Interactions in Primates*. M.E. Morbeck, H. Preuschoft, and N. Gomberg (eds.). New York: Gustav Fisher, pp. 75-94.

Rose, M.D. 1977. Interspecific play between free ranging guereza (*Colobus guereza*) and vervet monkeys (*Cercopithecus aethiops*). *Primates*, 18(4): 957-964.

Rowe, N. 1996. *The Pictorial Guide to the Living Primates*. New York: Pogonias Press.

Saj, T. 1998. *The ecology and behaviour of vervet monkeys in a human-modified environment*. University of Calgary: Unpublished MA thesis.

Saj, T., P. Sicotte, and J.D. Paterson 1999. Age-sex class differences in the time budget and feeding strategies of members of a crop and food-raiding vervet group in Entebbe, Uganda. *American Journal of Primatology*, 49(1): 98. Abstract.

Schenkel, R. and L. Schenkel-Hullinger 1967. On the society of free-ranging colobus. In: *Progress in Primatology*. Stark, Schneider and Kuhn (eds.). New York: Gustav Fisher, pp. 185-194.

Schlotterhausen, L. 1998. A comparison of the social and feeding behaviours between a wild and commensal group of bonnet macaques (*Macaca radiata*) in the Indira Gandhi Wildlife Sanctuary, South India. *American Journal of Primatology*, 45(2): 206. Abstract.

Siex, K.S. and T.T. Struhsaker 1999. Colobus monkeys and coconuts: a study of perceived human-wildlife conflicts. *Journal of Applied Ecology*, 36: 1009-1020.

Siex, K.S. and T.T. Struhsaker 1998. Ecology of the Zanzibar red colobus monkey: demographic variability and habitat stability. *International Journal of Primatology*, 20(2): 163-192.

Siegel, S. and N.J. Castellan, Jr. 1988. *Nonparametric Statistics for the Behavioural Sciences*. New York: McGraw-Hill Incorporated.

Spatz, C. 1993. *Basic Statistics: Tales of Distributions*. California: Brooks/Cole Publishing Company.

Stanford, C.B. 1998. *Chimpanzee and Red Colobus: The Ecology of Predator and Prey*. Cambridge: Harvard University Press.

Struhsaker, T.T. 1998. Zanzibar's endangered red colobus monkeys. *National Geographic*, November, vol. 194 (5): 73-81.

Struhsaker, T.T. 1997. *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. Florida: University Press of Florida.

Struhsaker, T.T. 1978. Food habits of five monkey species in the Kibale Forest, Uganda. *Recent Advances in Primatology*, 1: 225-248.

Struhsaker, T.T. 1975. *The Red Colobus Monkey*. Chicago: The University of Chicago Press.

Struhsaker, T.T., D.O. Cooney, and K.S. Siex 1997. Charcoal consumption by Zanzibar red colobus monkeys: its function and its ecological and demographic consequences. *International Journal of Primatology*, 18(1): 61-72.

Struhsaker, T.T. and L. Leland 1987. Colobines: infanticide by adult males. In: *Primate Societies*. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker (eds.). Chicago: The University of Chicago Press. pp. 83-97.

Struhsaker, T.T. and J.F. Oates 1979. Comparison of the behaviour and ecology of red colobus and black and white colobus monkeys in Uganda: a summary. In: *Primate Ecology: Problem-oriented Field Studies*. R.W. Sussman, (ed.) New York: John Wiley and Sons, pp. 103-122.

Suzuki, A. 1979. The variation and adaptation of social groups of chimpanzees and black and white colobus monkeys. In: *Primate Ecology and Human Origins: Ecological Influences of Social Organizations*. I.S. Bernstein and E.O. Smith (eds.). New York: Garland STPM Press, pp. 153-173.

Tanaka, T. and S. Nakao 1976. *Tanaka's Cyclopedoa* (sic) *of Edible Plants of the World*. Japan: Keigaku Publishing Company.

Teelen, S. 1994. *Group size and group structure of guereza, Colobus guereza occidentalis (Rocheburbe 1886), in the Kibale Forest, Uganda*. Technical University of Braunschweig: Unpublished Ph.D. thesis.

Teelen, S. and H. Klingel 1994. Population density of *Colobus guereza* in the Kibale Forest, Uganda. *American Journal of Primatology*, 33(3): 245. Abstract.

Terborgh, J. 1983. *Five New World Primates: A Study of Comparative Ecology*. New Jersey: Princeton University Press.

Thomas, S.C. 1991. Population densities and patterns of habitat use among anthropoid primates of the Ituri Forest, Zaïre. *Biotropic*, 23(1): 68-83.

von Hippel, F.A. 1998. Use of sleeping trees by black and white monkeys (*Colobus guereza*) in the Kakamega Forest, Kenya. *American Journal of Primatology*, 45: 281-290.

von Hippel, F.A. 1996. Interactions between overlapping multimale groups of black and white colobus monkeys (*Colobus guereza*) in the Kakamega Forest, Kenya. *American Journal of Primatology*, 38: 193-209.

Waser, P.M. 1987. Interactions among primate species. In: *Primate Societies*. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker (eds.). Chicago: The University of Chicago Press. pp. 210-226.

Waser, P.M. 1984. Ecological differences and behavioural contrasts between two mangabey species. In: *Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismal Biology of Prosimians, Monkeys, and Apes*. P.S. Rodman and J.G.H. Cant (eds.). New York: Columbia University Press, pp. 195-216.

Waterman, P.G. and K.M. Kool 1994. Colobine food selection and plant chemistry. In: *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge: Cambridge University Press, pp. 251-284.

Watkins, B.E., D.E. Ulrey, and P.A. Whetter 1985. Digestibility of a high-fiber biscuit diet by black and white colobus (*Colobus guereza*). *American Journal of Primatology*, 9: 137-144.

Wheatley, B.P., D.K. Harya Putra, and M.K. Gonder 1996. A comparison of wild and food-enhanced long-tailed macaques (*Macaca fascicularis*). In: *Evolution and Ecology of Macaque Societies*. J.E. Fa and D.G. Lindburg (eds.). Cambridge: Cambridge University Press, pp. 182-206.

Williams, J., R.T. Peterson, and N. Arlott 1995. *Collins Field Guide: Birds of East Africa*. Ontario: Harper Collins Canada, Limited.

Williams, R.O. 1949. *The Useful and Ornamental Plants in Zanzibar and Pemba.* Great Britain: St. Ann's Press.

Winkler, P. 1988. Feeding behaviour of a food-enhanced troop of Hanuman langurs (*Presbytis entellus*) in Jodhpur, India. In: *Ecology and Behaviour of Food-Enhanced Primate Groups.* J.E. Fa and C.H. Southwick (eds.). New York: Alan R. Liss, Incorporated, pp. 3-24.

Winkler, P. 1984. The adaptive capacities of the Hanuman langur and the categorizing of diet. In: *Food Acquisition and Processing in Primates.* D.J. Chivers, B.A. Wood, and A. Bilsborough (eds.). New York: Plenum Press, pp. 161-166.

Wooldridge, F.L. 1971. *Colobus guereza*: birth and infant development in captivity. *Animal Behaviour*, 19: 481-485.

Yeager, C.P. and R.C. Kirkpatrick 1998. Asian Colobine social structure: ecological and evolutionary constraints. *Primates*, 39(2): 147-155.

Yoshiba, K. 1968. Local and intertroop variability in ecology and social behaviour of common Indian langurs. In: *Primates: Studies in Adaptation and Variability.* P.C. Jay (ed.). New York: Holt, Rinehart, and Winston Incorporated, pp. 217 – 242.

APPENDIX A: ACTIVITY BUDGET CATEGORIES

Behaviour	Definition
Scan	Animal is inactive but with eyes open.
Sleep	Fully inactive, eyes closed.
Movement	Travel of at least one-body length.
Feed	Animal is masticating or ingesting a food source.
Social	Gregarious behaviour.
Out of Sight	Animal no longer visible to observer.
Other	Any behaviour that does not fall into the above categories.

APPENDEX B: TREE AND SHRUB SPECIES AVAILABLE IN THE ENTEBBE BOTANICAL GARDENS (list from Katende, 1998).

FAMILY	SPECIES (*eaten by subjects)	ORIGIN
Mimosaceae	*Aedzia zygia**	
Bombacaceae	*Adansonia digitata*	E. Africa
Mimosoideae	*Adenanthera pavonica*	W. Africa
Caesalpiniaceae	*Afzelia quanzensis*	Coastal Forests (?)
Coniferae/Araucariaceae	*Agathis alba*	T. America
Mimosaceae	*Albizia coriaria**	T. Africa
Mimosaceae	*Albizia glaberrima*	T. Africa
Mimosaceae	*Albizia grandibracteata* *	T. Africa
Mimosaceae	*Albizia gummifera**	T. Africa
Mimosaceae	*Albizia mallocophylla*	T. Africa
Mimosaceae	*Albizia zygia**	T. Africa
Euphorbiaceae	*Aleurites moluccana**	Malaya
Apocynaceae	*Alstonia boonei*	T. Africa
Myrtaceae	*Amomis caryophyllata*	America
Anacardiaceae	*Anacardium occidentale*	T. America
Sapotaceae	*Aningeria altiissima*	T. Africa
Loganiaceae	*Anthocleista vogeli*	T. Africa
Moraceae	*Antiaris toxicaria**	T. Africa
Euphorbiaceae	*Antidesma* sp.	Pacific Is.
Araucariaceae	*Araucaria angustifolia*	T. America
Araucariaceae	*Araucaria bidwillii*	Australia
Araucariaceae	*Araucaria caninghamii*	Australia
Araucariaceae	*Araucaria excelsa*	T. America
Palmae	*Archontophoenix alexandrae*	Australia
Palmae	*Areca catechu*	T. Asia
Palmae	*Areca concinna*	Ceylon
Palmae	*Areca katechu*	Pacific Is.
Palmae	*Arenga pinnata**	Malaya
Moraceae	*Artocarpus altilis*	Polynesia
Moraceae	*Artocarpus heterophylus*	T. Asia
Oxalidaceae/Averrhoaceae	*Avarrhoa carambola*	T. America
Malvaceae	*Azanza garckeana**	
Caesalpiniaceae	*Baikiaea insignis*	T. Africa
Bambusaceae/Gramineae	*Bambusa vulgaris*	T. Asia
Papilionaceae	*Baphiopsis parviflora*	T. Africa
Bischoffiaceae	*Bischoffia javanica*	T. Asia
Bixaceae	*Bixa orellana*	T. America
Sapindaceae	*Blighia unijugata**	T. Africa
Bombaceae	*Bombax kimenzae*	T. America
Palmae	*Borassus aethiopium*	T. Africa
Nynctanginaceae	*Bougainvelia alba*	T. America
Nynctanginaceae	*Bougainvelia formosa*	T. America
Euphorbiaceae	*Bridelia micrantha*	T. Africa
Moraceae	*Broussonetia papyrifera*	Pacific Is.
Caesalpiniaceae	*Brownea ariza*	W. Africa
Caesalpiniaceae	*Caesalpinia coriaria*	T. America
Mimosoideae	*Calliandra guildingii*	
Myrtaceae	*Callistemon citriinus*	Australia
Myrtaceae	*Callistemon rigidus*	
Myrtaceae	*Callistemon salignus*	America
Flacourtiaceae	*Caloncoba schweinfurthii*	T. Africa
Theaceae	*Camellia sinensis*	China/India
Annonaceae	*Cananga pinnata*	Malaya
Caricaceae	*Canangium odoratum*	T. America
Bursaraceae	*Canarium shweinfurthii*	T. Africa
Rubiaceae	*Canthium vulgare (Psydrax parviflora)**	T. Africa
Caricaceae	*Carica papaya*	T. America
Palmae/Arecacea	*Caryota mitis*	T. Asia
Palmae/Arecacea	*Caryota urens**	T. Asia
Rutaceae	*Casimiroa edulis*	Mexico

FAMILY	SPECIES	ORIGIN
Caesalpiniaceae	*Cassia fistula*	T. Asia
Caesalpiniaceae	*Cassia grandis*	T. America
Caesalpiniaceae	*Cassia nodoza*	W. Africa
Casuarinaceae	*Casuarina equisitifolia*	E. Africa
Celastraceae	*Catha edulis*	T. Africa
Bombacaceae	*Ceiba pentandra**	T. Africa (I)
Sapotaceae	*Chrysophylum cainito*	C. America
Lauraceae	*Cinnamomum camphora*	Asia
Lauraceae	*Cinnamomum zeylenica*	India
Rutaceae	*Citrus limonia*	India
Rutaceae	*Citrus sinensis*	China
Palmae	*Cocos nuclear*	T. America
Rubiaceae	*Coffee canephora*	T. Africa
Rubiaceae	*Coffee liberica*	T. Africa
Sterculiaceae	*Cola acuminata**	T. Africa
Combretaceae	*Combretum paniculata*	W. Africa
Boraginaceae	*Cordia millenii**	T. Africa
Lecythidaceae	*Couroupita guianensis*	Trinidad
Papilionaceae	*Craibia elliotii*	T. Africa
Rubiaceae	*Craterispermum laurinum*	T. Africa
Bignoniaceae	*Crescentia cejute*	T. America
Euphorbiaceae	*Croton megalocarpus**	T. Africa
Euphorbiaceae	*Croton sylvaticus (C. oxypetalus)**	T. Africa
Cupressaceae	*Cupressus funebris*	
Cupressaceae	*Cupressus sempevirens*	Mediterranean
Cycadaceae	*Cycas revoluta*	Asia
Caesalpiniaceae	*Cynometra alexandri*	T. Africa
Leguminosae	*Dalbergia sisoo*	India
Caesalpiniaceae	*Delonix alata*	
Caesalpiniaceae	*Delonix regia*	Madagascar
Dilleniaceae	*Dillenia indica*	T. Asia
Ebenaceae	*Diospyros discolor*	T. Africa (?)
Flacourticeae	*Dovyalis cafra*	
Flacourticeae	*Dovyalis hebecarpa*	India
Draceanaceae	*Dracaena strudneri*	T. Africa
Verbenaceae	*Duranta rapens*	T. America
Bombacaceae	*Durio zibethinus*	Malaysia
Meliaceae	*Ekebergia sensgalensis*	T. Africa
Palmae/Arecacea	*Elaeis guinensis*	T. Africa
Cycadaceae	*Encephalartos hildebrandtii*	T. Africa
Lauraceae	*Eriobotrya japonica*	China
Papilionaceae	*Erythrina abyssinica*	T. Africa
Papilionaceae	*Erythrina umbrosa*	Malaya
Caesalpiniaceae	*Erythrophleum suaveolens*	T. Africa
Myrtaceae	*Eucalyptus camaldulensis*	Australia
Myrtaceae	*Eucalyptus citriodora**	Australia
Myrtaceae	*Eucalyptus deglupta*	Australia
Myrtaceae	*Eucalyptus grandis*	Australia
Myrtaceae	*Eucalyptus maideni*	Australia
Myrtaceae	*Eucalyptus robusta*	Australia
Myrtaceae	*Eugenia bukobensis*	T. Africa
Myrtaceae	*Eugenia uniflora**	T. America
Rutaceae	*Fagaropsis angolensis**	T. Africa
Moraceae	*Ficus benjamina**	Asia
Moraceae	*Ficus cyatistipula*	T. Africa
Moraceae	*Ficus dawei*	T. Africa
Moraceae	*Ficus elastica*	India
Moraceae	*Ficus eriobotryoides (F. saussureana)*	T. Africa
Moraceae	*Ficus exasperata**	T. Africa
Moraceae	*Ficus natalensis**	T. Africa
Moraceae	*Ficus ovata*	T. Africa
Moraceae	*Ficus pseudomangifera*	T. Africa
Moraceae	*Ficus sur (F. capensis)**	T. Africa
Moraceae	*Ficus thonningii (F. stipilata)**	T. Africa
Flacourtiaceae	*Flacourtia jangomosa*	Malaya
Oleaceae	*Fraxinus viridis*	N. America

FAMILY	SPECIES	ORIGIN
Apocynaceae	*Funtumia africana**	T. Africa
Guttifera	*Garcinia mangostana*	Malaya
	Gmelina arborea	Asia
Tiliaceae	*Glyphea brevis*	T. Africa
Proteaceae	*Grevillea banksii**	Australia
Proteaceae	*Grevillea robusta*	Australia
Leguminosae	*Haematoxylon campechianum**	T. America
Simaroubaceae	*Harrisonia abyssinica*	T. Africa
Hypericaceae	*Harungana madagascariensis*	T. Africa
Euphorbiaceae	*Hevea brasiliensis**	T. America
Malvaceae	*Hibiscus rosa-chinense*	Asia
Bombacacceae	*Hura crepitus*	T. America
Flacourtiaceae	*Hydnocarpus anthelimintica*	Siam
Flacouriaceae	*Hydnocarpus laurifolia*	Malaya
Irvingiaceae	*Irvingia gabonensis*	T. Africa
Myrtaceae	*Jambusa caryophylus*	Molucca Is.
Euphorbiaceae	*Jatropha curcas*	T. America
Euphorbiaceae	*Jatropha multifida*	America
Cupressaceae	*Juniperus bermudiana*	Bermuda
Bignoniaceae	*Kigelia moosa*	T. America
Lythraceae	*Lagerstroemia indica*	China
Lythraceae	*Lagerstroemia speciosa*	T. Asia
Meliaceae	*Lansium domesticum*	Malaya
Sapindaceae	*Litchi chinensis*	China
Palmae	*Livingstonia chinense*	Malaya
Meliaceae	*Lovoa trichilioides**	T. Africa
Rhamnaceae	*Maesopsis eminii**	T. Africa
Magnoliaceae	*Magnolia grandiflora*	N. America
Sapindaceae	*Majedea fosteri*	T. Africa
Malphigiaceae	*Malphigia glabra*	T. America
Malphigiaceae	*Malphigia lubra*	Malaya
Anacardiaceae	*Mangifera indica*	T. Asia
Euphobiaceae	*Manihot grazior*	America
Bignoniaceae	*Makhamia lutea**	T. Africa
Euphobiaceae	*Margaritaria discodeus*	T. Africa
Meliaceae	*Melia azedarach*	Asia
Meliaceae	*Melia dubia**	Asia
Moraceae	*Melicia excelsa*	T. Africa
Magnoliaceae	*Michelia champaca**	T. Asia
Papilionaceae	*Milletia dura*	T. Africa
Annonaceae	*Monodora myristica*	T. Africa
Rubiaceae	*Morinda lucida**	T. Africa
Moraceae	*Morus mesozygia*	T. Africa
Cecropiaceae	*Musanga cecropioides**	T. Africa
Myrianthaceae	*Myrianthus arborea*	T. Africa
Papilionaceae	*Myroxylon balsamum*	T. America
Rubiaceae	*Nauclea diderrichii**	T. Africa
Rubiaceae	*Nauclea latifolia*	T. Africa
Sapindaceae	*Nephelium happaceum*	E. Asia
Mimosaceae	*Newtonia buchananii*	T. Africa
Cactaceae	*Opuntia speciosa*	T. America
	Pamentera sp.	
	Paylanthus sp.	
Lauraceae	*Persea americana*	T. America
Palmae	*Phoenix reclinata*	T. Africa
Euphorbiaceae	*Phyllanthus sp.*	T. Africa
Phytolacaceae	*Phytolaca dioica*	T. America
Apocynaceae	*Picralima nitida*	T. Africa
Myrtaceae	*Pimenta officenale*	T. America
Myrtaceae	*Pimenta racemosa*	
Pinaceae	*Pinus canariensis*	Canary Is.
Pinaceae	*Pinus caribeae*	West Indies
Pinaceae	*Pinus elliotii*	N. America
Pinaceae	*Pinus khasya*	Burmese
Pinaceae	*Pinus patula*	Mexico
Mimosaceae	*Piptadeniastrum africanum**	T. Africa
Apocynaceae	*Plumeria rubbra*	T. America

FAMILY	SPECIES	ORIGIN
Podocarpaceae	*Podocarpus latifolius**	T. Africa
Podocarpaceae	*Podocarpus usambarensis*	T. Africa
Arariaceae	*Polyscias fulva**	T. Africa
Verbenaceae	*Premna sp.**	
Anacardiaceae	*Pseudospondias microcarpa**	T. Africa
Myrtaceae	*Psidium cattleianum*	T. America
Myrtaceae	*Psidium guajaya*	T. America
Sterculiaceae	*Pteregota mildbraldii*	T. Africa
Leguminosae	*Pterolobium sp.*	T. Africa
	Pulmena fulva	
Myristicaceae	*Pycnanthus angolensis*	T. Africa
Palmae	*Raphia farinifera*	T. Africa
Apocynaceae	*Rauvolfia vomitoria**	T. Africa
Musaceae	*Ravenala madagascariensis*	Madagascar
Anacardiaceae	*Rhus sp.*	
Palmae	*Roystenia oleracea*	T. America
Palmae	*Roystenia regia*	T. America
Apocynaceae	*Saba comoroensis*	T. Africa
Salicaceae	*Salix babylonica*	Australia
Sapindaceae	*Sapindus saponaria**	T. America
Euphobiaceae	*Sapium ellipticum**	T. Africa
Euphobiaceae	*Sapium sebiferum*	China
Sapindaceae	*Sapondus sp.*	
Caesalpiniaceae	*Saraca indica*	India
Araliaceae	*Schefflera sp.*	Australia (?)
Caesalpiniaceae	*Schizolobium excelsa*	Pacific Is. (?)
Cactaceae	*Schlumbergera bridgesii*	T. America
Caesalpiniaceae	*Senna spectabilis*	T. America
Caesalpiniaceae	*Senna (Cassia) grandis*	
Solanaceae	*Solanum macrantherum*	Mexico
Bignoniaceae	*Spathodea campanulata**	T. Africa
Euphobiaceae	*Spondianthus preusii*	T. Africa
Anacardiaceae	*Spondias lutea**	T. America
Araliaceae	*Steganotaenia araliacea*	T. Africa
Sterculiaceae	*Sterculia dawei**	T. Africa
Meliaceae	*Swietenia mahogany*	West Indies
Euphobiaceae	*Synedenium gratii*	T. Africa
Myrtaceae	*Syzigium cuminii*	T. Asia
Bignoniaceae	*Tabebuia pentaphylla**	T. America
Bignoniaceae	*Tabebuia rosea*	T. America
Apocynaceae	*Tebernaemontana holstii*	T. Africa
Rutaceae	*Teclea nobilis**	T. Africa
Bignoniaceae	*Tecoma natans*	T. America
	Terbanaemontana holstii	
Combretaceae	*Terminalia catappa*	E. Indies
Combretaceae	*Terminalia ivorensis*	T. Africa
Combretaceae	*Terminalia mantaly*	
Combretaceae	*Terminalia superba*	T. Africa
Mimosaceae	*Tetrapleura tetraptera*	T. Africa
Euphorbiaceae	*Tetrorchidium didymostemon**	T. Africa
Sterculiaceae	*Theobroma cacao*	T. Africa
Papilionaceae	*Tipuana tipu*	T. America
Meliaceae	*Toon ciliata*	T. Asia
Ulmaceae	*Trema orientalis*	T. Africa
Meliaceae	*Trichilia africana**	T. Africa
Meliaceae	*Trichilia dregeana**	T. Africa
Meliaceae	*Trichilia prieuriana**	T. Africa
Moraceae	*Trilepisium madagascariense (Bosqueia angolensis)**	T. Africa
Cupressaceae	*Thuja occidentalis*	N. America
Rubiaceae	*Vangueria apiculata*	T. Africa
Verbenaceae	*Vitex sp.*	
Cupressaceae	*Widdringtonia whytei*	S. Africa

Plus 16 unidentified species

VINES AND CLIMBERS AVAILABLE IN THE ENTEBBE BOTANICAL GARDENS (list from Katende, 1998).

FAMILY	SPECIES	ORIGIN
Leguminosae	*Abrus cemascens*	
Passifloraceae	*Adenia cisampeloides*	
Apocynaceae	*Alafia grandis**	
Nynctanginaceae	*Bougainvelia alda*	T. America
Nynctanginaceae	*Bougainvillea glabra**	T. America
Combretaceae	*Combretum paniculata*	T. Africa
Vitaceae	*Cyphostema adervianle*	
Vitaceae	*Cyphostema cyphopetala*	
Rubiaceae	*Momordica foetida**	
Rubigceae	*Mondia whitei*	T. Africa
Apocynaceae	*Oncinotis sp.*	N. Africa
Passifloraceae	*Passiflora sp.*	
	Pentarrhinum insipidum	
	Peponium vagelii	
Araceae	*Philodendron sp.**	T. America
Piperaceae	*Piper scandens*	
	Pleopeltis excavata	
Apocynaceae	*Saba commorensis*	T. Africa
Dilleniaceae	*Tetracera potatoria*	India
Acanthaceae	*Thunberga grandiflora**	India
Urticaceae	*Urera cameronnensis*	

Additional Trees and Climbers (Identified by Makerere University Herbarium)

FAMILY	SPECIES	ORIGIN
Aristolochiaceae	*Aristolochia elegans* (vine)*	T. America
Boraginaceae	*Cordia abyssinica (C. africana)**	E. Africa
Papilionaceae	*Craibia rawraufi**	
	*Entadrophragma sp.**	T. Africa
Papilionaceae	*Erythrina excelsa**	E. Africa
Moraceae	*Ficus artocarpoides**	
Euphorbiaceae	*Manihot esculenta**	America
Myrianthaceae	*Myrianthus holstii**	E. Africa
Araliaceae	*Polysias zuwa**	
	*Teroi cocoa**	

APPENDIX C: UTILIZED PLANT FAMILIES

The guerezas fed off of thirty-one different plant families, including:

Acanthaceae	*Euphorbiaceae*	*Papilionaceae*
Anacardiaceae	*Leguminosae*	*Podocarpaceae*
Apocynaceae	*Magnotiaceae*	*Proteaceae*
Araceae	*Malvaceae*	*Rhamnaceae*
Arariceae	*Meliaceae*	*Rubiaceae*
Aristolochiaceae	*Mimosaceae*	*Rutaceae*
Bignoniaceae	*Moraceae*	*Sapindaceae*
Bombacaceae	*Myrianthaceae*	*Sterculiaceae*
Boraginaceae	*Myrtaceae*	*Verbenaceae*
Ceropiaceae	*Nyctaginaceae*	
Cucurbitaceae	*Palme*	

APPENDIX D: BREAKDOWN OF AVAILABLE FEEDING TREE BY SECTION

SPECIES	Bush A	Sec B/D	Sec L	Sec I	Sec G	Sec A	Sec K	Sec C	Sec M/O/P	Sec E	NF	Total
Albizia coriaria	-	-	-	5	-	-	-	-	2	-	-	7
Albizia grandibracteata	3	-	-	-	-	-	2	-	-	-	1	6
Albizia gummifera	-	-	-	-	-	-	-	-	-	-	2	2
Albizia zygia	-	-	1	-	-	-	-	-	-	-	-	1
Aleurites moluccana	-	-	-	-	-	-	1	-	1	1	-	3
Alafia grandis	1	-	-	-	-	-	-	-	-	-	-	1
Antiaris toxicaria	14	2	5	-	5	-	2	-	11	-	9	48
Arenga pinnata	-	-	-	1	8	-	-	-	2	1	59	71
Azanza garckeana	-	-	-	-	-	-	-	-	2	-	-	2
Blighia unijugata	2	2	1	-	-	-	-	-	-	-	1	6
Bougainvillea glabra	-	-	-	-	-	-	1	-	-	-	-	1
Canthium vulgare	12	1	1	6	2	-	-	1	1	1	8	33
Caryota urens	-	-	-	-	2	-	-	-	-	-	1	3
Ceiba pentandra	-	2	-	-	-	-	-	-	-	-	-	2
Cola acuminata	-	-	-	-	-	-	-	-	-	-	3	3
Cordia millenii	-	-	2	-	-	-	1	1	-	-	1	5
Croton megalocarpus	-	-	-	-	-	-	5	-	-	-	2	7
Croton sylvaticus	-	2	-	-	-	-	-	-	-	-	-	2
Entandrophragma sp.	-	-	-	-	-	-	-	-	11	-	-	11
Erythrina excelsa	-	-	-	-	-	-	-	-	2	-	2	4
Eucalyptus citriodora	-	1	-	4	4	-	-	-	2	-	1	12
Eucalyptus sp.	-	-	-	-	-	-	-	-	2	-	-	2
Eugenia uniflora	-	1	-	-	1	-	1	-	-	-	1	4

Appendex D, Continued

SPECIES	Bush A	Sec B/D	Sec L	Sec I	Sec G	Sec A	Sec K	Sec C	Sec M/O/P	Sec E	NF	Total
Fagaropsis angolensis	1	-	-	-	-	-	1	-	-	-	-	**2**
Ficus benjamina	-	-	-	-	-	-	-	-	1	-	1	**2**
Ficus exasperata	-	-	-	1	2	1	4	-	2	-	1	**11**
Ficus natalensis	3	1	-	-	2	-	-	-	2	-	3	**11**
Ficus sur	1	-	-	-	-	-	-	-	1	-	3	**5**
Ficus thonningii	-	1	2	3	-	-	-	-	3	-	1	**10**
Funtumia africana	-	-	-	-	-	-	-	-	-	-	2	**2**
Grevillea banksii	-	-	-	-	-	-	-	-	-	-	2	**2**
Haematoxylon campechianum	-	-	-	-	-	-	-	-	-	-	1	**1**
Hevea brasiliensis	-	44	-	-	-	-	-	-	1	-	1	**46**
Lovoa trichilioides	7	1	-	-	-	-	-	-	-	1	8	**17**
Maesopsis eminii	2	1	2	4	24	-	1	2	8	-	14	**58**
Markhamia lutea	-	-	-	-	-	-	-	5	4	-	-	**9**
Melia dubia	-	-	-	-	-	-	-	-	-	-	2	**2**
Michelia champaca	-	-	-	-	1	-	-	-	-	-	2	**3**
Morinda lucida	2	2	3	-	-	1	-	-	1	-	5	**14**
Musanga cecropioides	-	-	-	1	1	-	-	1	-	8	1	**12**
Nauclea diderrichii	1	-	-	-	-	-	-	-	4	-	-	**5**
Piptadeniastrum africanum	2	1	-	2	5	-	3	2	2	1	2	**20**
Podocarpus latifolius	1	5	-	-	-	-	-	-	-	-	-	**6**
Polyscias fulva	7	-	1	-	2	-	-	2	2	-	3	**17**
Premna sp.	-	-	-	-	-	-	-	-	2	-	-	**2**
Pseudospondias microcarpa	16	1	-	2	1	-	2	3	6	8	7	**46**
Rauvolfia vomitoria	1	-	-	-	-	-	-	-	-	-	5	**6**

Appendex D, Continued

SPECIES	Bush A	Sec B/D	Sec L	Sec I	Sec G	Sec A	Sec K	Sec C	Sec M/O/P	Sec E	NF	Total
Sapindus saponaria	-	-	-	-	1	-	-	-	1	-	1	**3**
Sapium ellipticum	26	5	9	1	4	-	1	-	4	-	16	**66**
Spathodea campanulata	-	-	-	5	3	-	-	-	11	-	2	**21**
Spondias lutea	-	1	-	-	1	-	-	-	-	-	-	**2**
Sterculia dawei	10	-	-	-	-	-	-	-	-	-	1	**11**
Syzigium sp.	-	-	2	-	-	1	-	-	-	-	-	**3**
Teclea nobilis	-	6	-	-	-	-	-	-	-	-	-	**6**
Tetrochidium didymostemon	2	-	-	-	-	-	-	-	-	-	5	**7**
Trichilia africana	-	-	-	-	-	-	-	2	-	-	-	**2**
Trichilia dregeana	3	3	-	-	-	-	-	-	-	-	5	**11**
Trichilia prieuriana	26	-	-	1	-	-	-	-	-	-	-	**27**
Trilepisium madagascariense	3	-	-	-	-	-	-	-	-	-	3	**6**
Section Totals	**146**	**83**	**29**	**36**	**69**	**3**	**25**	**19**	**91**	**21**	**188**	**710**

Trees Not Included Above

Identified by Makerere University Herbarium

Cordia abyssinica
Craibia rawraufi
Ficus artocarpoides
Myrianthus holstii

Located Outside Botanical Gardens

Manihot esculenta

No Record in Botanical Garden Survey

Aedzia zygia
Gmelina arborea
Polysias zuwa
Pseudospondias sp.
Tabebuia pentaphylla
Teroi cocoa

Vines

Aristolochia elegans
Momordica foetida
Philodendron sp.
Thunberga grandiflora

APPENDIX E: MANAGEMENT RECOMMENDATIONS AND IMPLICATIONS

Resident highly habituated, free-ranging primates provide a tourist attraction for the Entebbe Botanical Gardens. The high level of habituation provides a unique, personal experience for the public, who would most likely get only fleeting glances of guereza troops in the national parks. As a result the Gardens gains the increased entrance-fee profit from the public. In addition, the animals' habituation level provides a unique opportunity to study guerezas up-close.

Detrimental aspects of the guerezas residing in the Gardens include the human-guereza interactions. Although there was no observed physical contact between the humans and animals during the course of this study each of the three troops received attention from the humans and the attentions were rarely friendly. An additional detrimental aspect is the incorporation of exotic foods into the diet, which may have unobserved complications on the health of the animals.

A few measures are needed to ensure the survival of the guerezas and to increase the benefits to both the Gardens and to the public. These recommendations include:

1. Incorporation of indigenous guereza feeding trees (like *Celtis durandii* and *Markhamia platycalyx*) into the existing upgrades in the Gardens would provide additional food sources for the animals. In a similar vein, planting feeding trees with the arboreal

movement of the animals in mind could also easily be incorporated into the ongoing upgrades. Many sections of the Gardens are unused by the monkeys, which may be due, in part, to the lower density of both cover and feeding trees in those sections.

2. Group size and the fissioning of daughter troops need to be monitored. Although, the three troops fit within the existing mean group composition and size, the Para troop is in the upper size range for troops found in previous studies and shows indications that it may be growing (with the birth of a neonate and the emigration of an adult male during the course of the study). Access to the unique diet in the Botanical Gardens and the lack of predators could lead to an unsustainable rise in population (Saj 1998).

3. A present goal of the Entebbe Botanical Garden staff is increasing public education. At the time of the study, the on-site staff had limited knowledge of the plants in the Gardens and had virtually no information about the animals or ecology of the area. In this regard, teaching the guides and gate workers about the animals, ecology, and conservation would provide a valuable public service to both the foreign and Ugandan visitors. It may be feasible to have the Entebbe Botanic Garden staff attend zookeeper classes routinely sponsored by the Uganda Wildlife Education Center (UWEC). In addition, an arrangement between the Gardens and tour companies would be beneficial to both parties by reducing the entrance fee for the tours and allowing the Garden staff to join the on-site bird- and primate-watching lectures. The production of educational signs and pamphlets (some are already in production) to be distributed when the gate fee is paid would provide another opportunity for public education. In addition, programs for the area schools could

be created as an effective means of education. The schools are already going to UWEC and, a matching education program could be combined with the Gardens.

General management recommendations for areas with primates utilizing exotic species include:

1. Overall animal density (as well as individual troop size) requires monitoring as troop density has been found to increase with the incorporation of exotic foods into the diet, especially in areas of human habitation.

2. The availability of known dietary species (both native and exotic) needs to be monitored. Very little information is presently known about exotic food choices (or the long-term effects of novel foods in the diet) and with the rise of exotics found in the diets of nonhuman primates, additional data is required to have a clearer understanding of how these animals adjust to changing availability of plant species.

3. As the effects of incorporating exotic species into the ecology of an area is unknown national parks, wildlife preserves, landowners, and individual farmers need to be encouraged to develop the cultivation of native species into viable crops rather than the incorporation of exotic species.