# Ecological and behavioural flexibility of vervet monkeys (*Chlorocebus pygerythrus*) living in a savanna-woodland fragment near Kigoma, Tanzania

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# DEDICATION

In loving memory of my father, for all his love towards me and other primates: Massimo D’Adamo (1951-2007). Baci dalla tua zippa scimmietta.

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# ABSTRACT

Primates habitats are being increasingly fragmented by human activities worldwide. The behavioural flexibility exhibited by vervet monkeys (*Chlorocebus pygerythrus*) is assumed to be crucial in the species ability to persist in habitats heavily altered by humans. From July to October 2015 vervet monkeys were studied in a savanna-woodland fragment near Kigoma, Tanzania, to increase our understanding of how primates can survive in anthropogenically altered habitats. Data were obtained on the activity budget, diet, ranging patterns and habitat use of two neighbouring groups living in areas with different degrees of human disturbance: Kitwe (28-33 individuals) and Jakobsen (21-23 individuals). Significant intergroup differences were found in activity budget, ranging patterns and diet. The group occupying the less altered habitat (Kitwe) spent significantly more time moving and had significantly greater day journey length. The group occupying the most heavily altered habitat (Jakobsen) lived in greater population density and spent significantly more time foraging, playing and engaged in sexual activity. Mean home range size (95% KDE) and mean day travel length were greater for Kitwe group (38.8 ha, 2585.2 m) than for Jakobsen group (15.6 ha, 1727.8 m). Comparatively, the group living in the most altered habitat (Jakobsen) included a larger number of food species in their diet (N=42), ate significantly more fruits, flowers, shoots, invertebrates, mature leaves and human processed foods, and included a larger percentage of human derived foods (39% of their diet) while the group living in the less disturbed habitat (Kitwe) included less food species in their diet (N=16), ate a significantly greater amount of seeds, and included a lower percentage of human derived foods (8.6% of their diet). Results show that vervet monkeys use flexible dietary strategies, one of them being the ability to access the human derived food commonly available in their habitat. The data obtained in this study contributes to developing conservation strategies that can ensure the long-term conservation of the vervet monkeys and possibly other species that share this fragmented habitat.

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# 1 INTRODUCTION

## 1.1 Theoretical background

Primate natural habitats are being destroyed, modified and fragmented by human activities at unprecedented rates causing worldwide decline in primates (Fahrig, 2003; Sodhi and Ehrlich, 2010) and even local extinction of primate populations (Marsh and Chapman, 2013; Sodhi and Ehrlich, 2010). For this reason, human-modified landscapes have become crucial refuges for primates (Marsh, 2003; Marsh and Chapman, 2013) and it has been proposed that such landscapes may actually be necessary for their effective conservation (Riley, 2007). This stresses the importance of studying the behavioural ecology of primates in human modified landscapes (including fragmented habitats) to understand how a primate species can survive, which in turn is important for its conservation (Chapman et al., 2016; Onderdonk and Chapman, 2000).

The capacity to modify behaviour in an adaptive way over time and space in different environments, termed behavioural flexibility, is important for primates in order to cope with changes in their environment (Jones, 2006). However, to generalize how primates respond to fragmentation is difficult because different groups within a single species may react differently to similar fragmentation pressure (Boyle et al., 2009; Irwin, 2007; Marsh, 2003). Studying primates living in different kinds of fragmented habitats is crucial to deepen our understanding of the behavioural and ecological strategies that may allow them to survive in modified habitats and assess the extent of their behavioural flexibility (Jones, 2006). Furthermore, if effective conservation of primates is to take place, it is necessary to conduct more research in disturbed habitats to learn what factors may limit primate adaptability. Compared to studies in relatively undisturbed habitats, little research has been conducted on primates living in fragmented habitats (Bicca-Marques, 2003; Estrada and Coates-Estrada, 1996; Marsh and Chapman, 2013; Onderdonk and Chapman, 2000).

Vervet monkeys (Chlorocebus pygerythrus) exist in east Africa, from Ethiopia and Somalia to South Africa (Kingdon, 2008). They are able to live in much drier habitats than any other member of their genus, occupying forest-grassland mosaics, miombo woodland, open woodland and arid savanna (Kingdon, 2008; Struhsaker, 1967c). Besides occupying habitats relatively undisturbed by humans (Baldellou and Adan, 1998; Struhsaker, 1967c), they live in habitats with secondary vegetation (Chapman, 1985; Foord et al., 1994), highly fragmented habitats (Baranga et al., 2013), cultivated areas (Saj et al., 1999) and even rural (Legesse and Erko, 2004) and urban areas (Albert et al., 2014; Kingdon, 2008). The vervet monkeys' impressive ability to live in human dominated landscapes, contrary to most primate species, is assumed to be related to their behavioural flexibility. For example, they are capable of high dietary plasticity, foraging away from arboreal refuge, adjusting their group size and even lowering the intensity of their alarm calls to hide from predators (Albert et al., 2014; Chapman et al., 2016; Kavanagh, 1980).

Vervet monkeys are semi-terrestrial, opportunistic omnivores (Struhsaker, 1967c). They consume predominantly plants, with a large proportion of fruits, but also eat invertebrates and occasionally vertebrates and their products (Albert et al., 2014; Enstam and Isbell, 2007; Estes, 1991; Lee and Hauser, 1998; Skinner and Chimimba, 2005; Struhsaker, 1967b; Whitten, 1988). Although vervets can expand their diet when exploring new areas, they usually maintain a relatively stable diet despite significant changes in food plant densities, which suggests consistency in food choice (Brennan et al., 1985; Cambefort, 1981; Kavanagh, 1980; Lee and Hauser, 1998).

### 1.2 Previous studies

Vervets have been studied extensively in relatively undisturbed habitats over the last 60 years. Such studies have been conducted in Kenya: Amboseli National Park: (Cheney, 1981; Hall and Gartlan, 1965; Isbell et al., 1990; Lee, 1984; Lee, 1987; Struhsaker, 1967a; Struhsaker, 1967b; Struhsaker, 1967c); South Africa: Windy Hodge Game Park (Baldellou and Adan, 1998) and Ethiopia: Bole Valley (Dunbar and Dunbar, 1974). With the increase of human modified landscapes, the focus over the last 40 years has shifted towards studying vervets in disturbed habitats; with some of the first studies conducted in areas near tourist lodges in Amboseli (Brennan et al., 1985; Lee et al., 1986) and more recent ones in human activity and agricultural areas in South Africa: Samara Private Game Reserve (Pasternak et al., 2013) and Blydeberg (Barrett, 2009a), and Uganda: Entebbe (Saj et al., 1999; Saj et al., 2001) and Lake Nabugabo (Chapman et al., 2016).

Studies on vervets living in human modified landscapes have found many similarities in how the monkeys respond to changes in their habitats: they include human derived foods (Brennan et al., 1985; Chapman et al., 2016; Lee et al., 1986a; Saj et al., 1999; Saj et al., 2001), spend less time foraging (Brennan et al., 1985; Chapman et al., 2016; Lee et al., 1986a; Saj et al., 1999), reduce home range size and mean day travel length (Brennan et al., 1985; Saj et al., 1999). Such studies also found that vervets foraging on human food had larger group sizes and higher population densities compared to unprovisioned groups (Brennan et al., 1985; Chapman et al., 2016). These studies have provided important information on the species range of adaptations and its behavioural flexibility. However, not all habitats where vervet monkeys exist are represented in these studies and the extent of their behavioural flexibility is only partially known.

Primate populations living in human modified landscapes face very different challenges from conspecifics in less disturbed environments. For example, physical injuries observed in groups of vervet monkeys with access to human food were suspected to be the result of an increase in intragroup aggression during food-raids (Brennan et al., 1985; Lee et al., 1986b). In addition, vervets also suffered from interaction with humans. People harass the monkeys (Brennan et al., 1985; Chapman et al., 2016; Lee et al., 1986; Saj et al., 1999; Saj et al., 2001), use dogs to chase them (Chapman et al., 2016; Saj et al., 2001) and ultimately kill them (Kasso and Bekele, 2014; Saj et al., 2001). Furthermore, there are serious public health risks associated with the interaction between humans and monkeys, such as the possibility of disease transmission between the two, and monkey bites to humans. An increase in the human-vervet conflict has thus repeatedly been reported in human altered landscapes (cf. Barrett, 2005; Brennan et al., 1985; Lee et al., 1986; Saj et al., 1999; Saj et al., 2001). Because of this, it is important to extend primate research to populations with access to human derived food and use the data obtained to help in designing strategies to minimize the human-monkey conflict.

### 1.3 Present study

This study investigated the behavioural flexibility of wild vervet monkeys living in a human modified landscape. Next to baboons, vervets are the most extensively distributed and abundant of all monkey species in Africa and one of the most successful primates in the world (Estes, 1991; Struhsaker, 1967c). The vervet monkey is one of four species of the genus *Chlorocebus* that has been classified as highly disturbance-tolerant (Albert et al., 2014; Barrett, 2009b) and is listed as of Least Concern on the IUCN list (Kingdon, 2008).

In the present study, two groups of wild vervet monkeys that occupy different parts of a savanna woodland fragment were chosen with the aim of investigating the behavioural and ecological flexibility that makes them able to persist in this disturbed habitat. Savanna woodland habitat is underrepresented in vervet studies and thus comparing the behavioural ecology of vervet groups living in this same habitat but occupying areas with different levels of human disturbance will enhance our knowledge of the extent of the species ecological and behavioural flexibility. Learning what makes this species successful in adapting to changes is important to understand what makes primates able to survive in continuously expanding human anthropogenical landscapes and aid in their conservation.

The objectives of the present study were:

1. To understand how the behaviour of the vervet monkeys is constrained by the ecological characteristics of their modified habitat.
2. To recommend strategies that can serve for the long-term conservation of the vervet monkeys and other species that share their fragmented habitat.

The following hypotheses were tested:
*Hypothesis 1:* The most altered area within the habitat is expected to be of less ecological quality.
Prediction:

a) The least altered area will have higher abundance of trees, higher density of key food species and lower amount of human activity signs than the most altered area.

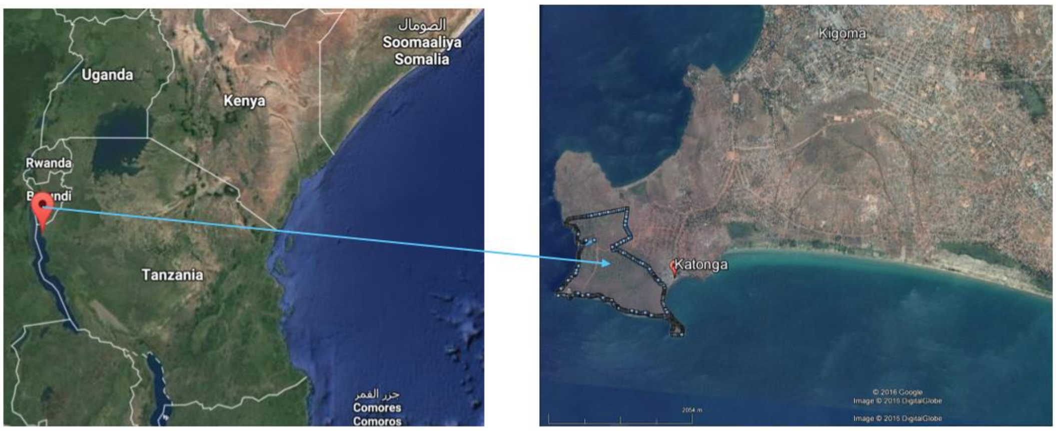
*Hypothesis 2:* The availability of human-derived food is expected to influence the activity budget and diet of the vervet monkeys.
Predictions:

a) The group living in the most heavily altered area will spend less time foraging than the group living in the least altered area.
b) The group living in the most heavily altered area will have a higher dietary diversity than the group living in the least altered area, including a larger amount of food species and items, as well as more human derived foods in their diet.

# 2 METHODS

## 2.1 Study area

The study area (4°54' 47S 29° 36' 14E) is a savanna-woodland fragment of 1.03 km$^2$ on the shore of Lake Tanganyika, about 14 km west of Kigoma town within Kigoma Municipality in western Tanzania. The study area is delimited on the west and south by the lake, on the east by two villages (Katonga and Kamara) and on the north by an expanse of grassland (Figure 2.1).

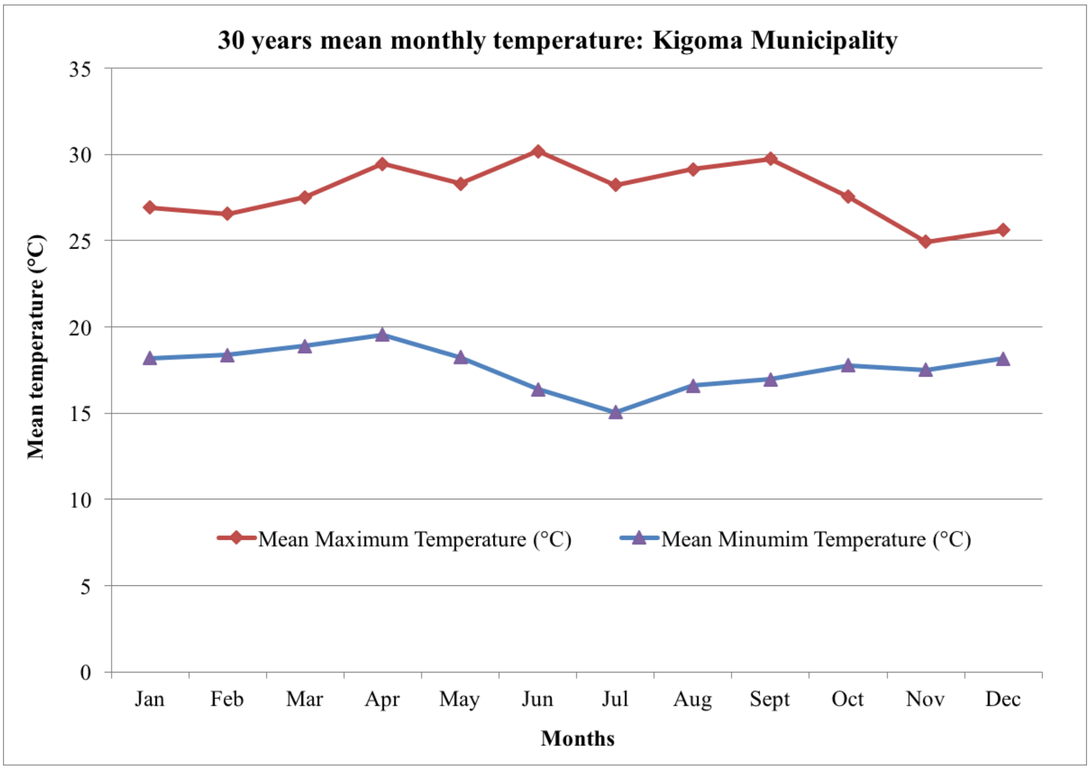


Western Tanzania

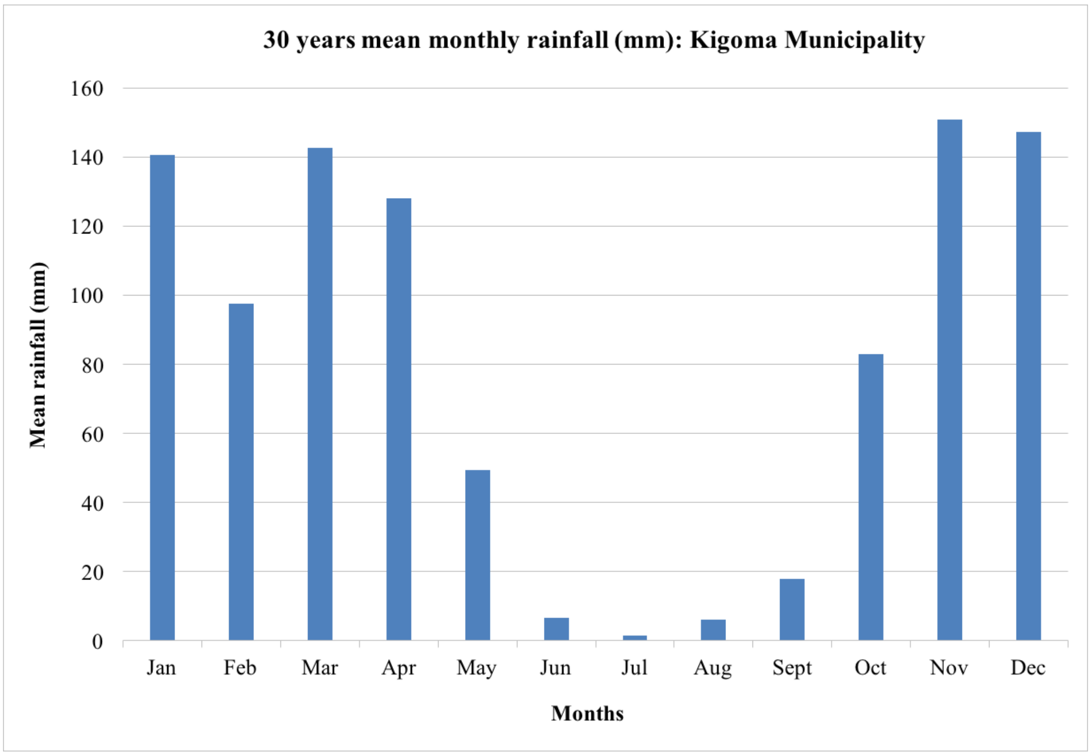
Miombo-woodland fragment (1.03 km$^2$)

**Figure 2.1.** Map of the study area

Altitude ranges from 708 m to 825 m. a.s.l. The climate has a dry season from May to October and a wet season from November to April (Figure 2.2). A dry month is defined as having <100 mm of rainfall (Hernandez-Aguilar 2009). The closest site where climatological data were available is Kigoma town (from 1980 to 2010: Meteorological Directorate of Tanzania). The mean annual rainfall is 971 mm, with 17% falling during the dry season. Average monthly maximum temperature was highest in June (30.2℃) and lowest in November (24.9℃), and average monthly minimum temperature was highest in April (19.5℃) and lowest in July (15.1℃).



a)



b)

**Figure 2.2.** a) Mean monthly maximum and minimum temperatures (ºC) and b) Mean monthly rainfall (mm) obtained from 30 years of climate data (1980 to 2010).

The vegetation of the study area is secondary savanna miombo woodland, dominated by trees from the genera *Brachystegia* and *Julbernardia* (Fabaceae) with patches of grassland, wooded grassland, bushland, and rocky and sandy beaches along the shores of Lake Tanganyika (Appendix I). The area has experienced a series of human modification events that led to a reduction of plant biomass until the Jane Goodall Institute Tanzania (a non-governmental organization) began to protect it in 1994, initiating the Lake Tanganyika Catchment Reforestation and Education (TACARE) project. This is a conservation project that offers sustainable natural resource management education and training, aiming to promote conservation values while actively addressing human needs and endorsing the active participation of local people. The Jakobsen family began working with TACARE in October 1995, when they acquired the property in the North part of the study area. Prior to their acquisition 20 years ago, this part was depleted of most large trees, but since then no more trees have been cut down and the vegetation has re-grown.

The study area is home to other species besides vervet monkeys, such as zebra (*Equus quagga),* genet (*Genetta angolensis*), African wildcat (*Felis silvestris*), otter (*Aonyx capensis*), forest duiker (*Cephalophus natalensis*), central African rock python (*Python sebae*), water cobra of Lake Tanganyika *(Boulengerina annulata stormsi)* and monitor lizard (*Varanus niloticus*). Other species, such as leopards (*Panthera pardus*), used to be present in the area but have not been seen in more than ten years. Except for humans, no other primates live in the study area.

The study area consists of two continuous and connected parts with different levels of anthropogenic alteration. The south part, Kitwe (least altered), comprises 0.87 km$^2$ of municipal land. It is owned and protected by the Kigoma Municipality under the status of reserved land. It is also protected by the Jane Goodall Institute Tanzania. Since 1995 it has been a recreational area where only low impact activities are allowed (hiking, beach bathing, fishing, collecting mushrooms and dead wood). This south part is surrounded by two villages: Katonga (983 households with 5075 inhabitants) and Kamala (1812 households with 9039 inhabitants) (National Bureau of Statistics (NBS) and Office of Chief Government Statistician (OCGS), 2012). Both villages are inhabited by farmers and fishermen and most households include small agricultural plots and fishing camps. The north part, Jakobsen (most heavily altered), is a 0.16 km$^2$ private land called Jakobsen's Beach that provides tourist accommodation. It includes the following human-made areas: one office with a washing room area, paths, ornamental gardens, one four-room guesthouse, three small cottages, two campsites with one camp kitchen and four bedded tents. It has a maximum capacity to accommodate 50 visitors at the same time. However, the total area occupied by these structures is only about 400 $m^2$ and the remaining is natural vegetation and two sandy beaches.

## 2.2 Study subjects

Two groups of vervet monkeys (*Chlorocebus pygerythrus*) living in the study area were the focus of this study (Table 2.1). The present study is the first to have been conducted on these primates. Jakobsen group consisted of 23 individuals over the entire study period and occupied the most heavily altered part of the study area. Kitwe group consisted of a minimum of 28 individuals over the entire study period and occupied the least altered part of the study area. The observation distance was kept at a minimum of ten meters to minimize direct contact with the animals. Jakobsen group was already habituated to humans because of the presence of tourists and workers. Kitwe group was gradually habituated to the presence of researchers over the course of the study, and after the first month human observers were allowed at a ten meters' distance. During this research the primates did not get any formal provisioning, but both groups were observed stealing food from, and given food by humans.

**Table 2.1.** Group size and composition.

| **Categories** | **Kitwe (least altered)** | **Jakobsen (heavily altered)** |
|---|---|---|
| Group size (range) | 28-33+ | 21-23 |
| Group composition | 5+ M, 8+ F, 10+ J, 6+ I<br>Births: 6 + U Deaths: U<br>Emigrations: U | 4M, 6F, 7J, 6I<br>Births: 6 Deaths: U<br>Emigrations: U |

M, number of adult males; F, adult females; J, juveniles; I, infants; +, possibly more individuals; U, Unknown.

This study complies with the International Society of Primatologists requirements for the ethical treatment of primates.

## 2.3. Data collection and analysis

Research was conducted from the 14th of July 2015 to the 14th of October 2015. Data were collected with the help of a local field assistant from dawn to dusk (7:00 am – 7:00 pm) five days a week, alternating between the two groups. All data were tested for normality using Shapiro-Wilks test and statistical significance was set at $p \leq 0.05$. The following data were recorded:

### 2.3.1 Vegetation

Vegetation data were collected once during the study, following the vegetation sampling standard procedure using nested quadrats (Stohlgren, 1995). Transects were placed in each part of the study area aligned along the Lake shore (north west). Due to the different size of the two parts of the study area, it was decided to have different number of plots in each part. In Jakobsen, three plots were placed along one straight transect. In Kitwe, nine plots were placed in one L-shaped transect. (Appendix II). Vegetation plots of 20 x 50 m were placed every 250 m from the start of each transect. Nested subplots were used to include sampling shrubs, saplings and herbs, grasses and sedges.

The following data were collected in each plot: vegetation type (grassland, wooded grassland, woodland, bushland, sandy beach, rocky beach, human altered area), topography (flat, gentle slope, moderate slope, steep slope), soil type (rocks, rocks and sand, sand), canopy cover and ground cover (estimated to the nearest 5% following Hernandez-Aguilar, 2006), evidence of vervet monkeys and/or other mammals (faeces or sightings), evidence of human activities (garbage, snares, roads and constructions), and Global Positioning System (GPS, Garmin GPSmap 64st) location (taken in the middle of the square plot). All trees with a diameter at breast height (DBH) ≥ 5 cm were recorded in 20 x 50 m plots, all shrubs and saplings were recorded in 15 x 20 m nested plots, and all herbaceous plants (grasses, sedges and herbs) were recorded in 2 x 0.5 m subplots. All plants were taxonomically identified by an experienced botanist on site. The few individual plants that could not be identified on site were collected and dried in the field for taxonomical identification at the University of Dar es Salaam, Tanzania.

Species diversity within sites was calculated using the Shannon Wiener Index, and species similarity between sites was tested using the Jaccard Index. After categorizing trees into different DBH classes, size (DBH) of trees was compared using Mann Whitney U test. The number of different species and the number of individuals from each species were calculated per hectare to get the frequency of the species and correct for different sample sizes.

### 2.3.2 Activity budget

Activity data were collected using instantaneous scan sampling (Altmann, 1974) at 15-minutes intervals. Data were collected during the first five minutes of the interval to record the first activity that lasted ≥ 5 seconds for up to five adults or juveniles in sight during scans. Each activity was recorded scanning the group from left to right to avoid the overrepresentation of eye-catching activities (Fashing, 2001). Individuals were identified as: adult male, adult female and juvenile. Infant behaviour was not recorded.

The following behaviours were recorded: resting, moving, foraging, grooming, playing, displaying aggressive behaviour, sexual activity and other. Resting was recorded when an individual was calm, stationary or inactive either sitting or lying down. Self-grooming and sleeping were included in the resting category. Moving was recorded when an individual changed spatial position and included walking, jumping, running and climbing. Foraging was recorded when an individual located, captured and consumed a food item, and included manipulating the substrate (searching through leaves or digging for insects) to get food. Drinking was also included in this category. Grooming was recorded when an individual used the hand(s) to explore or to clean the body of another monkey. Playing was recorded when an individual approached another monkey and/or used an object not used for foraging in a playful manner described by Struhsaker (1965) and Fedigan (1972). Aggression was recorded when an individual interacted in an agonistic context, and included chasing, biting, grabbing, displacing and making threatening gestures. Sexual activity was recorded when an individual engaged in copulatory behaviour. All other activities that did not fit into the previous mentioned categories, such as defecating, play-mothering and vocalizing, were recorded in the category “other”. Group counts were done opportunistically when the monkeys gathered together or crossed areas without vegetation.

Merging the age-sex classes, the total activity budget for each group was calculated to time percentages dividing the number of behavioural records for each activity category by the total number of activity records per day, creating daily and overall activity budgets. The behavioural activity categories were kept separate throughout the analysis to assess possible variations between groups. To test for differences between groups, activity budgets were analysed using One-way ANOVA.

### 2.3.3 Diet

The following dietary data were collected for those individuals recorded feeding during each activity scan sample:

Food categories: natural (naturally occurring food species), cultivated (crops and garden plants) and human processed (foods that have been cooked or altered by humans, such as bread or spaghetti). The last two categories are referred to as human derived foods.

Food items: seeds, young leaves, mature leaves, fruits, flowers, bark, shoots, stalks, roots, invertebrates and human processed foods; life form: tree, shrub, herb, climber, grass/sedge. Leaf litter was recorded when individuals foraged from heaps of leaves on the ground (Harrison, 1984) and no further distinction could be made. Invertebrates could not be identified, as vervets usually snatched these animals and rapidly ingested them before we got a chance to examine the species closely (Chapman et al., 2016) and thus they were simply recorded as invertebrates (Kavanagh, 1978).

Samples of unidentified plant species the monkeys ate were collected and dried in the field for taxonomical identification at the University of Dar es Salaam, Tanzania. The exact type of human processed foods was recorded whenever possible (e.g. bread, ugali (maize porridge), margarine). Human food types that could not be identified were recorded as unknown from human source.

Dietary composition, diversity, daily and overall diet were calculated to percentages using the proportion of different food species and items consumed by the monkeys. Diet composition was analysed using G test. Dietary diversity was analysed using Shannon Wiener and Evenness using Past. One-way ANOVA was used to compare the daily and overall consumed food items.

### 2.3.4 Ranging patterns

GPS locations of each group were taken during every scan sampling. Data were recorded even when the group was not visible as long as cues of their presence (vocalizations, characteristic movements in the tree tops) could be confirmed (Mekonnen et al., 2010).

Day travel length was obtained analysing only full-day follows (days where each group was followed from dawn until it settled in its sleeping site at dusk), using the shortest point-to-point movements for each group between consecutive GPS locations (Mekonnen et al., 2010). Day travel lengths were measured using two commands in Geospatial Modeling Environment (GME) Version 0.7.3 (Beyer, 2015) (*convert.pointstolines* and *addlength*) following (Mekonnen et al., in review) and plotted in ArcGIS 10.3.

Tools (HRT) version 2.0 (Rodgers et al., 2015) in ArcGIS 10.3. Home range was estimated using fixed Kernel Density Estimation (KDE) that measured utilization distribution (Worton, 1989). For this study, home range was defined as 95% KDE and core areas as 50% KDE (the most intensively used areas). However, home range was also estimated using the minimum convex polygon (MCP) method to enable comparisons with earlier studies using fixed mean points (Rodgers et al., 2015) as 95% MCP. Each group’s total distance travelled per day was calculated and compared using One-way ANOVA with SPSS data editor. All results were double checked in R.

### 2.3.5 Habitat use

The following data were collected for each focal individual during each activity scan sample:

Vertical use of space (sensu Enstam and Isbell, 2004): ground level (0 m), shrub layer (0.5-3 m), lower canopy (3.1-10 m), middle canopy (10.1-20 m) and upper canopy (>20 m). Vegetation type used: grassland, wooded grassland, woodland, bushland, sandy beach, rocky beach and human activity area (Appendix I). Vertical use of space and vegetation type use were analysed using G test.

# 3 RESULTS

## 3.1 Vegetation

A total of 2.25 km of transects were sampled for the whole study area (Table 3.1). A total of 36 different plant species were recorded, of which ten were found in both parts of the study area, 21 were only present in Kitwe, and five were only present in Jakobsen (Appendix III). As expected, species diversity was higher in Kitwe (H'= 2.30) than in Jakobsen (H'= 1.51). Presence-absence data between the two study parts showed a partial overlap in species composition (Jaccard similarity index = 0.58).

**Table 3.1.** Vegetation composition.

| | **Kitwe** (least altered) | **Jakobsen** (heavily altered) |
|---|---|---|
| Area sampled | 1.75 km | 0.5 km |
| No. of species (no. of food species) | 31 (13) | 15 (11) |
| No. of total trees counted | 596 | 273 |
| Mean DBH of food species (cm) | 12.8 | 11.4 |
| No. of food trees counted | 485 | 264 |
| Key food species[a] density per ha | 33.9 | 20.3 |

[a]Key food species: *Julbernardia globiflora, Brachystegia sp., Pterocarpus angolensis, Burkea Africana*.

The study area was dominated by small trees, mostly between 5.1 and 20 cm. In Kitwe 88.1% and in Jakobsen 91.9% of the trees belonged to this size class (Figure 3.1. Kitwe: 88.1%, Jakobsen: 91.9%). Mean tree size (DBH) was significantly different between the two parts of the study area (Mann Whitney U = 68014, z = -3.89, p =1.0104E-04; mean size Kitwe = 12.38 ± SD 11.60, mean size Jakobsen = 9.10 ± SD 4.78).

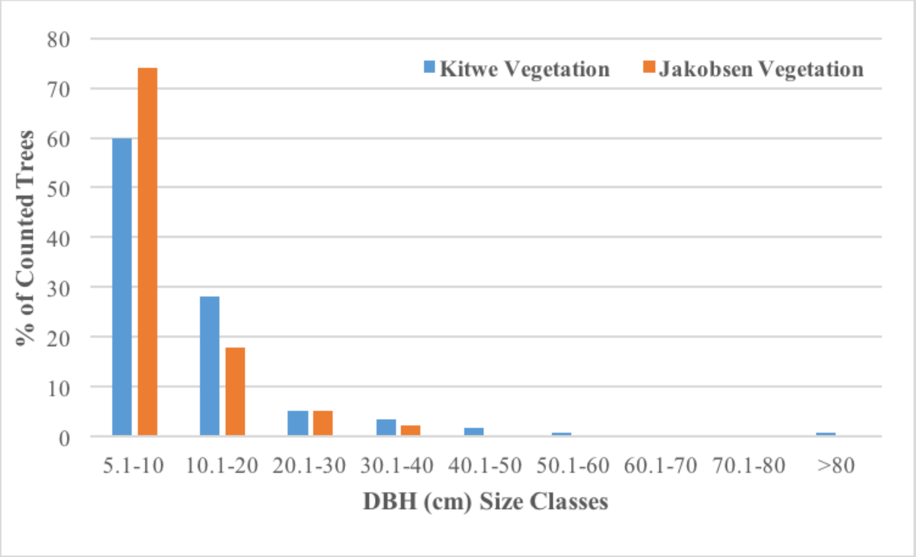


**Figure 3.1.** Tree size (DBH) distribution in the two parts of the study area: Kitwe and Jakobsen.

### 3.2 Activity budget

A total of 252 hours of observation were recorded (Jakobsen group: 138 hours, Kitwe group: 114 hours), comprising 4234 individual scans (Jakobsen group: 2478, Kitwe group: 1713).

Kitwe group spent significantly more time moving (Figure 3.2; ANOVA, F = 41.39, p = 2.24E-06) compared to Jakobsen group. Jakobsen group spent significantly more time foraging (ANOVA, F = 9.34, p = 0.00599), playing (ANOVA, F = 11.3, p = 0.00296), engaging in sexual activity (ANOVA, F = 15.04, p = 0.00087) and other activities (ANOVA, F = 22.54, p = 0.000109) compared to Kitwe group. However, the two groups did not differ significantly in time spent resting (ANOVA, F = 0.012, p = 0.913), grooming (ANOVA, F = 2.008, p = 0.171) or engaging in aggression (ANOVA, F = 0.175, p = 0.68).

Kitwe group spent the greatest proportion of time moving (Figure 3.2; 46.7 %), followed by resting (23.2 %), foraging (20.2 %), playing (4%), grooming (4 %), engaging in aggressive activity (1.3 %) and other activities (0.5 %). Jakobsen group also spent most of their time moving (Figure 3.2; 30.9 %), followed by foraging (26.4 %), resting (24.1 %), playing (7.9 %), grooming (5.3 %), engaging in aggressive activity (1.5 %) and other activities (3.1 %).

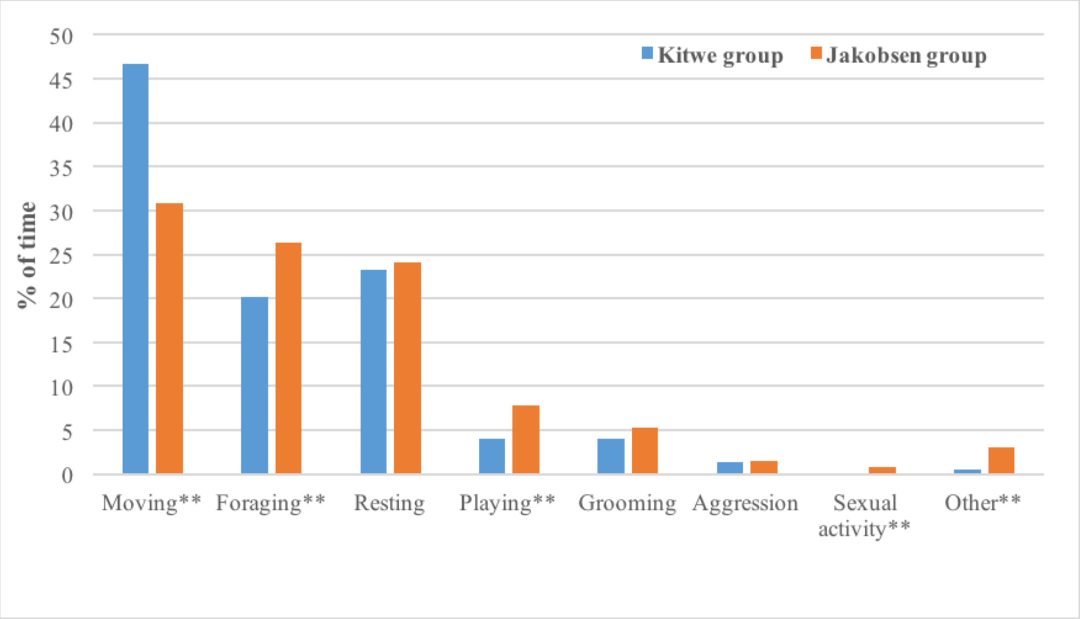


**Figure 3.2.** Activity budget of the two study groups. *p < 0.05; **p < 0.01.

### 3.3 Diet

Diet composition was significantly different between the two groups (Figure 3.3; G test: df = 2, G = 31.25, p = 1.64E-7). The largest proportion of their diet came from natural foods (Kitwe: 91.4%, Jakobsen: 61.1%). Human processed foods were eaten almost four times more by Jakobsen group (23.2%) than by Kitwe group (8.0%). Cultivated foods were rarely observed eaten by Kitwe group (0.6%), but frequently eaten by Jakobsen group (15.8%).

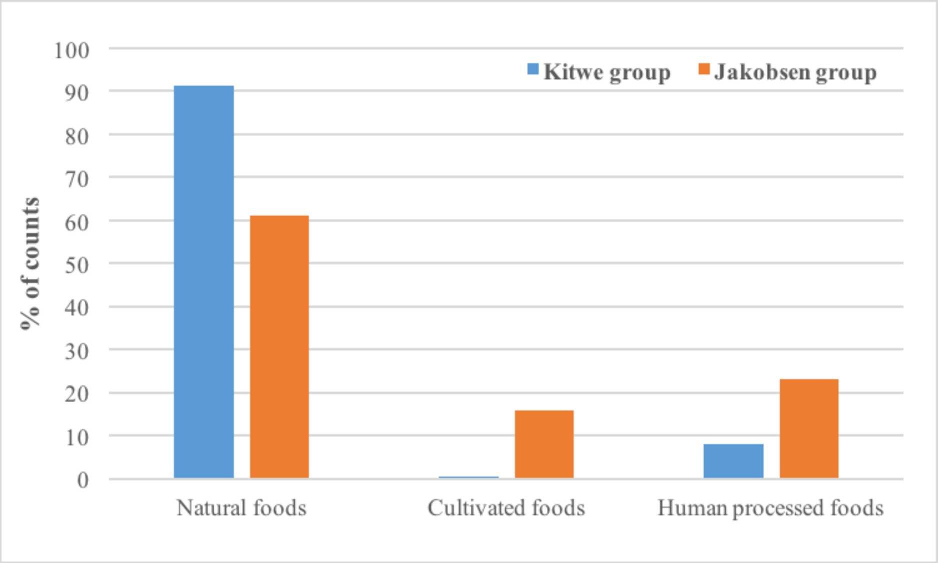
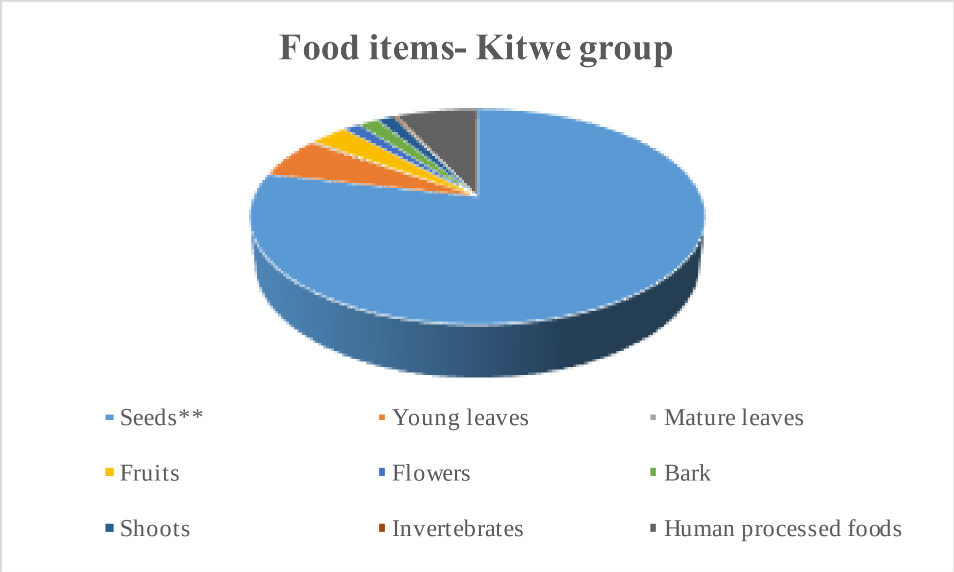


**Figure 3.3.** Percentage of food categories included by the two study groups.

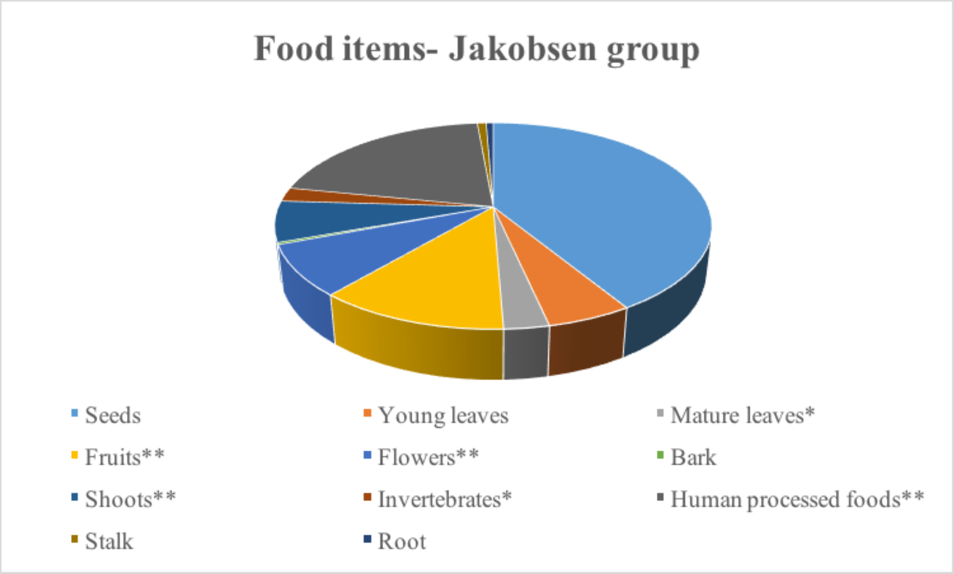
Kitwe group ate significantly more seeds (Figure 3.4; ANOVA, F = 90.04, p = 4.81e-09) compared to Jakobsen group. Jakobsen group ate significantly more fruits (F = 12.88, p = 0.00173), flowers (ANOVA, F = 11.44, p = 0.00281), shoots (ANOVA, F = 11.7, p = 0.00257), human processed foods (ANOVA, F = 9.51, p = 0.00563) invertebrates (ANOVA, F = 5.68, p = 0.0267) and mature leaves (ANOVA, F = 5.34, p = 0.0311) compared to Kitwe group. No significant intergroup differences in the amount of bark (ANOVA, F = 2.09, p = 0.163) and young leaves (ANOVA, F = 0.16, p = 0.696) observed eaten were found.

Seeds accounted for the largest proportion of the diet of both groups (Figure 3.4; Kitwe: 78.6%, Jakobsen: 41.3%), followed by human processed foods (Jakobsen: 20.5%, Kitwe: 7.0%). Kitwe group ate more young leaves (Figure 3.4; Kitwe: 6.1%, Jakobsen: 5.3%) and bark (Kitwe: 1.7%, Jakobsen: 0.3%). Jakobsen group ate more fruits (Figure 3.4; Kitwe: 3.2%, Jakobsen: 11.9%), flowers (Kitwe: 1.4%, Jakobsen: 8.0%), shoots (Kitwe: 1.4%, Jakobsen: 6.4%), mature leaves (Kitwe: 0.3%, Jakobsen: 2.8%) and invertebrates (Kitwe:

0.3%, Jakobsen: 2.2%). Only Jakobsen group was observed eating stalks and roots (Figure 3.4; 0.8% and 0.6% respectively).



a)



b)

**Figure 3.4.** Percentage of food items eaten by Kitwe group (a) and Jakobsen group (b). $*p < 0.05$; $**p < 0.01$.

Jakobsen group consumed a significantly higher number of different food species - including natural and human derived foods (Appendix IV; N = 42) than Kitwe group (N = 16). Food species diversity was higher for Jakobsen group (H’ = 2.63, Evenness = 0.27) than for Kitwe group (H’ = 1.55, Evenness = 0.22). The most consumed plant species was *Brachystegia sp.* in Kitwe, accounting for 55.5% of the diet, and *Julbernardia globiflora* in Jakobsen, accounting for 28.6% of the diet. The top ten plant species for each group are presented in Table 3.2.

**Table 3.2.** Top ten most consumed plant species in both groups.

| Species | Kitwe group<br>(% of counts) | Jakobsen group<br>(% of counts) |
|---|---|---|
| *Brachystegia sp.* | 56.03 | 12.18 |
| *Julbernardia globiflora* | 21.84 | 28.57 |
| *Diplorhynchus condylocarpon* | 3.74 | 3.01 |
| *Elaeis guineense* | 2.87 | 2.26 |
| *Pterocarpus angolensis* | 2.01 | 5.86 |
| *Burkea africana* | 0.86 | (0.30) |
| *Senna siamea* | 0.86 | (0.30) |
| *Ficus lutea* | 0.57 | 1.35 |
| *Pterocarpus tinctorius* | 0.57 | (-) |
| *Strychnos innocua* | 0.57 | (0.15) |
| *Brassica oleracea* | (-) | 0.75 |
| *Parinari curatellifolia* | (-) | 0.60 |
| *Albizia lebeck* | (-) | 0.45 |
| *Mangifera indica* | (-) | 0.45 |

Values listed in parentheses are for comparison only and not top ten most eaten for that group (-, absent).

### 3.4 Ranging patterns

Kitwe group covered a total area of 38.82 ha (Figure 3.5; 95% KDE), with three core areas constituting 9.64 ha. Jakobsen group covered a total area of 15.6 ha over the same period, with two core areas constituting 4.87 ha. The home ranges of the two groups are separated by a minimum distance of 560 m and this in-between area was never observed to be used by either group. Based on the mean group size and 95% KDE of each group, Jakobsen group had an estimated population density of more than twice as many animals/km$^2$ compared to Kitwe (Jakobsen: 146 individuals/km$^2$; Kitwe: 78.6 individuals/km$^2$).

Day travel length varied between 903.4 m and 3880.1 m for Kitwe group and between 1049.2 m and 2097.4 m for Jakobsen group. Kitwe group had a significantly longer mean day travel length compared to Jakobsen group (ANOVA, F = 11.73, p = 0.00254; Kitwe: 2585.2 m; Jakobsen: 1727.8 m).

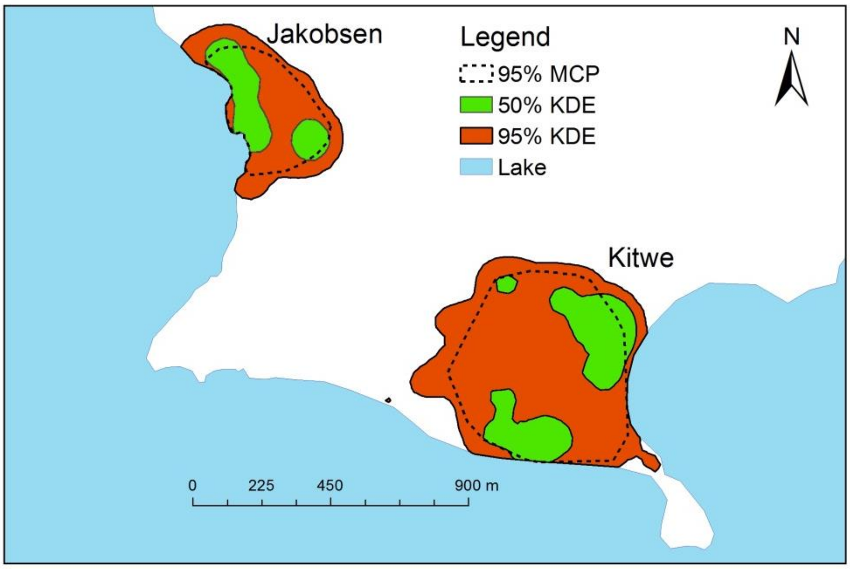


**Figure 3.5.** Home ranges analysed using 95% KDE for the two study groups.

### 3.5 Habitat use

Time spent in different vegetation types was significantly different between the two study groups (G test: d.f. = 6, G = 112.14, p = 7.26E-22). Kitwe group spent almost three times more of their time in woodland than Jakobsen group (Figure 3.6). Kitwe spent 88.8% of their time in woodland, 6.0 % in wooded grassland, 3.6% in rocky beach, 1.1% in grassland and 0.4% in bushland. Jakobsen spent 47.8% of their time in human activity area, 32.4% in woodland, 10.5% in sandy beach, 6.2% in wooded grassland, 1.6% in bushland and 1.4% in rocky beach.

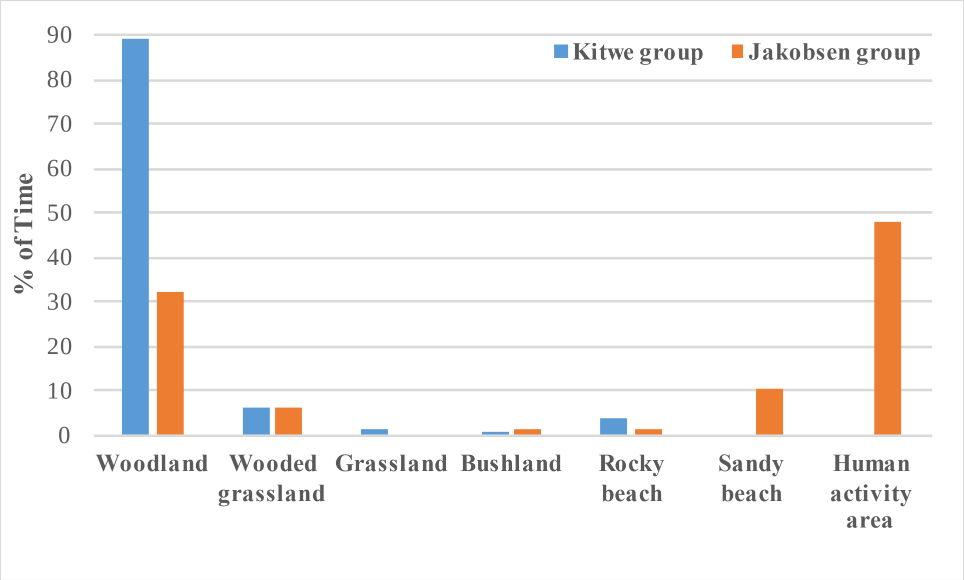


**Figure 3.6.** Percentage of time spent in different vegetation types by the two study groups.

The most used vertical strata for both groups was the ground level (Kitwe: 54.2%, Jakobsen: 64.0%) and they exhibited a similar pattern of strata use (Figure 3.7). The rest of the time Kitwe spent 13.9% in the low canopy, 13.0% in the middle canopy, 12.7% in the shrub layer and 6.1% in the upper canopy, while Jakobsen group spent 12.0% of their time in the middle canopy, 10.7% in the low canopy, 9.7% in the shrub layer and 3.5% in the upper canopy. They two groups did not differ significantly in the amount of time spent in different vertical strata categories (G test: d.f. = 4, G = 2.37, p = 0.668).

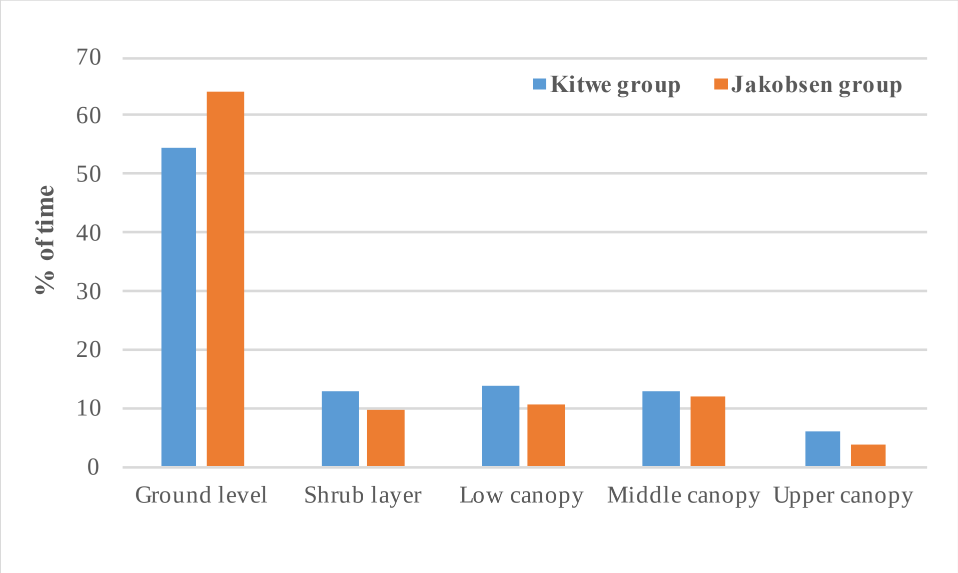


**Figure 3.7.** Percentage of time spent in different vertical strata by the two study groups.

# 4 DISCUSSION

This thesis reports the first study of vervet monkeys in a human-altered savanna woodland fragment in Tanzania. The two study groups showed significant differences in activity budget, diet, ranging patterns and habitat use, likely as a result of the contrasting ecological conditions of the areas occupied by each group. Similarly to other studies, the vervets in the present study showed behaviours that indicate ecological flexibility in response to human disturbance. They readily exploited human derived foods, including what appeared to be novel food sources. Both groups seemed to adjust their daily travel pattern to increase access to human foods. The group in the most altered area (Jakobsen) included a higher amount of human derived foods than the group in the least altered area (Kitwe), and intensively used specific places where human sources were predictably obtainable.

## 4.1 Vegetation

The study area was dominated by trees of small size classes, most of them between 5.1 and 20 cm in DBH. Middle class trees were rare and there were only a few large trees in the area. The absence of middle class trees can be explained by the previous overharvesting of the area, and the abundance of small trees is an indication of regeneration since conservation of the area began. Kitwe was protected first and accordingly had more trees between 10.1 and 20 cm in DBH, while Jakobsen had more trees between 5.1 and 10 cm in DBH. Miombo-woodlands, the vegetation of the study area, are characterized by requiring a long time to reach the sapling phase (at least eight years) and by having a low success of seed establishment (Campbell, 1996). With many of the trees preferred by the vervets only producing fruits after reaching a large size, the cutting of large trees likely had, and continues to have, a great impact on the vervets food availability in the study area (Chapman et al., 2016). As expected, the least altered area had a higher species diversity compared to the most heavily altered area. The area also had lower amount of human activity signs, higher tree abundance and key food species density (Table 3.1). This supports hypothesis 1.

## 4.2 Activity budget and behavioural patterns

Food abundance and distribution affects the vervets activity budget, causing large variations in time spent foraging, resting and moving, while social activities seem less prone to fluctuations (Saj et al., 1999). During the dry season, vervets have been observed to increase the time spent resting at the expense of feeding, adjusting their activity in accordance to the

**Table 4.1**. Comparative data from this and previous studies on vervet monkeys living under different levels of human disturbance.

| Study site/ groups | Country | Duration of study | Season | Habitat | Degree of disturbance[c] | N | Mean group size[d] | MDTL (m) | HRS (ha) | Density (ind/km$^2$) * | Human food obtention strategy[e] | Foraging[g] | Moving | Resting | Social (total, excluding other) | Food species eaten (N) | Fruits | Seeds | Flowers | Leaves | Animal prey | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Katonga (Kitwe group) | Tanzania[a] | Jul - Oct 2015 | D | Savanna woodland | M | 1 | 30.5 | 2585.2 | 38.8 | 78.6 | FR | 20.2 | 46.7 | 23.2 | 9.3 | 16 | 3.2 | 78.6 | 1.4 | 6.4 | 0.3 | This study |
| Katonga (Jakobsen group) | Tanzania[a] | Jul - Oct 2015 | D | Savanna woodland and human modified landscape | H | 1 | 22 | 1727.8 | 15.6 | 141 | FR, HO | 26.4 | 30.9 | 24.1 | 15.5 | 42 | 11.9 | 41.3 | 8.0 | 8.1 | 2.2 | This study |
| Lake Nabugabo | Uganda[a] | Jun 2011 - May 2014 | B | Wetland and human modified landscape | H | 1 | 25.3 | - | 11.6 | 218.1 | FR, HO | 34.3 | 21.2 | 18.3 | - | 49 | 77 | - | 7.6 | 4.0 | 10.6 | (Chapman et al., 2016) |
| Samara Private Game Reserve | South Africa | Feb - Nov 2010 | B | Open dwarf shrub land, woodland, grassland | M | 2 | 26.6 | 2580 | 119 | 22.4 |  | 31.7 | 24.6 | 33.5 | 10 | 26 | - | - | - | - | - | (Pasternak et al., 2013) |
| Blydeberg, Northern Province | South Africa | May 2003 - Apr 2004 | B | Mixed and sour lowveld bushveld | M | 1 | 33 | - | 77 | 42.9 | FR, CR | 42 | 15 | 17 | 26 | 42 | 48.9 | 18.4 | 1.4 | 1.4 | 3.9 | (Barrett, 2009; Willems et al., 2009) |
| Entebbe | Uganda | Jul - Sept 1997 | D | Agricultural areas and settlements | H | 1 | 21 | 596 | 12 | 175 | FR, CR, HO | 26.3 | 14.2 | 44.3 | 10.7 | - | - | - | - | - | - | (Saj et al., 1999; Willems et al., 2009) |
| Windy Hodge Game Park | South Africa | Oct 1997 - Jun 1998 | B | Riverine forest and bushveld mosaic | U | 1 | 11 | - | - | - |  | 32.8 | 18.4 | 30.6 | - | - | - | - | - | - | - | (Baldellou and Adan, 1998; Chapman et al., 2016) |
| Amboseli (O-lengia groups) | Kenya | Apr 1978 - Jan 1980 | B | Open grassland, mixed bushland and woodland | U | 3 | 16 | - | 25 | 64 |  | 36.5 | 26 | 32 | 6.5 | - | - | - | - | - | - | (Lee et al., 1986)<br>(Saj, 1999) |
| Amboseli (Ol Tukai, Lodge group) | Kenya | Jul - Oct 1980 | D | Semi-arid savanna and human modified landscape | H | 1 | 28 | - | 13 | 215.4 | FR, HO | 18.5 | 16.5 | 43 | 20 | - | - | - | - | - | - | (Lee et al., 1986) |
| Amboseli (Ol Tukai, Lodge group) | Kenya | Jul – Oct 1983 | D | Semi-arid savanna and human modified landscape | H | 1 | 43 | 456 | 8 | 537.5 | FR, HO | 18.9 | 16.5 | 43 | 19.9 | 23 | - | - | - | - | - | (Brennan et al., 1985) |
| Amboseli | Kenya[b] | Apr 1978 - Feb 1980 | B | Semi-arid savanna | U | 3 | 20.6 | - | 23.4 | 88 |  | 40 | 25 | 32 | 5 | 44 | - | - | - | - | - | (Lee, 1984)<br>(Chapman et al., 2016) |
| Bole Valley | Ethiopia | May 1971, May - Jul, Sept - Oct 1972 | B | Gallery forest, forest, open grassland | M | 1 | 19 | 700 | 29.5 | 64.4 |  | 28 | 28.9 | 31.8 | 11.4 | - | - | - | 17.6 | 18.7 | 7.4 | (Dunbar and Dunbar, 1974; Willems et al., 2009) |
| Amboseli | Kenya | Jun 1963 - Jun 1964 | B | Semi-arid savanna | U | 4 | 24 | - | 27.3 | 87.9 |  | 35.4 | 14.3 | 36.8 | 13.6 | 37 | 11.5 | 24.9 | 14.9 | 22.5 | 7.7 | (Struhsaker, 1967c; Willems et al., 2009) |

Season: D, Dry; W, Wet; B, Both; [c], degree of disturbance: L, Low, M, Medium, H, High.; N, number of groups; MDTL, Mean day travel length; HRS, Home range size; *,calculated based on mean group size; [e] , Human food obtention strategy: FR, Food-raid; CR, Crop-raid; HO, Handouts. Blanks: the monkeys were observed eating only natural occurring foods. [g], includes feeding and foraging; Food species eaten: N, Number; -, missing info or not comparable; [a], excluding infants; [b], only immatures; [d], when more than one study group under the same disturbance degree the groups have been merged. Crop raid: the monkeys stole crops from farms. Food-raid: individuals supplement their natural diet with food obtained from human activity areas (Brennan et al., 1985). Hand-outs: the monkeys were given food by hand from human. References: besides the mentioned references, data was extracted on: Mean group size obtained from Chapman, 2016 page 79. Mean group size and mean home range size obtained from Lee 1984 page 249. Mean group size obtained from Dunbar, 1974 page 41.
Activity budget data estimated from Lee, 1986 page 233, Figure 1. Number of food species obtained from Brennan, 1985 page 39.

high temperature: resting during mid-day and feeding and travelling in the cooler hours of the day (morning and afternoon) to avoid overheating (McFarland et al., 2014). A similar pattern was observed in the timing of resting events within the two study groups during the present study.

Contrary to what was expected, Jakobsen, the group with highest availability of human derived food, spent significantly more time foraging than Kitwe group. It was expected that Jakobsen group spent less time foraging because of the predictability and high energetic content of the human derived food they have available. This does not support the prediction (a) under hypothesis 2. Time spent in different activities strongly correlates with nutrition in primates with a varied diet, having to balance foraging costs and nutritional benefits (Agetsuma, 1995). Studies have found that primates with access to urban, rural and human activity areas spent significantly less time feeding than their counterparts living in an undisturbed habitat (e.g. *Papio cynocephalus*, (Altmann and Muruthi, 1988); *Papio anubis*, (Quick, 1986) *Macaca radiata*, (Singh and Vinathe, 1990). This has also been found in vervets (Brennan et al., 1985; Lee et al., 1986; Saj et al., 1999). One of the reasons why Jakobsen group spent more time foraging than Kitwe group may be related to the high tolerance of humans to the monkeys' activities in this area, not restricting the time the monkeys spent at the garbage pits and allowing them be more selective of the human derived food.

Compared to other studies, both groups in the present study spent a large amount of time moving (Table 4.1). However, Kitwe group spent a larger time moving than Jakobsen group. This may be related to the higher amount of seeds included in the diet of Kitwe group, since seed eating requires intensive searching through their home range. A seed based diet increased moving time in Yakushima macaques (Agetsuma, 1995). Isbell and Young (1996) reported that resource scarcity increased intragroup scramble competition in vervets and, by consequence, daily travel distance. Thus, the higher group size and resource scarcity in Kitwe may result in longer daily travel distances.

Jakobsen group spent twice the amount of time playing compared to Kitwe group (Table 4.1). Lee (1984) found that the vervet groups with the lowest overall food density decreased social interactions, including play and Saj et al. (1999) found that the higher energetic value of human food makes individuals meet their metabolic demands faster, liberating time for other activities. These results could explain why Jakobsen group, having higher availability of human derived food, could afford more playing time and why Kitwe group, with lower overall food availability, had less time for highly energetic social interactions. In support of Kitwe group having less time for social interactions, this group did not show any sexual activity during the present study and play-mothering behaviour (Hrdy, 1976; Lancaster, 1971; McKenna, 1979) by juveniles was less frequently observed in Kitwe than in Jakobsen group.

### 4.3 Diet

Food availability and nutritional value are important variables shaping the activity budgets of vervets (Lee, 1984), as are human processed foods (Saj et al., 1999). Human processed foods (e.g. spaghetti, bacon) will often be of higher energetic value than cultivated foods (e.g. tomato, banana), given the addition of refined starches and the removal of toxins by heating or refining processes (Saj et al., 1999). The high energetic content of human derived food makes vervets with access to it able to meet their metabolic demands sooner, thus freeing time for other activities, as well as possibly affecting daily travel length and home range size (Brennan et al., 1985; Lee et al., 1986; Saj et al., 1999). The dry season is a time of lower primate food availability in savanna woodlands in western Tanzania (Hernandez-Aguilar, 2006; Hernandez-Aguilar, 2009). In the present study, both groups ate mostly natural foods, but there were significant differences in diet composition. As expected, the diet composition of Jakobsen group included a greater amount of human derived foods, both cultivated and processed (Figure 3.3), as well as of food items (Figure 3.4), and also included more than twice the number of food species compared to Kitwe group, resulting in a diet of higher species diversity (Appendix IV). This supports the prediction (b) under hypothesis 2.

The vervet monkeys in the present study exhibited a high degree of dietary plasticity, willing to include new human processed foods in their diet (Figure 3.3, 3.4; Table 3.2; Appendix IV). But even with wide access to energetic human processed foods, the vervets still foraged mostly on natural foods. The reasons for this may be related to nutrition (protein content may be lower in the available high-carbohydrate human foods than in wild foods: (Saj et al., 1999) and to costs associated with human food consumption (see below).

Seeds accounted for the largest proportion of the diet in both study groups (Figure 3.4). Their habitat is dominated by *Brachystegia* and *Julbernardia* trees (Campbell, 1996) and species from these two genera have seeds available during the dry season, and where consequently consumed in large quantities by both groups. The lower availability of fruit in the dry season can lead to more seed eating because preferred foods (fruits) are not available. Jakobsen group ate a lower proportion of seeds than Kitwe group, which may be a result of their smaller home range containing less seed producing trees and the higher inclusion of human derived foods.

The second most eaten food item by both groups was human processed foods. Jakobsen group ate significantly more human processed foods. One of the most fought over foods was the energy rich margarine (containing more than 700 calories per 100g). Interestingly, the inclusion of a potential new item in the diet of the vervets during this study was observed: individuals from Jakobsen group obtained a salad with bacon. The group fought over it, rapidly eating everything except the bacon. The adult individuals showed no interest in the bacon, but three juveniles did. After putting the bacon in their mouth and spitting it out several times, one of the juveniles ingested it. He then took another piece. The other two juveniles looked at him and suddenly all three were eagerly eating the bacon and finished it all. This behaviour indicates flexibility to include new foods. Further, it supports previous findings that inclusion of novel foods is more common in juveniles, as they typically engage in more risk-taking and exploratory behaviour compared to adults (Fairbanks, 1993; Saj et al., 1999).

Jakobsen group ate significantly more fruits, flowers, shoots and invertebrates compared to Kitwe group. This likely reflects differences in ecological conditions: Jakobsen had flowering trees available, fruits from garbage pits, and shoots from gardens. In addition, there were plenty of invertebrates near the garbage pits and the surface of buildings made invertebrates easy to spot. In contrast, in Kitwe garbage was not available, human constructions were limited to huts largely made of natural materials (dirt and grass) and there were less flowering trees.

In this study, Jakobsen group ate significantly more mature leaves than Kitwe group. Young leaves are higher in protein and preferred over mature leaves by primates (Glander, 1982; Mekonnen et al., 2010; Milton, 1979; Oates, 1977). Wrangham and Waterman (1981) found that the vervets ate exclusively young leaves even if they had access to mature leaves, suggesting that higher amounts of indigestible fibre, phenolics and tannins influence food item choice. In this study, vervet monkeys in Kitwe group spent less time foraging on mature leaves. Juveniles in Jakobsen group were observed to forage on leaf litter (containing mature dry leaves). This was not observed in Kitwe. Given the low nutritional content of dry leaves, it is possible that they were ingested because they contained invertebrates (caterpillars, pupae, galls). If this is correct, the invertebrate contribution may be underestimated in the present study.

### 4.4 Ranging patterns

Primates living in fragmented habitats tend to have smaller daily travel distances and home ranges compared to conspecifics living in continuous habitats (Bicca-Marques, 2003; Boyle et al., 2009; Boyle and Smith, 2010; Tutin, 1999). However, this is not the case for vervet monkeys. Instead, their home range is highly variable (ranges from 8 to 119 ha, see Table 4.1). In the present study, Kitwe, the group living in the least disturbed area, had a larger home range (38.8 ha) and a significantly longer mean day travel length (2585.2 m) compared to Jakobsen, the group occupying the most disturbed area (15.6 ha and 1727.8 m; Table 4.1). Home range and day travel length decrease in response to foreseeable allocation of human food (Altmann and Muruthi, 1988; Brennan et al., 1985; Lee et al., 1986; Saj et al., 1999). Thus, the higher predictability of human derived food availability (e.g. in garbage pits) for Jakobsen group compared to Kitwe group could be one of the reasons for the former group having smaller home range and day travel length.

Results from the present study agree with previous primate studies reporting that the group living in the smallest, more disturbed area travelled shorter daily and overall distances, revisited locations with high food availability throughout the day more frequently and moved in a more uniform way than their conspecifics living in the larger and less disturbed area (Boyle and Smith, 2010; Brennan et al., 1985; Saj et al., 1999). When comparing the present study only with other studies that provide data for the dry season, Kitwe group had a larger mean day travel length than that reported in other studies (Table 4.1). Time spent travelling increases in habitats with widely dispersed food sources (Isbell et al., 1998) and deciduous savanna woodlands in Tanzania are characterized by dispersed primate food sources, especially during the dry season (Suzuki, 1969). Even though plant phenological data were not obtained during the present study, observations during the present study agree that natural food is scattered within the home range of both study groups.

Both groups slept in proximity to areas that offered potential food supplies. Jakobsen group had garbage pits within their core areas, while one of the three Kitwe group's core areas was adjacent to Katonga village. This facilitated food raiding. Jakobsen group acquired human derived foods by food-raiding and occasional handouts, while Kitwe group food-raided from households but was not given handouts. Brennan et al. (1985) reported that vervets living at high population density in a tourist lodge had a range too small to provide enough natural food to sustain the group and concluded that human derived food was important for the group's survival. Similarly, the density of individuals in Jakobsen group was twice as high as Kitwe group and thus human derived foods are likely to be important, particularly during the dry season.

### 4.5 Habitat use

Vervets select vegetation types non-randomly (Chapman, 1987) and availability of food resources is one important factor in this selection (Chapman, 1985). Kitwe group spent most time in woodland and Jakobsen group in human activity areas. But since the percentage of each vegetation type within the home range of both groups was not assessed in the present study, it is not possible to adequately evaluate differences in vegetation type use by the study groups. The differences in vegetation types used by both study groups can partially be explained by the distinct structure of the two parts of the fragment: Kitwe does not have human activity areas except for the Katonga village, while a large part of Jakobsen group home range is composed of human activity areas.

Both groups exhibited a similar use of the vertical strata. In agreement with vervets being semi-terrestrial monkeys, the ground level was the most used strata. This is probably also influenced by the food availability and the ecological characteristics of the habitat: the dry season has less tree cover and more food is located on the ground.

### 4.6 Recommendations for conservation

Similar to other studies, the results from the present study suggest that vervet monkeys can successfully survive in human modified landscapes including fragments. Despite the encouraging evidence of their ecological flexibility, however, the vervet monkeys long term survival is at risk because of conflicts with humans (Altmann and Muruthi, 1988). Because of their ability to exploit human altered habitats, including agricultural areas, vervet monkeys are considered pests by local people in several places in Africa (Brennan et al., 1985; Lee et al., 1986; Lee and Priston, 2005; Saj et al., 2001) and the financial loss for the farmers from crop-raiding has led to actions against vervets spanning from harassment to population displacement and even eradication (Saj et al., 2001). In addition, vervet monkeys are sometimes used as tourist attraction, encouraging people to engage with the monkeys by giving them food, resulting in less fear of humans and aggressive behaviours toward humans when not provided (Brennan et al., 1985; Lee et al., 1986; Lee and Priston, 2005).

Access to human derived food has potentially high risks for monkeys not only because it increases human-monkey conflict but also because it increases the possibility of disease transmission from humans (Barrett, 2009a; Brennan et al., 1985; Chapman et al., 2016; Fourie et al., 2015; Lee et al., 1986; Saj et al., 1999; Saj et al., 2001). Other costs of consuming human foods are higher aggression levels and seemingly more frequent injuries among the monkeys (Saj et al., 1999). A study on Barbary macaques and visitor-directed aggression in Gibraltar, Spain, found biting of humans to be dependent on tourist density: with more tourists getting bitten when the visitor numbers were higher (Fa, 1992). Food provisioned vervets displayed antagonistic behaviour towards people, particularly during hand-feeding interactions, and bites pose a serious health hazard and risk of various zoonoses for humans (Brennan et al., 1985; Chapman et al., 2016; Fa, 1992).

In line with previous studies (Brennan et al., 1985; Chapman et al., 2016; Saj et al., 1999), but for this study in particular, the following conservations measurements are suggested to be implemented to reduce the human-monkey conflict: discourage any contact between monkeys and people, keep human disturbance to a minimum, completely stop handouts, place inexpensive barriers in garbage pits and food preparation facilities, restrict human contact, cut provisioning, keep the number of tourists and visitor low, provide information to tourist on how and why to avoid contact with the monkeys and discourage the monkeys from food-raiding. The TACARE regeneration project from the Jane Goodall Institute Tanzania is a step that aids the conservation of the vervets in this study and the protection given to the area needs to be continued and become more active (e.g. planting more vervet food species in the study area). Finally, education is recommended to take place to reverse the idea of vervet monkeys being pests. The vervets important ecological role (e.g. as seed dispersers) and their value to attract tourist interest can be used to highlight the value of the species for the local community. Educating people is a key step in changing the prognosis of primate survival.

# 5 CONCLUSION

The results of the present study confirmed that vervet monkeys are able to live in areas with high levels of human activity by exhibiting high degree of ecological flexibility: adjusting their ranging patterns, activity budget and habitat use in accordance to the availability of food in time and space, taking advantages of feeding opportunities and readily exploiting human derived foods. It is necessary to implement conservation measurements and work with the local community and with the tourists to prevent the now low-level human-monkey conflict from increasing and allow the long-term survival of the monkeys in the fragment.

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# APPENDIX

**I.** Vegetation type definitions.

| **Vegetation type** | **Description** | **References** |
|---|---|---|
| Grassland | Grass dominated<br>Shrubs and trees make up <2% of canopy cover | (Pratt et al., 1966) |
| Wooded grassland | Grass dominated with scattered trees<br><20% canopy cover<br>Woody plants ≤6 meters tall | (Pratt et al., 1966) |
| Woodland | Grasses and herbs dominate ground<br>High tree density (mostly deciduous) and low shrub density with open or continuous not thickly interlaced canopy cover >20% | (Pratt et al., 1966) |
| Bushland | Shrub canopy <6 meters tall<br>Canopy cover >20% | (Pratt et al., 1966) |
| Rocky beach | Shoreline with sandbed and rocks made of sediments deposits<br>Rocks often covered with biota | (Pearse et al., 1942) |
| Sandy beach | Shoreline with sandbed made of sediments deposits<br>No rocks<br>Biota often not apparent | (Pearse et al., 1942) |

**II.** Vegetation plots sampled in the study area (J, Jakobsen; K, Kitwe; 1-9, plot number).

**III.** <u>Species composition</u>

| **Species** | **Kitwe**<br>(least altered) | **Jakobsen**<br>(heavily altered) |
|---|---|---|
| *Afzelia quanzensis* | P | P |
| *Albizia antunesiana* | P | - |
| *Anisophylla boehmii* | P | P |
| *Annona senegalensis* | P | - |
| *Boscia salicifolia* | - | P |
| *Brachystegia boehmii* | - | P |
| *Brachystegia microphylla* | P | - |
| *Brachystegia spiciformis* | - | P |
| *Bridelia duvigneaudii* | P | - |
| *Burkea africana* | P | P |
| *Chrysophyllum bengalensis* | P | P |
| *Combretum molle* | P | - |
| *Combretum zeyheri* | - | P |
| *Crossopterix febrifuga* | P | - |
| *Dalbergia nitidula* | P | P |
| *Diplorhynchus condylocarpon* | P | P |
| *Hexalobus monopetalus* | - | P |
| *Julbernardia globiflora* | P | P |
| *Lannea schimperi* | P | - |
| *Margaritaria discoidea* | P | - |
| *Markhamia obtusifolia* | P | - |
| *Ochna mossambicensis* | P | - |
| *Ozoroa insignis* | P | - |
| *Parinari curatellifolia* | P | P |
| *Pericopsis angolensis* | P | - |
| *Phyllanthus engleri* | P | - |
| *Pseudolachnostylis maprouneifolia* | P | P |
| *Psydrax parviflora* | P | - |
| *Pterocarpus angolensis* | P | P |
| *Pterocarpus tinctorius* | P | - |
| *Rothmania engleriana* | P | - |
| *Sterculia mhosya* | P | - |
| *Strychnos cocculoides* | P | - |
| *Strychnos innocua* | P | - |
| *Vitex mombassae* | P | - |
| *Ximenia americana* | P | - |

(P, Present; -, Absent)

**IV.** Consumed food species in both study groups.

| Food | Source | Kitwe group (least altered) | Jakobsen group (heavily altered) |
|---|---|---|---|
| *Albizia antunesiana* | NF | - | P |
| *Albizia lebeck* | NF | - | P |
| *Ananas comosus* | CF | - | P |
| *Anisophyllea boehmii* | NF | - | P |
| *Arachis hypogaea* | HDF | - | P |
| *Avena sativa* | HDF | - | P |
| Bacon | HDF | - | P |
| Bread | HPF | P | P |
| *Brachystegia sp.* | NF | P | P |
| *Brassica oleracea* | NF | - | P |
| *Burkea africana* | NF | P | P |
| *Citrullus lanatus* | CF | - | P |
| *Citrus sinensis* | CF | - | P |
| *Cucurbita maxima* | CF | P | - |
| *Chloris ciliata* | CF | - | P |
| *Cucurbitaceae* | CF | - | P |
| *Cyperus papyrus* | NF | - | P |
| *Dalbergia nitidula* | NF | P | - |
| *Daucus carota subsp. Sativus* | CF | - | P |
| *Digitaria brazzae* | CF | - | P |
| *Diplorhynchus condylocarpon* | NF | - | P |
| *Diplorhynchus monopetalus* | NF | P | P |
| *Elaeis guineense* | NF | P | P |
| *Ficus lutea* | NF | P | P |
| *Ficus sycomorus* | FF | - | P |
| *Gallus gallus domesticus* (eggs) | HDF | - | P |
| *Hexalobus monopetalus* | NF | - | P |
| Invertebrates | NF | P | P |
| *Ipomoea batatas* | CF | - | P |
| *Julbernardia globiflora* | NF | P | P |
| *Khaya senegalensis* | NF | P | - |
| *Lactuca sativa* | CF | - | P |
| Leaf litter | NF | - | P |
| *Lonchocarpus capassa* | NF | - | P |
| *Loudetia flavida* | NF | P | - |
| *Mangifera indica* | NF | - | P |
| *Musa sapientum* | CF | P | P |
| *Oryza sativa* | HDF | - | P |
| *Parinari curatellifolia* | NF | - | P |
| *Persea americana* | CF | - | P |
| *Pterocarpus angolensis* | NF | P | P |
| *Pterocarpus tinctorius* | NF | P | P |
| *Rothmannia engleriana* | NF | P | - |
| *Saccharum officinarum* | CF | - | P |
| *Senna siamea* | NF | P | P |
| *Sinarudinaria alpina* | NF | - | P |
| Spaghetti | HPF | - | P |
| *Solanum lycopersicum* | CF | - | P |
| *Solanum tuberosum* | CF | - | P |
| *Strychnos innocua* | NF | P | P |
| *Tagetes erecta* | CF | - | P |
| Unidentified from human source | HDF | - | P |
| Ugali | HDF | P | P |

(NF, Natural Foods; CF, Cultivated Foods; HDF, Human Processed Foods; P, present; -, absent).