ANGLIA RUSKIN UNIVERSITY

THE INFLUENCE OF AGE, SIZE AND SEX ON FEEDING IN YELLOW BABOONS: SEXUAL SEGREGATION BUT NOT AS WE KNOW IT

AMANI KITEGILE

A Thesis in partial fulfilment of the requirements for Anglia Ruskin
University for the degree of Doctor of Philosophy

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"……He who understands baboons would do more towards metaphysics than Locke…"
Charles Darwin

(A quote from Baboon Metaphysics: The evolution of social mind, the book by Dorothy L Cheney and Robert M Seyfarth)

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ABSTRACT

ANGLIA RUSKIN UNIVERSITY

FACULTY OF SCIENCE AND TECHNOLOGY

DOCTOR OF PHILOSOPHY

THE INFLUENCE OF AGE, SIZE AND SEX ON FEEDING IN YELLOW BABOONS: SEXUAL SEGREGATION BUT NOT AS WE KNOW IT

By Amani Kitegile

August 2016

Yellow baboons are sexually size dimorphic mammals living in permanent stable mixed-sex troops: Puzzling in the context of our current theory on group living, sexual dimorphism and sexual segregation! This study is the first to investigate how male and female baboons live together despite body size differences. It hypothesizes they use subtle differences in diet and behaviour predicting that Subadult males will be more similar to adult females than larger bodied adult males. Testing this required looking at the behaviour of baboons in new ways by building on long-term research in an area high in abundance and diversity of baboon food species and habitats in Mikumi National Park (Tanzania)

Data on dietary profile, space use and activity budgets from three-age-sex classes were collected using focal follows with instantaneous and one-zero recording: 70 individuals in 2 troops, over 270 days across 2 years.

Findings demonstrate that baboon diets are diverse not just in terms of species. A range of plant parts and types (including sap and forbs) were eaten plus vertebrates and, especially, invertebrates. Food was packaged in a variety of ways with different processing requirements. Exotic food from a highway was also eaten although only made a very minor contribution to overall diet. Subadult males were more similar to adult females than adult males in their dietary profile (particularly in terms of parts and packages) and activity budgets (particularly in terms of relative allocation of time and number of activities but not synchrony). There were differences between age-sex classes in space use but no consistent patterns emerged.

These findings suggest that adult male and female baboons are able to live together and avoid "classic" sexual segregation despite large difference in body size by subtle differences in what they eat but not in where and how they allocate their time for feeding.

Keywords: Yellow baboon, Mixed-sex troop, Sexual dimorphism, Age-sex class, Sexual segregation, Mikumi.

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Chapter 1 Introduction

1.1 Introduction

This study investigates feeding in yellow baboons (*Papio cynocephalus*) in new ways to increase our knowledge of their dietary and foraging adaptations and explore the question: How can male and female baboons live in stable mixed-sex groups despite large differences in body size? This introductory chapter explains why this question arises in the context of our current understanding of group living, sexual dimorphism and sexual segregation. A conceptual framework is developed to identify potential explanatory mechanisms. Lastly, it gives the structure of thesis along with the summary of topical contents of each chapter.

1.2 Background

1.2.1 Sexual segregation in mammals

In mammals, adult males are usually the larger sex (Fairbairn, 1997). This pattern is associated with sexual selection favouring larger males (Darwin 1871, cited in Stephens and Wiens, 2009; Trivers, 1972). Sexual differences in body size often result in important physiological, ecological and behavioural differences between the sexes. For example, differences in dietary retention rates leads to differences in activity budgets (Ruckstuhl, 1998; Perez Barberia and Gordon, 1998) with larger bodied males spending more time resting (Ruckstuhl, 1998) while smaller bodied mammals (females) spend more time moving (Ruckstuhl, 1998). Sex differences in body size can influence habitat use (Ruckstuhl and Neuhaus 2002; Bowyer 2004; Hay et al., 2008), and may also lead to differences in nutritional and energetic requirements hence differences in food choices by sexes (Illius and Gordon, 1987). When variation in energy nutritional requirements is sufficiently large, males and females have differing resource requirements and use different strategies to detect and acquire food (Breed et al., 2006). Consequently selection will result in mating and social systems where sexes live in different types of social groups and/or use different habitats or similar habitats in differing ways. This phenomenon is referred to as sexual segregation (Ruckstuhl and Neuhaus 2000, 2002; Breed et al., 2006).

Classic sexual segregation is defined as "differential use of space (and often habitat or forage) by sexes outside the mating system" (Bowyer, 2004, pp. 1040; Ruckstuhl, 2007, pp. 245). However, a consensus on what is or is not sexual segregation remains lacking

(Ruckstuhl and Neuhaus, 2000; Bowyers et al., 2002). In species with classical sexual segregation, the sexes are highly dimorphic in size and the mating systems and social organisations reflect selection for this dimorphism. The extent and nature of sociality in a species is predicted to be a selective consequence of differing resource pressures on the sexes and the reproductive fitness differences that select for sexual dimorphism.

In mammals, sexual segregation occurs either as social segregation (sexes live in separate age-sex class groups) or as habitat segregation (age-sex class live in and utilize different habitats (Conradt, 1998; Ruckstuhl and Neuhaus, 2000; 2002; Ruckstuhl, 2007; Hay et al., 2008). Habitat segregation also occurs as spatial segregation when sexes use different areas of the same habitat (Conradt, 1998; Hay et al., 2008). Sexual segregation may also result from sex differences in activity budget and movement (Ruckstuhl, 1998) as well as weather sensitivity in temperate climates areas (Conradt et al., 2000; Bowyer, 2004). Because sexual segregation occurs in a variety of forms a number of hypotheses have been developed to explain the selective pressures leading to sexual segregation.

1.2.2 Hypotheses on occurrence of sexual segregation in mammals

Behavioural and ecological research on species with sexual segregation has resulted in five non-independent hypotheses to explain occurrence of sexual segregation (Ruckstuhl, 2007). These are: i) predation risk/reproductive strategy hypothesis, ii) scramble competition hypothesis, iii) forage selection hypothesis, iv) activity budget hypothesis and, v) social factors hypothesis (social preference and social affinities hypotheses) (Ruckstuhl and Neuhaus, 2000; 2002; Ruckstuhl, 2007). These hypotheses can be assigned into two categories; i) habitat segregation hypotheses and ii) social segregation hypotheses (Ruckstuhl, 2007). Both categories associate the occurrence of sexual segregation with either sex related constraints of body size on nutritional and/or energetic requirements or sex differences in reproductive investment.

1.2.2.1 Habitat Segregation hypotheses

Of the five widely used hypotheses for sexual segregation, three have been classified as habitat segregation hypotheses (Ruckstuhl, 2007). These are: predation risk/ reproductive strategy mostly studied on ungulates such as mule mountain deers (*Odocoileus hemionus hemionus*) (Main and Coblentz, 1990; 1996; Main et al., 1996); forage selection studied on southern mule deer (*Odocoileus hemionus fuliginatus*) (Bowyer, 1984) and bighorn sheep (*Ovis canadensis*) (Ruckstuhl, 1998); and scramble competition hypotheses studied on red deer (*Cervus elaphus*) (Clutton-Brock et al., 1987; Main et al., 1996). Table 1.1 describes each of the three main habitat segregation hypotheses.

Habitat segregation predicts that differences in energy and nutritional requirements between sexes result from sex differences in body size and reproductive investment (Ruckstuhl, 2007). Outside of breeding seasons risk taking and/or predator avoidance as well as decisions on where, when and what resources to use are predicted to differ by sex in relation to differences in body size and reproductive investment (Ruckstuhl, 2007).

Table 1.1 Main hypotheses explaining habitat sexual segregation in sexually size dimorphic mammals.

HYPOTHESIS	SOURCE OF SEGREGATION	EXPLANATION/CONCEPT	SUPPORTED BY	STUDY SPECIE
Predation risk-Reproductive strategy	Sex difference in reproductive investment	Males compete for access to females: and risk predation to maximize energy. Females invest in offspring; and sacrifice forage quality for habitats with lower predation risk.	Main *et al*., 1996; Main and Coblentz, 1990; 1996 Hay *et al*., 2008. Ruckstuhl and Neuhaus, 2002.	Mountain mule deer (*Odocoileus hemionus hemionus*) African buffalo (*Syncerus caffer*)
Forage selection	Sex difference in forage selection	Males have larger rumen and lower passage rate, because of that they are more efficient in digestion of even lower quality forage. To them, food quantity is important than its quality. Females are less efficient in digestion of forage, because of smaller rumen and higher passage rate. For females the quality of forage is important that its quantity.	Bowyer, 1984 Post et al, 2001 Ruckstuhl, 1998; 2007; Ruckstuhl and Neuhaus, 2000	Southern mule deer (*Odocoileus hemionus fuliginatus*) Bison (*Bos bison*) Bighorn sheep (*Ovis canadensis*)
Scramble Competition	Sex difference in tolerance over forage biomass	Males cannot tolerate lower forage biomass because of allometric relationship of bite-size to body-size ratio. Hence, they are less competitive than females. Females have higher allometric relationship of bite-size to body-size ratio, hence can tolerate lower forage biomass and exploit it more efficiently than males.	Clutton-Brock et al., 1987; Main *et al*., 1996; Ruckstuhl and Neuhaus, 2002.	Red deer (*Cervus elaphus*)

1.2.2.2 Social Segregation hypotheses

Two hypotheses addressing social (sexual) segregation are currently widely studied and supported empirically. These are: activity budget hypothesis (red deer-*Cervus elaphus*; Conradt, 1998; bighorn sheep-*Ovis canadensis*; Ruckstuhl, 1998): and social preference hypothesis (Alpine ibex-*Capra ibex ibex*; Bon, 1991 cited in Ruckstuhl, 2007; Bon and Campan, 1996). Details of these social segregation hypotheses are given in Table 1.2. A number of other hypotheses addressing social segregation have been developed. These include the: oddity effect hypothesis (Rodgers et al., 2011): avoidance of intraspecific aggression in mixed sex group hypothesis (Ruckstuhl, 2007); and the weather sensitivity hypothesis (Conradt et al., 2000). These additional hypotheses are not considered further here.

The activity budget hypothesis argues that sexes differ in patterns of movement and activities (Ruckstuhl, 2007) due to differences in decision making and time allocation, while resources and habitats used don't necessarily differ. How resources are used, and when differs due to differences in nutritional and energetic requirements that make synchrony of activities impossible (Ruckstuhl, 2007). The social preference hypothesis argues that sexual segregation is driven by age-sex-specific preferences in association. This hypothesis predicts that there are advantages in associating with animals of similar size, age and/or sex (Ruckstuhl, 2007). Both the activity budget and social preference hypotheses have been empirically tested in social segregated mammals (Michelena et al., 2004; Perez-Barberia et al., 2005).

Table 1.2 Main hypotheses explaining social sexual segregation in sexually size dimorphic mammals

HYPOTHESIS	SOURCE OF SEGREGATION	EXPLANATION/CONCEPT	SUPPORTED BY	STUDY SPECIE
Social Preference	Sex difference in social affinities	Males' preference is access to oestrus females. Males form same-sex peer groups to learn fighting skills, establish dominance and interact with potential rivals.	Bon 1991; Bon et al., 2001 Bon and Campan, 1996; Pérez-Barbería et al., 2005	Alpine Ibex (*Capra ibex ibex)* Mouflon sheep (*Ovis gmelini*)
Activity Budget	Incompatibility of activity budget between sexes	Females have less efficient digestion and compensate with longer foraging times than males. Males have more efficient digestion than females, and will spend more time ruminating or resting. Differences inactivity budgets results in groups with similar activity budgets.	Ruckstuhl, 1998,1999 Michelena et al., 2004 Conradt, 1998; Ruckstuhl and Neuhaus, 2000	Bighorn sheep (*Ovis canadensis*) Merina sheep (*Ovis aries)* Red deer (*Cervus elaphus*)

1.2.2.3 Variation in occurrence of sexual segregation in mammals

Sexual dimorphism in size or body mass is fundamental to hypotheses explaining or predicting sexual segregation (Ruckstuhl and Neuhaus, 2000). The hypotheses addressing sexual segregation predict that the degree of sexual segregation increases with increase in sexual body size and/or mass dimorphism (Ruckstuhl and Neuhaus, 2000). Habitat segregation is predicted to be more pronounced in extremely sexually size dimorphic species than in less sexually size dimorphic species (Ruckstuhl and Neuhaus, 2000). Similarly the activity budget hypothesis predicts incompatibility of activity budgets with synchrony of behaviours for group living should be greater in species with strong sexual size dimorphism (Ruckstuhl and Neuhaus' 2000; Ruckstuhl, 2007). Sexual segregation in any form is more likely and is expected in species with sexual size dimorphism and should be uncommon or absent in species with slight size dimorphism and in monomorphic species (Ruckstuhl and Neuhaus 2000) (Figure 1.1).

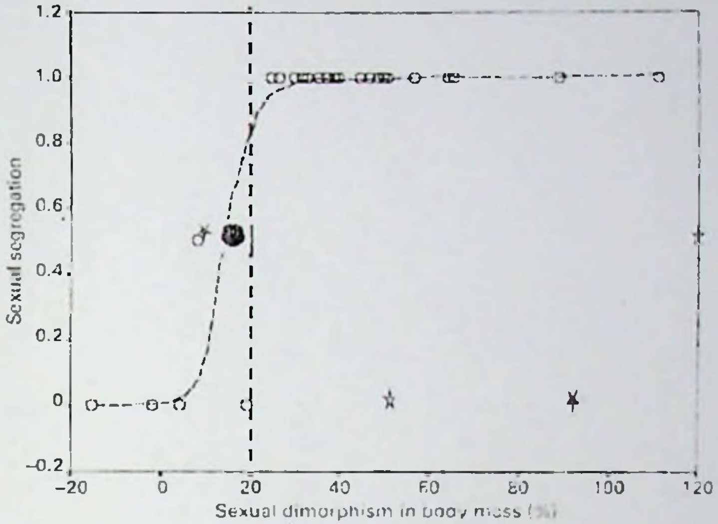


Figure 1.1 Sexual segregation in relation to sexual body size dimorphism in social ruminants compared to primates. Modified from Figure 5, Ruckstuhl and Neuhaus (2002) with points for selected primate species added (stars). The original figure is a logistic regression plot of the effect of sexual body mass dimorphism on sexual segregation in social ruminants (0= no segregation occurs; 0.5 = sometimes live in mixed-sex groups, temporarily segregated or sometimes solitary; 1 = segregation occurs and the bold dashed line represents the 20% threshold above which segregation is expected according to the assumptions of the activity budget hypothesis of sexual segregation). Data points (stars) for 6 primate species were added to the outputs (not regression analyses): yellow baboons (yellow star; Cawthon, 2006), spider monkeys (brown star, Smith, 1996), chimpanzee (grey/black star, Kingdon, 2013), white headed capuchin (white star, Long, 2009), Orangutan (green star, Cawthon, 2005) and hamadryas baboon (blue star, Shefferly, 2004).

Despite the predicted relationship between sexual dimorphism in body size and classic sexual segregation, a number of species have pronounced sexual size dimorphism but little or no sexual segregation as classically defined. In particular, many diurnal primates such as baboons live in permanent mixed sex groups that coordinate locations and activities despite exhibiting pronounced sex size dimorphism (Watts, 2005). There are also some monomorphic species where sexual segregation occurs in absence of sexual size dimorphism. For instance sexual segregation occurs in monomorphic temperate bats (*Myotis daubentonii*) (Altringham et al., 2005) and in Iberian noctule bats (*Nyctalus noctule*) (Popa-Lisseanu et al., 2009).

The lack of classic sexual segregation in highly social group-living diurnal primates with clear and pronounced sex/size dimorphism presents a problem for the existing theoretical structure. Ungulates have been the major group in which sexual segregation has been empirically studied (Ruckstuhl, 1998; Conradt, 1998; Ruckstuhl and Neuhaus 2000; Perez-Barberia *et al.*, 2005; Calhim et al. 2006) and it is from this group that the explanatory hypotheses have been derived. Diurnal primates differ from ungulates in a number of ways especially in terms of life history, female reproductive investment and degree and pattern of sociality (Norton per comm). This study addresses the absence of classical segregation in diurnal primates in relation to these differences.

1.2.3 Sexual segregation in non-human primates

Sexual segregation in some form occurs in a range of primates. This is associated with the type of social system exhibited by a species and the related mating systems (Watts, 2005). In most cases, primate sexual segregation occurs in the form of social segregation where, typically males forage separately from female groups except during mating season. One exception to this is harem groups where males forage separately except for the breeding male holding the harem as is the case for western gorillas (*Gorilla gorilla*) (Harcourt and Greenberg, 2001), hamadryas baboon (*Papio hamadryas*) (Shefferly, 2004). Spatial segregation in primates occurs in form of fission-fusion social systems and can be clearly observed in spider monkeys (*Ateles geoffroyi*) (Abondano and Link, 2012; Rodrigues, 2014) chimpanzees (*Pan troglodytes*) (Chapman and Wrangham, 1993) and orangutans (*Pongo spp*) (van Schaik, 1999; Delgado and van Schaik, 2000; Singleton and van Schaik, 2002), in all these species females typically forage alone or with dependant offspring, juvenile offspring and close female relatives while males are either solitary or in male groups. In Squirrel monkeys (*Saimiri spp*) males are approximately 20% larger than females live and forage in unisex-groups peripheral to the core group of females and their young (Boinski, 1987). Similar form of sexual segregation is exhibited in nocturnal grey mouse lemur (*Microcebus murinus*) which is largely monomorphic. However, males and females forage together during the day, but form unisex sleeping groups during the night (Radespiel et al., 2001). Possibly classic social sexual segregation occurs in mandrills (*Mandrillus sphinx*), where adult females and young live in cohesive permanent hordes, while males are solitary joining females hordes only during breeding seasons (Abernethy et al., 2002).

1.2.4 Group living in non-human primates

There are a number (see Table 5, Smith and Jungers, 1997) of diurnal primate species with marked sex size dimorphism comparable to ungulates, however they exhibit neither habitat nor social sexual segregation as classically defined (Figure 1.1). For instance, yellow baboon males average 21.8kg and are almost twice the weight and size of females averaging 11kg (Altmann, 1993 cited in Cawthon, 2006). Similarly, in hamadryas baboons *(Papio hamadryas)*, average males weigh about 21.5kg, while females weigh 9.9 kg (Shefferly, 2004) and orangutan, in which males weigh as much as 75 kg while females weigh 38.5kg only (Cawthon, 2005a). Many diurnal primate species have a social system with cohesive mixed-sex groups containing overlapping generations (Watts 2005). Such groups are not sexually segregated as classically defined as they are permanent and synchronous in space and time. Behaviour is sufficiently synchronous in order to maintain group cohesion. Cohesive groups are maintained through synchronization of activity in primate species with different mating systems and social organizations such as hierarchical as in gelada (*Theropithecus gelada*) and hamadryas baboons (Swedell, 2012). Polyspecific association with mixed species occurs in many Neotropical and African rain forest monkeys (Heymann, 2011). In terms of sexual segregation the form of sociality, which is most anomalous is that defined by multi-male female bonded primate societies of which the chacma (*Papio ursinus*), olive (*Papio anubis*) and yellow baboons are archetypical examples (van Schaik, 1996; Baniel et al, 2016).

The function and evolution of complex sociality in primates has been a focus of extensive research interest (van Schaik, 1983; Dunbar, 2009). Group living poses theoretical challenges to the hypothesis that selection operates on differential reproductive success of individuals. Living in groups imposes fitness costs on individuals through the cooperative and coordinating behaviours by which social groups are maintained. Individuals must cooperate with those they are competing with for reproductive success (Conradt and Roper, 2000). Extensive research and well supported theoretical models suggest that benefits to individual fitness in groups exceed the competitive costs of living in these groups through: association with and support of relatives (kin selection), protection against predators and increased efficiency for acquiring resources (Conradt and Roper, 2000). Such cooperation even with relatives requires reciprocity and results in complex social networks (van Schaik, 1983; Janson and van Schaik, 1988).

The type of sociality in a species is related to the mating system and the balancing of the different reproductive fitness needs of the sexes. For primates the general premise is that females invest in offspring and need to forage efficiently and safely while males invest in access to and mating with females (Trivers, 1972; Watts 2005). In classic sexual segregation, the fitness costs of males and females grouping together exceed that of living separate lives except for mating purposes. The drivers for this sexual segregation are the differing resource needs related to the energetics of body size (van Schaik, 1983; Ruckstuhl, 1998) and the differing resource demands on the separate sexes related to reproductive investment (Trivers, 1972). Female bonded multi-male sexually dimorphic primate societies are anomalous, as the costs of size do not prevent males from permanently associating with and being a part of female groups. This leads to the question; how do males offset the costs of permanent group membership and how do females offset the cost of competition for resources from males? In addition to resource competition from males, females also must reduce the risks from male reproductive competition especially in the form of infanticide (Palombit, 2000; Watts 2005).

1.2.5 Yellow baboon social organization and behaviour

Yellow baboons along with the similar chacma and olive baboons are typical Female-bonded multi-male societies (van Schaik, 1996; Baniel et al., 2016) living in cohesive permanent mixed-sex troops (Norton et al., 1987). Females are permanent members of natal troops containing dependent and maturing offspring and establishing strong social bonds with related females (Bentley-Condit and Smith 1999; Silk et al., 2004). Females form dominance hierarchies with matrilineal inheritance (Bentley-Condit and Smith 1999). Males have prolonged sexual and physical maturation, and do not form permanent dominance hierarchies; after maturation they disperse from natal troops and join new troops, competing for mating (Samuels et al., 1987; Bentley-Condit and Smith 1999; Silk et al., 2004). Because males move between troops, male troop membership is fluid but there are always adult males in a troop and individual males are rarely living away from a troop (Noë and Sluijter, 1995). An important aspect of baboon sociality is that there is no rigid seasonality to reproduction though there can be reproductive synchrony in females (Cawthon, 2006).

The complex sociality of mixed sex baboon troops with pronounced sexual dimorphism must have mechanisms that allow the sexes to meet their divergent reproductive and resource needs while maintaining the benefits of group living. Compared to ungulates with classic sexual segregation, baboons living in permanent mixed sex groups have a much more diverse and complex diet and resource landscape (Norton et al., 1987). Food resources occur in spatial and temporal patches at a variety of scales and in very diverse packages that pose a range of harvesting and processing problems. These complex resource conditions can allow animals of differing size and sex to vary resource use; behaviourally and in space and time, while maintaining the synchronous behaviours that maintain group cohesion.

1.3 Conceptual framework, research hypothesis and objectives

1.3.1 Conceptual framework

The diet of yellow baboons is extremely diverse especially in Mikumi National Park where this study was conducted. Resource diversity results from discrete wet/dry seasonality, a complex topography patchy seasonal fire, and a high floral diversity. Baboon foods are patchy in space and time and present differing harvest and processing problems for baboons. The food packages used by baboons range from very small seeds and similar that can be harvested and consumed rapidly, to very large fruits roots and pods that require strength and time to harvest, open process and consume (Norton et al., 1987: Rhine et al., 1989).

This resource diversity presents multiple simultaneous feeding options many of these options occur in the same habitats and within the same locations. This enables multiple opportunities for meeting the challenges of nutritional demand and energy requirement. Animals with differing resource needs due to body size and sex differences can utilize different options of resource while synchronizing movement and location. Thus, a mechanism for maintaining stable mixed-sex baboon troops while accommodating the differing needs dictated by size and sex is expected to be sex and size differences in dietary profile by using different food sources, type, parts and packages in differing ways. Such dietary and foraging differences are seen directly in classic sexual segregation and when comparing species of differing size. For example, large bodied animals have lower metabolic requirements, hence consume larger quantity of low quality food, while smaller bodied animals with higher metabolic requirements, and feed on a high quality diet (Ruckstuhl, 2007; Pérez-Barbería et al., 2008). In the case of baboons such dietary differences can be accommodated within the confines of a cohesive troop.

Differences by size/age and sex in spacing behaviour/spatial position (i.e. use of height levels and horizontal positions) is another mechanism for spatial segregation within troops. Because baboons are partly arboreal they can alter position in three dimensions. For example, trees with fruit can be utilised within the canopy at different heights and (for fallen fruit) at ground level. This form of spatial segregation is generally not available for species with classic sex segregation (Norton per comm). Under these conditions small sized individuals can occupy higher height levels, because higher strata produce fruits with superior nutrient content with higher concentrations of protein and sugar, and potentially lower concentrations of toxin (Houle et al., 2014). Thus animals in the same location and food patch can segregate by both height and food patch quality. In some species, larger sized individuals cannot tolerate lower plant biomass due to their lower body to bite size ratio, hence will move to the peripheries (Grassi, 2000; Ruckstuhl, 2000). In baboons this could lead to males with a larger bite size distributing themselves separately from smaller adult females and Subadult males. Thus individuals can spatial segregate within the same location through different spatial positions relative to other troop members and also relative to varying resource distribution within patches. Another driver for this mechanism could be avoidance of intersexual (size based) competition with dominant/larger individuals occupying preferred areas while less preferred but still resource rich positions are used by smaller or subordinate animals.

Social segregation occurs in baboon troops driven by the sex based differences in reproductive investments and the costs of reproductive efforts (Trivers, 1972). Female networks, matrilineal hierarchies and social networks are complex and clearly separate from the male social interactions (Samuels et al. 1987; Bentley-Condit & Smith 1999). Males rarely interact with each other except during conflicts for status or access to females and Male engagement with females socially is largely limited to associations when a female is receptive or to form relationships for future reproductive access (Palombit, 2000). Adult females maintain close relationships and proximity to one another and to dependant offspring and between them and Subadult males, especially during resting and moving. These social differences in age, sex, reproductive status and size, allow for segregation of like individuals with a cohesive troop. Because the diverse environment permits multiple resource tactics within the same locations like individual can synchronize their activity while maintaining the cohesiveness of the troop. Classic sexual segregation is absent but can occur at a micro level within the confines of group living.

1.3.2 Aims and objectives

In yellow baboons, body size varies with age and sex classes of individuals. Adult males are usually larger than Subadult males and adult females. However, the body size of adult female is relatively similar to that of sub adult male. Differences in body size between sexes and age classes in yellow baboons are important for understanding their foraging behaviour. Therefore, in this study age-sex classes (i.e. adult males, adult females and Subadult males) of baboons are used as the measure for difference in body size between them. The main aims of this thesis are to further our knowledge of the dietary profile and foraging behaviour of yellow baboons and use this knowledge to explore the question: How do sexually size dimorphic baboons maintain stable mixed-sex groups despite large differences in body size? These aims are addressed by collecting detailed data on diet and foraging behaviour and testing the main research hypothesis that: yellow baboons are able to maintain permanent stable mixed sex groups despite sexual dimorphism due to subtle differences in their dietary profile and spacing behaviour and through synchronization of their activity budget. This is achieved through completing the following objectives:

1. Describing the overall feeding behaviour of yellow baboons in relation to their dietary profile (i.e. food sources, types, parts and packages consumed) and spacing behaviour (i.e. use of vertical and horizontal positions) during feeding and their diurnal activity budget (Chapter 3).
2. Assessing variation in feeding behaviour in terms of food sources, types, parts and package consumed (dietary profile) by individuals of different age-sex classes (Chapter 4).
3. Assessing variation in use of vertical heights and horizontal positions (spacing behaviour) during feeding by individuals of different age-sex classes (Chapter 5).
4. Assessing for variation in diurnal activity budget in terms of time allocated to different activities, number of activities performed and activity synchrony between individuals of different age-sex classes (Chapter 6).

1.4 Thesis structure

This thesis has seven chapters. **Chapter two** describes the general methods used in this study. It includes description of study area and study sites, data collection techniques and recording procedures as well as data analysis. **Chapter three** is a benchmark results chapter for the succeeding chapters. It provides general but detailed results on dietary profile of yellow baboons, spacing behaviour during feeding and their activity budget. **Chapter four** is the result chapter on age-sex differences in dietary profile. It encompasses age-sex differences in consumption of food sources, types, parts and packages. **Chapter five** presents results on age-sex differences in spacing behaviour. It covers age-sex difference in use of height levels and horizontal positioning within and away from the vicinity of other troop members during feeding. Also provided in this chapter are results spacing behaviour of yellow baboon in relation to presence of nearest neighbours. **Chapter six** presents results on age-sex differences in diurnal activity budget. It elucidates age-sex difference in time allocated to different activities, number and types of activities performed at the same time. The chapter also presents results on degree of activity synchronization between age-sex classes. **Chapter seven** provides general discussion and conclusions on study findings as well as recommendations.

Each result chapter 4-6 introduces the specific questions addressed in that chapter, describes the specific chapter aims and a reviews of the relevant literature. Methods for the questions addressed in the chapter, are provided along with details of data analysis. Moreover each of these chapters provides prediction for expected patterns of sexual segregation within groups. Result sections present the test of these predictions, followed by a discussion and summary of the results.

Chapter 2 Study Area and General Methods

2.1 Introduction

This study was conducted in Mikumi National Park (MINAPA), Tanzania. The main period of data collection began in September 2010 and finished in November 2012, covering two full ecological years each with four seasons (two dry and two wet seasons). Preliminary work was conducted from June to August 2010, during which reliability of method for data collection and identification of individual baboons especially adult males, females and Subadult males were conducted.

This chapter gives detailed description of geography and vegetation (section 2.2.1) and climate (section 2.2.2) of MINAPA in general and introduces the study area (section 2.2.3). The chapter also provides detailed description of study animals (section 2.3), and methods of data collection (section 2.4). The chapter ends with an overview of data management and analysis (section 2.5) and sampling effort (section 2.6). Further descriptions of methods are given in the result chapters as appropriate.

2.2 Study site

2.2.1 Geography and vegetation

With an area of 3230 km², MINAPA (Figure 2.1; inset) is the fifth largest National Park in Tanzania after Ruaha, Serengeti, Katavi and Mkomazi National Parks respectively. Situated in the central eastern Tanzania, the park is about 20 km away from the small town of Mikumi, and about 70 km south west of Morogoro Municipal, which is the closest large town. The park extends from longitude 37°00’ to 37°30’E and latitude 7°00 to 7°45’S (Mofulu, 2005; Gunn, 2009; Anon 1, 2012). The altitudinal range of MINAPA is highly variant, ranging from 430m a.s.l in the southern plains to 1270m a.s.l in Malundwe Mountain (Lovett and Norton, 1989).

In the south, MINAPA is bordered by Selous Game Reserve, Udzungwa Mountains National Park, Mikumi open area and Mikumi town bordered the park in south west (Mofulu, 2005). While in the north, the Park is bordered by another protected area the Uluguru Natural Reserve, Doma village as well as Doma and Mkata open areas (Mofulu, 2005; Annon 1, 2012).

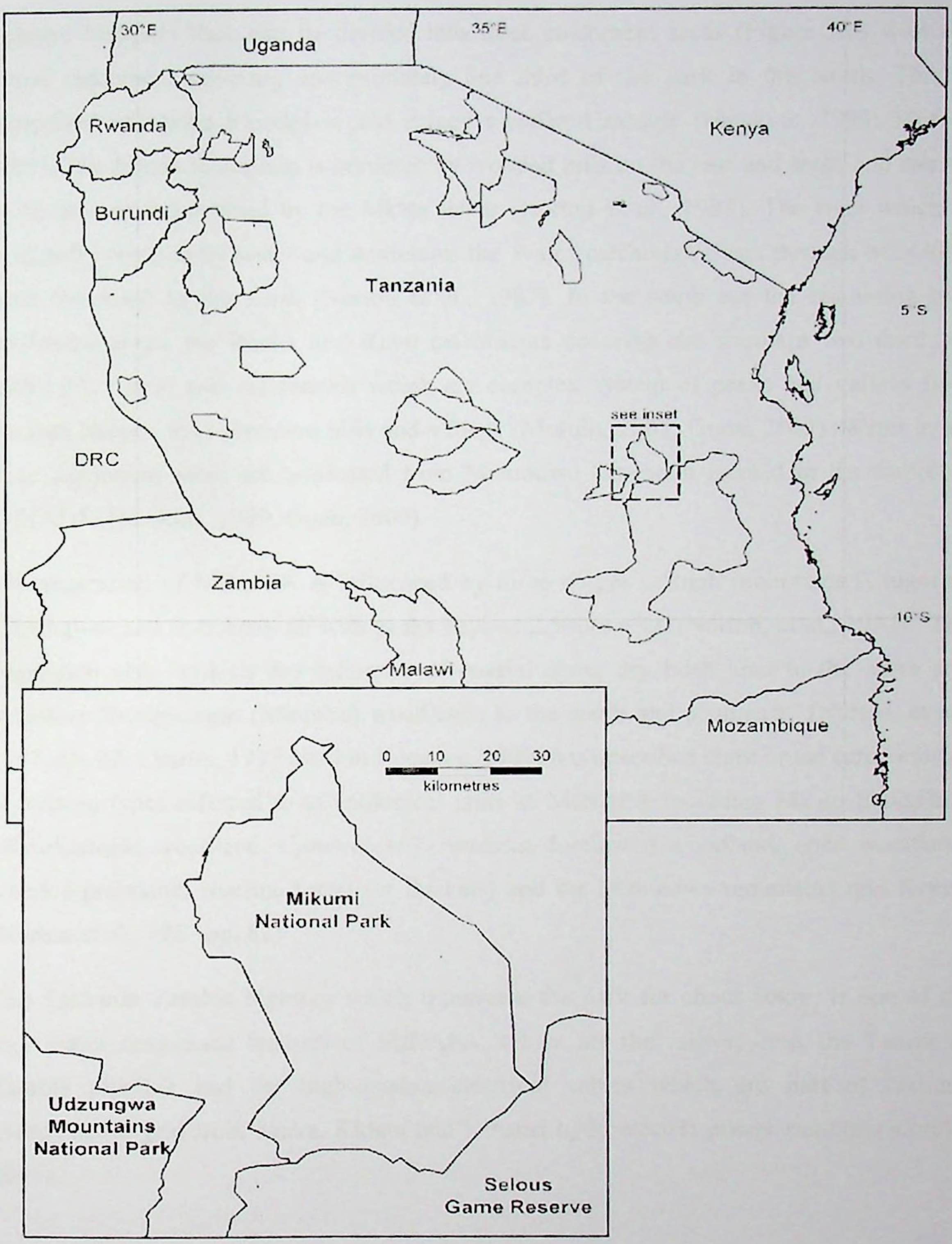


Figure 2.1 Position of Mikumi National Park within Tanzania (inset) in relation to the wider Mikumi Selous Ecosystem (source: Mofulu 2005).

Mikumi National Park can be divided into three catchment areas (Figure 2.2) with the Wami catchment covering approximately one third of the park in the North. This is comprised of Mkata Floodplain and mixed woodland mosaic (Hawkins, 1999: Mofulu 2005). The Mkata floodplain is bordered by wooded hills on the east and west, and named so because it is traversed by the Mkata River (Norton et al., 1987). The river which is seasonally covered by water and dominates the Wami catchment flows through MINAPA from the south to the north (Norton et al., 1987). In the south are the remaining two catchment areas, the Ruaha and Ruvu catchments covering the southern two thirds of MINAPA. These two catchments which are complex system of peaks and valleys flow through steeper, mid-elevation hills and valleys (Mofulu, 2005; Gunn, 2009). Water in all three catchment areas are originated from Malundwe Mountain located in the centre of MINAPA (Hawkins, 1999; Gunn, 2009).

The vegetation of MINAPA is influenced by three ranges of high mountains (Ulugurus, Udzungwas and Rubehos), all with peaks beyond 2,500m a.s.l. (Norton, et al., 1987). The vegetation also "reflects the influence of coastal zone, dry bush land to the north and extensive *Brachystegia* (Miombo) woodlands to the south and southeast" (Norton, et al., 1987, pp. 82: Lyaruu, 1997 cited in Venance, 2009) has described eight broad categories of vegetation types referred to as ecological units in MINAPA including Mkata floodplain, "*Brachystegia* woodland, *Combretum-Terminalia* dominated woodland, open woodland, wooded-grassland, riverine forest (or thickets) and the Malundwe mountains rain forest" (Norton et al., 1987,pp. 82).

The Tanzania–Zambia highway which transverse the park for about 50km, is one of the four major man-made features of MINAPA, others are the railway line, the Tanzania-Zambia pipeline and the high-tension electrical cables which are part of national hydroelectric grid from Mtera, Kidatu and Kihansi hydroelectric power stations (Mofulu, 2005).

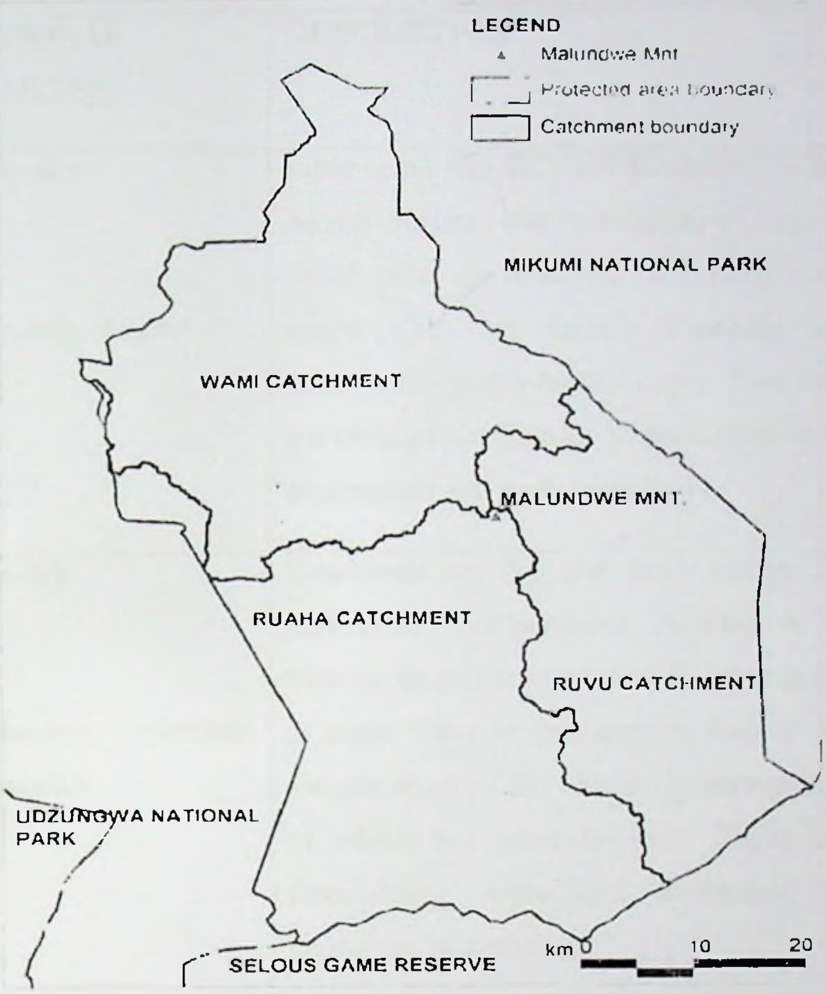


Figure 2.2 Three water catchments of MINAPA: Wami, Ruaha and Ruvu (source: Gunn 2009).

2.2.2 Climate

Mikumi National Park has a unimodal pattern of climate although rainfall patterns are highly variable (Norton 1994, ABRU unpublished rainfall records). The wet season usually lasts from December to May (although in some years it may start as early as October) and the dry season from June to November. For years up to 1997, average annual rainfall for MINAPA has been 860mm (Norton, 1994 – up to 1997); however, from 1998 it has increased to 889mm of which around 95% fell in wet season with peak rainfall been in April (ABRU unpublished rainfall records). The dry season corresponds to the coolest time of the year with the average annual temperature being 25.5°C.

Long-term research in the park identifies an "ecological year" in MINAPA which is divided into four seasonal quarters; early dry, late dry, early wet and late wet (Table 2.1).

Table 2.1 Definition of seasonal quarters of MINAPA (modified from Hawkins 1999).

SEASONAL QUARTER	DESCRIPTION
Early dry June, July, August	Little or no rain falls and temperatures are relatively cool. Cover density declines due to foraging of large ungulates and fire. Fires which occur are relatively cool. Early burns may occur late in the quarter, but are usually localised and leave considerable unburned or partly burned cover. Free standing water is abundant for most of the quarter in permanent water holes, watercourses. depressions and buffalo wallows
Late dry September, October, November	Conditions are dry and dusty except for possible rain in late November. Temperatures increase as the quarter progresses. Electric storms are common in latter parts of the quarter. usually at night. Fires in this quarter tend to be hot late burns which remove most of the remaining perennial and annual cover. most of which has gone to seed. There is a gradual decline in freestanding water and increasing faunal dependence on permanent waterholes.
Early wet December, January, February	Rain falls regularly in this quarter. Temperatures are hot and humidity is high. Grass flushes occur especially in burned areas. There is rapid growth of herbaceous species. Grass height and density increases through the quarter, replacing herbaceous cover. Water is commonly available. however. early in the quarter the pattern and amount of rains may result in the intermittent availability of rain pools, and other water sources.
Late wet March, April, May	Rain falls in short showers on most days, with occasional days of heavy rain. Rains decline in frequency and intensity at the end of the quarter. Temperatures decrease as the quarter progresses. In many areas the cover is dense and high, especially from grasses. Freestanding water is abundantly distributed

2.2.3 Study area (Viramba range)

The range of Viramba troops, which was the main study area for this research, is located within the central floodplain and the easterly hills (Norton *et al.*, 1987; Mofulu, 2005; Figure 2.3).

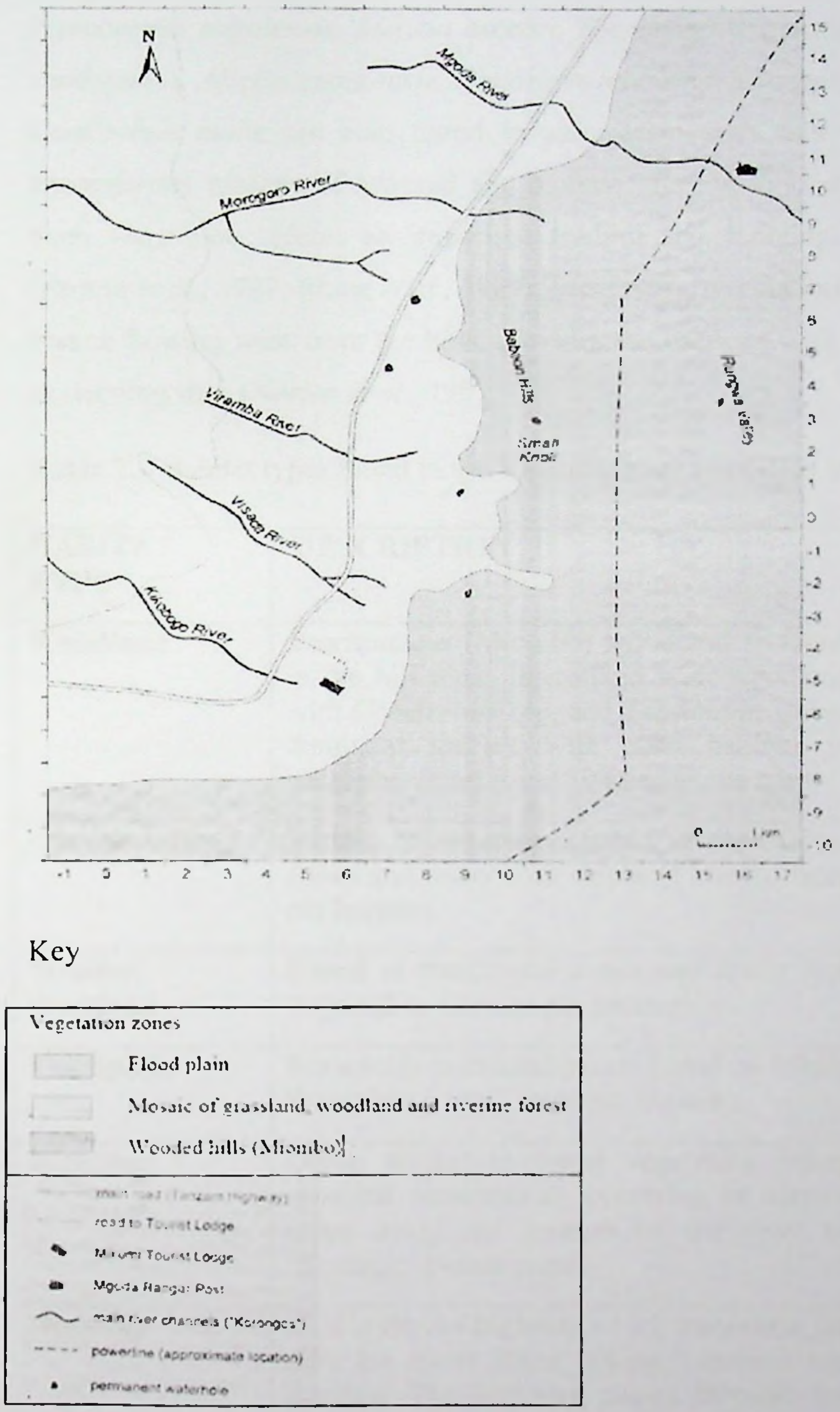


Figure 2.3 Study Area (Viramba troop range) (source: Hawkins 1999).

The habitat types in the study area (Table2.2; Mofulu, 2005; Norton *et al.*, 1987; Hawkins, 1999) include all the habitats and vegetation types found within the Park except for Afromontane forest (Lovett and Norton, 1989). Important tree species in the area for defining the mosaic of habitat types in which yellow baboons are adapted to are, *Brachystegia spiciformis, B. boehmii, B. microphylla and Pericopsis angolensis*. However, *Pterocarpus angolensis, Melicia excelsa, Pseudolachnostylis maprouneifolia, Xerroderis stuhlmannii, Afzelia quanzensis, Diplorhynchus condylocarpon, Annona senegalensis* and *Combretum molle* are also found in association with this vegetation. The area also encompasses patches of lowland and montane forests, thickets, riverine and grasslands. Such vegetation creates an important feeding and foraging zone for yellow baboons (Norton *et al.*, 1987; Rhine *et al.*, 1989). Moreover, riverine forests resulting from drainage system flowing west from the hills, provides the baboons with potential tree refuges used as sleeping sites (Norton *et al.*, 1987).

Table 2.2 Habitat types found in the Viramba range (modified from Hawkins, 1999).

HABITAT TYPE	**DESCRIPTION**	**Appendix 2.5, HABITAT codes**
Woodland	*Brachystegia* (Miombo) woodland is found in the hill tops intermixed with woodland with *Combretum spp*, and *Terminalia spp* as dominant species, with other habitats in transition zones (over 30 trees per hectare)	4, 5
Open woodland	Mosaic of vegetation found in transitional zones and lower foot slopes (11 to 30 trees per hectare)	3
Wooded grassland	Found in transitional zones and lower foot slopes (2 to 10 trees per hectare)	2
Floodplain	Seasonally inundated plains found on Mkata floodplain (1 to 2 trees per hectare)	1
Riverine	Dense thicket to forest vegetation lining seasonal watercourses occurring in narrow strips along the courses of the river or 'Korongo' (water pond)	6, 7, 9
Highway	This is the A4 highway which transverse the park for about 50km linking Tanzania and Zambia. The highway passes through the major part of study area.	10

2. 3 Study animals

2.3.1 History of long-term baboon research in MINAPA

Yellow baboons studied for this research belong to well habituated troops called Viramba. The original Viramba troop (V0) was habituated in 1975 and has been observed and studied ever since. One of the main themes of this research has been into baboon foods and feeding (Rhine et al., 1989; Rhine et al., 1986; Norton et al.,1987; Johnson, 1989 and Diego, 2003). These studies have documented the diversity, breadth and flexibility of the Viramba baboons in terms of habitats used and species eaten. They have also highlighted the role of cheek pouches in yellow baboons. It is this theme in the long-term baboon research in MINAPA in particular that has stimulated and enabled the exploration of the behaviour of yellow baboons in new and more details ways needed for this study.

During the period of long-term baboon research in MINAPA, the Viramba study animals have undergone a number of fission and fusion events, accompanied with changes in population size (Figure 2.4; Hawkins, 1999; ABRU unpublished records). The first split was in 1978 when V0 split into two troops, V1 and V2. In 1979, 15 members from V1 left and formed their own troop V3, which kept shrinking. In 1989, members of V3 troop tried to merge with V2 without success, leaving only two surviving members of original V3. In 1994, the remaining members of V1 reunited with V2 and form V4 which stayed united until early August 2010, when it split into V5 and V6. The preliminary survey for this work was conducted on V4 (in June to August 2010). The main data were collected on V5 and V6 (September 2010 to November 2012).

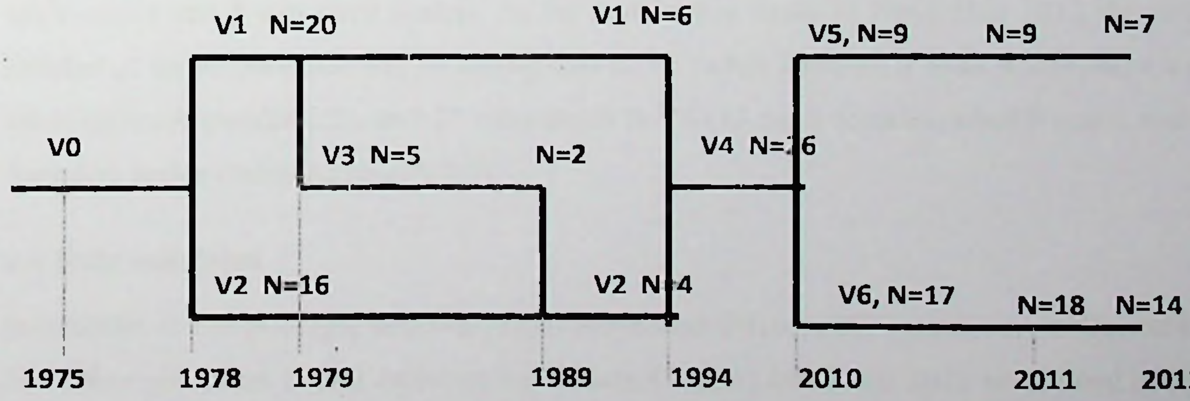


Figure 2.4 Population history of original and subsequent study troops (N= number of adult females)

2.3.2 Age-sex classes

Subjects for data collection in this study were mainly Adult males, Females and Subadult males. Females were defined as adults after first menstruation cycle: males were defined as adults after transfer to another troop and/or start consorting, whereas they were defined as subadult when reaches five (5) years of age (Table 2.3).

Table 2.3 Description of age and sex classes of subjects for data collection

AGE-SEX CLASS	DEFINITION	Appendix 2.5 AGE/SEX codes
Adult Female	Females were defined as adults after first menstruation cycle	1 to 3
Adult Male	males were defined as adults after transfer to another troop or and start consorting	6 to 10
Subadult males Male	defined as sub adult when reaches five (5) years of age	4 & 5

2.3.3 Troop sizes and composition

At the start of main data collection period for this study in 2010 there was a total of 79 individuals in the Viramba troops (Appendix 2.1); 37 individuals in V5 (including 9 adult females, 4 adult males and 6 sub adult males) and 42 in V6 (including 17 adult females, 7 adult males and 5 sub adult males). At the end of this study in November 2012 the total number of individuals was 61; 24 individuals in V5 (adult females, 3 adult males and 4 sub adult males-Appendix 2.2); and 37 individuals in V6 (13 adult females, adult 6 males and 4 Subadult males males-Appendix 2.3).

2.4 Data collection

In addition to the principle observer, from September 2010 to 2011 data were collected by two other observers (Hana Juricova and Hilary Conlan) and from 2011 to the end of the study in November 2012 data were also collected by Nicola Rodgers and Blaise Martay. In this study we checked for inter observer reliability by qualitative assessment whereby during pilot study principle investigator and Guy Norton (director of the long-term baboon research) collected data on the same subject at the same time, and compared and discussed the validity of the collected information. At various times during data collection, principle observer and Guy Norton did the same with Hana, Hilary, Nicola and Blaise.

2.4.1 Sampling technique

Behavioural data were collected using focal sampling technique, this method is generally considered among the most effective for studying animal behaviour particularly for recording primate activities (Altmann, 1974).

Follows were collected daily. The day began by locating the target troop at its sleeping site. Sleeping sites were usually already identified and the research team was able to arrive at the sleeping site at (or before) 06:30. Once the troop was located, 16 minute follows of individual subjects were conducted from 07:00 (the approximate time of sunrise). Follows were conducted until 17:00 when the troop had usually reached that evenings sleeping site. A day was divided into four time periods of two and half hours each (i.e. early morning; mid-morning to early afternoon; mid-afternoon and late afternoon to early evening; Table 2.7). A maximum of 9, sixteen minute subject follows could be conducted in a single period of the day. Subject follows were 16 minutes duration, divided into 2 minutes intervals. The number of subjects followed in a day ranged between 20 and 24 individuals depending on troop size (Appendix 2.4). The selection of the subject to follow was constrained to insure every individual was only followed once a day and in different periods on different days of the week.

Since data were collected from two different troops, individuals in a single troop were followed for 4 continuous days in a week. After these 4 days, observations were switched to the other troop. When the target troop could not be located at a sleeping site the troop was searched for 4 hours after which time the search was abandoned. Searching for the following days target troop resumed from 15:00 (approximately 3 hours prior to sunset).

Subjects were selected using the random rotary system, whereby the name of each adult female, male and sub adult males in a troop was written in a piece of paper. The papers were then put in a container which was shaken; a single name was then randomly chosen and listed in a day period from which it will be followed. The chosen name was then excluded from other papers and the exercise was repeated for the remaining names until a complete list of individual to be followed in a certain period of a day was complete. Depending on troop size, a single period of the day would be consisted with five or six focal subjects. The rotary random selection technique used was useful as it helped researcher to avoid bias that would have been caused by oversampling of most visible individuals. See Appendix 2.4 for an example follow rota used.

2.4.2 Recording techniques

Once the intended troop was located the information described below was recorded although not all these data were used in the analyses for this thesis: an example data sheet in presented in Appendix 2.5 and a detailed field protocol sheet in Appendix 2.6.

On top of data sheet the following were recorded troop (V5 or V6), name and identification number of subject to be followed, age-sex class (Table 2.3), Julian calendar, seasonal quarter (Table 2.1), time, location (GPS), habitat type, weather condition and food patches. Position of focal subject within the troop was recorded at the beginning and end of the 16 minutes follow (Table 2.4) were recorded.

Thereafter, during 16 minutes follow feeding, foraging and other predefined behaviours of interest performed by the focal subject were recorded within two minutes interval using One-zero technique by giving a tick (√) if behaviour occurred and left blank if it did not When a behaviour involved food consumption; the species, part and package were also recorded within 2 minutes interval. Other information such as the position of focal individual in relation to ground level (vertical height) (Table 2.5) was recorded at the end of 2 minutes interval.

The use of One-zero sampling technique in this study is justified from the fact that , the technique allows the accurate recording of the occurrence or non-occurrence of multiple behaviours which vary considerably in frequency of behavioural bouts, flurries as well as in typical durations (Bernstein, 1991 cited in Crockett and Ha, 2010). It is also useful in enhancing reliability when data are collected by multiple observers as it is easier to score and analyze, and it has higher inter-observer reliability than other techniques (Crockett and Ha, 2010). With smaller interval lengths, One-zero results correlate well with instantaneous (point) samples and continuous measures of frequency and duration making it possible for direct comparison of results with other studies (Rhine and Ender, 1983 cited in Crockett and Ha, 2010; Suen and Ary, 1984). The principle limitation of one-zero is that it is inappropriate for comparing frequencies of different behaviours within subjects (as it is technically possible for all behaviours to have occurred in 100% of intervals). This limitation is offset by the ability to examine the associations of different behaviours especially between subjects in different categories (e.g. age and sex categories).

Data were collected on pre-prepared data sheets (Appendix 2.5). Other equipment taken into the field was a pen or pencil for marking, a timely beep watch, pair of binocular, GPS, clip board, plastic bags (for plant species collection) and list with names and identification number of all individuals in the two troops.

Table 2.4 Positions of focal individuals in relation to the vicinity of other troop members.

CATEGORY	DESCRIPTION	Appendix 2.5, POSITION codes
Centre	Following Altmann (1979); Troop Centre of Mass was defined as the centre of the circular, elliptical or ovoid space encompassing troop members and offset toward the greatest concentration of troop members (the Centre of Mass will be drawn away from the geometric centre toward the largest masses of troop members).	1
Periphery	Individual position with no neighbours within 5m and other troop members do not occur on all sides of that position. To leave the periphery an individual can only move in limited directions to move toward other troop members.	2
Behind	Defined when troop direction can be assigned (due to troop moving or directional orientation) as a position away from troop centre opposite to troop direction. Individual has no neighbours within 5m but is visible to other troop members.	3
In front	Defined when troop direction can be assigned (due to troop moving or directional orientation) as a position away from troop centre in same direction as troop direction. Individual has no neighbours within 5m but is visible to other troop members.	4
Away	Individual has no neighbours and is not positioning or moving in relation to other troop members. Will be only partially visible or not visible to other members.	5

Table 2.5 Height of focal individuals in relation to the distance from ground level

CATEGORY	DESCRIPTION	Appendix 2.5
Below ground /Korongo	A height below ground level, in a watercourse or natural ditch/trench (Korongo is Swahili for a ditch/trench or seasonal watercourse)	0
Up to 1m (Ground)	A vertical height up to 1m from ground level	1
Up to 2m (Intermediate)	A vertical height up to 2m from ground level	2
Beyond 2m (Canopy)	A vertical height above 2m from ground level	3

2.4.3 Identification of food species

Scientific names were used to record species consumed. Most species could be identified in the field but were usually cross checked with the list of plant species by Norton *et al.* (1987). All unidentified plant species that were observed to be fed by baboons were collected put in a plastic bag for future identification back in the office with the assistance from Mikumi herbarium, Animal Behaviour Research Unit (ABRU) plant guides and botanist from Sokoine University of Agriculture (SUA).

2.5 Data management and analyses

2.5.1 Data entry

Raw data were entered directly into already prepared template of IBM SPSS Statistics Data Version 20.0 in two main data files. The first file called "*data entry activity.sav*" was divided into two parts; the first part was for subject, habitat and weather information and contained one line of data per follow. The second part which contained eight lines of data per follow (16 minutes follow in 2 minutes interval); bore information of associate behaviour for feeding and foraging behaviour. The second file named "*data entry food.sav*" contained eight lines of data per follow on food resource and how they were consumed. Follow number on both files were used as a reference code for much information belonging to the same follow in the two files. The two data files were then merged to form one major data file which contains all the information on feeding and other activities. The major file was then used for data analysis on various research questions in their relevant result chapters.

2.5.2 Data analyses

Data analyses were carried out using IBM SPSS Statistics Data Version 20.0. The primary method of data analyses used in Chapters 4, 5 and 6 are Generalized Estimating Equations (GEE). In this study they were used to test specific predictions rather than in a multi-model approach. Word equations can be usefully used to summarize these analyses (Hawkins, 2014; Grafen and Hails 2002). Specific word equations are given in the results chapters as appropriate but the general form of these word equations is:

Response variable = Age-sex class + Subject ID

Where: Age-Sex was treated as a fixed categorical explanatory variable and Subject ID as random explanatory variable. Subject ID was included as a random variable in order to take into account that individual baboons contributed multiple data points. As the model includes both fixed and random variables it is an example of a "mixed model".

Two versions of this basic word equation were developed which summarize the two approaches used to analyse data: Follow level and interval level. The follow level version of the word equation was used with data where behaviour was either recorded during a follow or not (Word Equation A). The interval level version was used with data where the proportion of intervals within a follow that a behaviour occurred was recorded (Word Equation B). Depending on context analyses were conducted on all follows (n=3838) or feeding follows only (n=3074). Feeding Follows were follows in which feeding was observed to occur at least once during the follow. See below, as defined in the last paragraph of this section.

Word Equation A: behaviour (recorded/not recorded)=age-sex class +subject ID

Where the response variable was assumed to be a binomial distribution with trial size of 1 and binary logistic model was used as a logit link function.

Word Equation B: behaviour (proportion of interval recorded)=age-sex class +subject ID

Where the response variable was assumed to be a binomial distribution with trial size of 8 and logistic model was used as a logit link function.

GEEs are part of the Generalized Linear Model (Garson 2013 cited in Hawkins, 2014) which has become increasingly recognised by biologists over the last decade as a useful statistical tool (e.g., Thurfjell et al., 2014; Prima et al., 2017). The Generalized Linear Model was first developed in the 1970s by Nelder and Wedderburn (1972) but it is only more recently, with the developments in personal computing power and software, that its wider use has become possible.

The use of GEEs has several advantages over more traditional analyses such as Anova or Kruskal-Wallis Anova, (Grafen and Hails, 2002; Hawkins, 2014) which have been exploited in this thesis:

- Subject ID can be included as a random factor which allows the follow, rather than the individual, to be used as the unit of analysis thus increasing power without pseudo-replication.
- Non-normal parametric models, such as binary and binary logistic models, can be easily used with the choice of an appropriate link function. In this study logit was used as link function
- Investigation of parameter estimates allows assessment of where the differences lie within the overall model. While post-hoc tests can be used with Anova to achieve the same ends, this is not the case with non-parametric Kruskal Wallis, therefore this advantages in particularly useful when working with on-normal data.
- Models can be developed by adding additional variables. Although beyond the scope of this PhD, the data management and analyses done here will facilitate including variables such as, group or season, to answer questions in the future.

The justification for using these two basic approaches to the analysis is as follows. The two word equations above were used to address age-sex class variation at two different levels. Firstly, Equation A is used to consider how often feeding was observed to occur in a follow in relation to total follows (follows which include intervals in which feeding occurred and also those follows where feeding did not occur). Secondly, Equation A was applied to the feeding follows to address variation in use of variable categories (e.g. plant as food source) by given age-sex class on feeding follows (follows which include intervals in which feeding occurred). This analysis focused on addressing how feeding differed between age-sex classes when occurring in follows (proportion of variable occurrence to total follows). Because the primary focus of this study was to evaluate differences in feeding between age-sex classes. Finally, Equation B was applied to assess rate of variable category use within feeding follows rate measured as mean percent of intervals used by age-sex class. This address age-sex class variation in occurrence of behavioural variable within a single feeding follow.

A critical significance level of 0.05 was used to interpret results. "Test of Model Effects" was used to assess overall significance. When overall significance was found, "Parameter Estimates" were used to assess where these differences lie. Error bars represent the standard error of the mean, unless explained otherwise.

2.6 Sampling effort

A total of 3838 follows were conducted in 270 observational days. The distribution of follows by age-sex class, troop, year, seasonal quarter and period of the day is given in Tables 2.6 and 2.7.

Table 2.6 Number of follows by age-sex class across both study groups and years with number of subjects in brackets.

Age-Sex Class	**Number of follows**		
	Overall	**By Troop**	
		V5	**V6**
Adult Male	756 (24)	205 (10)	551 (14)
Adult Female	2307 (34)	727 (11)	1580 (23)
Sub Adult Male	775 (14)	458 (8)	317 (6)
Total	3838 (72)	1390 (29)	2448 (43)

Table 2.7 Number of follows by age-sex class by year, ecological seasons and period of the day.

Age-Sex class	Number of follows										
	By Year			By Seasonal Quarter				By Period of the Day			
	2010	2011	2012	ED	LD	EW	LW	1	2	3	4
Adult Male	20	254	482	233	206	97	220	235	129	246	146
Adult Female	69	829	1409	650	655	286	716	688	416	835	369
Sub Adult Male	11	250	514	259	231	98	187	217	155	257	146
Total	100	1333	2405	1142	1092	481	1123	1140	700	1338	661

Seasons as defined above: ED= Early dry; LD=Late dry; EW= Early wet; LW= Late wet. Periods of the day; 1=early morning (07:00 to 09:30); 2=Mid-morning to early afternoon (09:30 to 12:00); 3=Mid-afternoon (12: 00 to 14:30) and 4=late afternoon to evening (14:30 to 17:00).

Chapter 3 Diet, Space and Activity

3.1 Introduction

3.1.1 Aim

The aim of this chapter is to addresses objective one of this study (Chapter 1. section 1.3.2). It is the benchmark result chapter which describes the following overall amount of feeding, dietary profile, space use and activity budgets in the Viramba baboons. Overall amount of feeding is described in relation to seasonal quarter and habitat. Dietary profile is described in terms of by food sources (plant, animal and exotic), food types (tree, shrubs, forbs, grasses, etc.), food parts (fruits, seeds, roots, leaves etc.) and food packages (no process/process/large/small etc.). Space use considers both of height in relation to ground and horizontal position relative to the centre of the troop. For activity budget the main behavioural activities are presented and the extent with which they were performed by yellow baboons was analysed. The variables introduced in this chapter are used in subsequent chapters to assess the nature and extent of sexual segregation within the confines of the permanent groups in which baboons live.

Feeding and foraging behaviour of baboons in MINAPA has been extensively studied through the ABRU project since 1975 (Rhine and Westlund 1978, Rhine et al. 1986, Norton et al., 1987, Rhine et al., 1989, Chapter 2, section 2.3.1). This long-term research has established a detailed knowledge of diet composition in terms of plant species used, food sources, and the complex diverse nature of the diet in terms of the multiple food types (e.g. trees, forbs, grasses), food parts (e.g. fruit, flowers, leaves) and the food package array available to baboons (Norton et al. 1987; Diego, 2003). The overall result of these studies and on-going work is to show that there are multiple foraging options and choices available to baboons and that the actual food and forage options used can vary across time and also between troops and individuals. From these insights, new problems and questions arise and some of these are addressed in this study.

3.2 Methods

This section provides information specific to this Chapter and supplements the information on the study area, data collection and analyses provided in Chapter 2.

The follow was used as the basic unit of analysis. Data were considered at one or both of the following levels as defined in section 2.5.2:

- Follow level data: Behaviour recorded (occurred) or not recorded (did not occur) during the follow. Data are presented as number and as percentage of total follows. Thus, feeding follows were defined as follows in which feed ("intake" or "intake chews", Appendix 2.6) was recorded at least once in a follow (i.e. in at least one of the eight intervals in a follow).
- Interval level data: Proportion of intervals a behaviour was recorded during a follow. These data are presented as mean proportions with standard errors. For example as the mean proportion (or number) of intervals in which feeding occurred for all follows.

Definitions of categories used for Food Sources, Food Types, Food Parts and Food Packages are based on the variables collected on the "Food List" section of the data sheet (Chapter 2, Appendices 2.5 and 2.6). Definitions of categories for Heights and Positions are given in Tables 2.5 and 2.4. Categories for Activity Budgets are given in Box 3.1, and additionally in Appendix 2.6.

Box 3.1 Definition of activity behaviours used in data collection

ACTIVITY	DEFINITION	Appendix 2.5
Rest	A state of being inactive can be sleeping or just sitting doing nothing	REST/INACTIVE
Move	A state of walking from one point to another in more than 5m, unless the subject is in a single tree. It is different from shift, which is walking in less than 5m unless in a single tree.	MOVE
Feed	It involves process of putting food into mouth and chewing it, it also includes foraging activities (i.e. search for food, harvest and processing it).	INTAKE and INTAKE CHEW
Social	It involves activities such as grooming (either being groomed or grooming others) and affiliation.	AFF + SEXUAL + GROOM + GROOM -
Vigilance	Looking around the environment it includes looking away from the troop (visual away) and/or sentry.	VISUAL AWAY VISUAL TROOP SENTRY
Other	It includes all other activities not specified above such as urinating, defecating, alarm barking, running, calling, drinking etc.	DRINK OTHER

3.3 Results

3.3.1 Overview of the Amount of Feeding

A total of 3838 individual follows were conducted and analysed, of these, the baboon subjects were recorded feeding in one or more intervals (i.e. feeding follow) in 3074 follows, equivalent to 80.1% of all follows (i.e. 3838 follows). The mean percent of intervals in which feeding occurred was 53.8% for all follows (n=3838); and 67.7% of feeding follows (n=3074).

3.3.1.1 Feeding in seasonal quarters

Table 3.1 shows that the percent of follows with feeding ranged from 74.2% of all follows in the late wet season to 83.9% in the late dry season. Table 3.1 also shows that the number of follows within seasons was similar for 3 of the 4 seasons with the early wet season being under sampled (12.5% of total follows) compared to the other 3 seasons (% total follows seasonal mean for early dry, late dry and early wet = 29.2%, range 1.5%). But, percent of follows with feeding within seasons does not vary in relation to the total follows within season.

Table 3.1 Variation in feeding across seasonal quarters. For example for Early dry: Percent feeding follows of all follows in seasonal quarters (387 as a percent of 481 = 80.4%); Percent feeding follows of all feeding follows (387 as a percent of 3074 = 12.6%); Percent feeding follows of all follows (387 as a percent of 3838 = 10.1%).

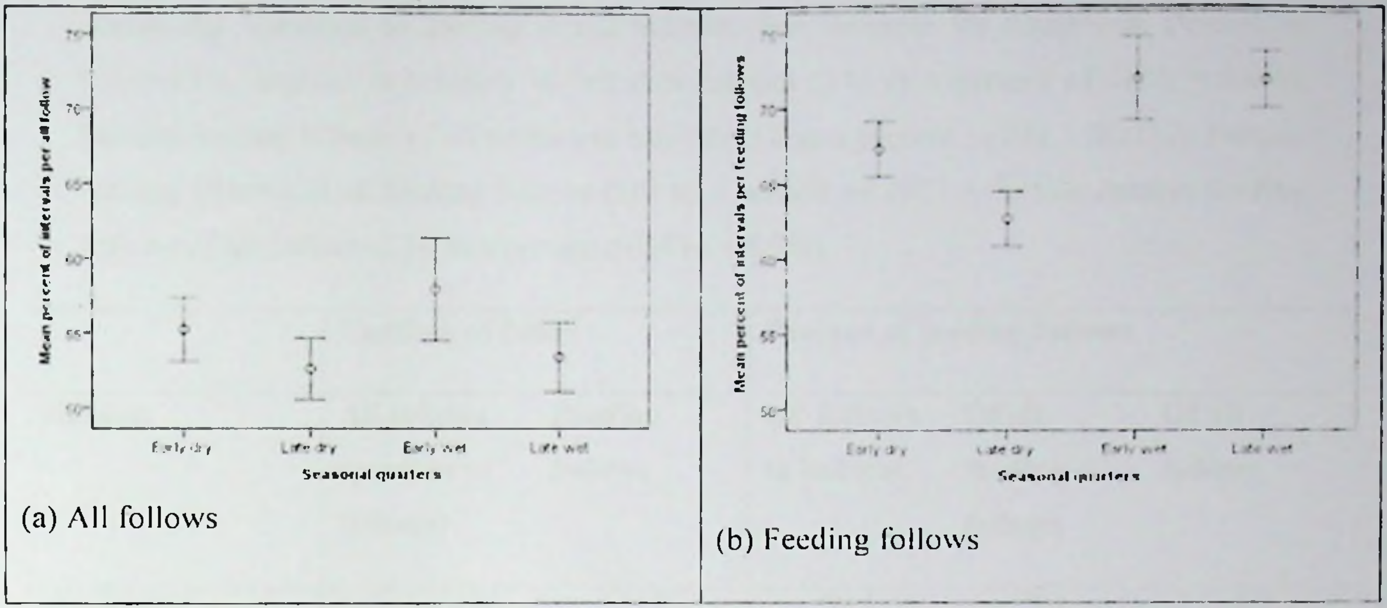
	Number of follows		**Percent feeding follows**		
Seasonal quarters	**All follows**	**feeding follows only**	**Of all follows in seasonal quarter**	**Of all feeding follows**	**Of all follows**
Early wet	481	387	80.4	12.6	10.1
Late wet	1123	834	74.2	27.1	21.7
Early dry	1142	937	82.0	30.5	24.4
Late dry	1092	916	83.9	29.8	23.9
Total	**3838**	**3074**		**100.0**	**80.1**

Feeding across seasonal quarters was also assessed as percent of intervals with feeding per follow within seasonal quarter (seasonal follows). Figure 3.1a shows the mean percent of intervals with feeding for all follows in seasonal quarters (number of focal animal follows in that seasonal quarter) and Figure 3.1b shows the mean percent of intervals with feeding for feeding follows in seasonal quarter (number of follow focal animal was recorded feeding at least once in a follow). Mean percent of intervals with feeding within seasonal follows ranged from 52.6% in the late dry season to 57.9% in the early wet season (Figure 3.1a). The overall mean was 54.8% of intervals with feeding.

The percent of intervals with feeding in only those follows in which feeding occurred (feeding follows) (Figure 3.1b) showed a seasonal range from 62.7% in late dry to 72.9% in late wet and early wet. The overall mean was 68.5% feeding intervals in feeding follows. The number of intervals with feeding is greater for seasonal feeding follows than it is for total seasonal follows as would be expected. The proportion of feeding to total follows within a season varied. The proportion of feeding to total follows within the late wet season was lower than other seasons (Table 3.1).

Moreover, patterns of feeding by proportion (mean percent) of intervals with feeding also varied across seasonal quarters. With all follows, feeding was proportionally higher in early wet seasons with the mean 57.6% of intervals with feeding, followed by early dry season (Figure 3.1a). However, proportion feeding intervals within feeding follows only (Figure 3.1b) showed that, baboons had the highest mean percent of intervals with feeding in wet seasons (early and late wet) than dry seasons (early and wet dry). Thus in wet seasons subjects fed at a higher rate when they were feeding than in dry seasons.

In the early wet season the proportion of feeding follows to total follows was similar to those of the dry seasons (despite a much smaller sample size) but feeding rate within follows was higher and similar to that of the late wet season rates. In the late wet season, baboons fed in a much lower proportion of total follows but at a much higher rate when feeding.



(a) All follows

(b) Feeding follows

Figure 3.1 Mean percent of intervals per follow in which feeding was recorded by seasonal quarters (a) all follows: Early dry [N=1142], Late dry. [N=1092], Early wet [N=481] and Late wet [N=1123] (b) Feeding follows only by season: Early dry [N=937], Late dry [N=917], Early wet [N=387] and Late wet [N=834].

3.3.1.2 Feeding in different habitat types

During this study, when baboons were observed and recorded as feeding, they did so almost exclusively in natural habitats. Table 3.2 shows that 70% of all follows occurred in Wooded Grassland (52%) and Open Woodland (18%). The highway was the least used habitat (3.8% of all follows) while grassland (6.4%) and woodland (6.2%) were also infrequently visited. Feeding in natural habitat was recorded in 95.7% of feeding follows and in 76.6% of all follows. Proportionally, feeding follows varied between 81.3% (open woodland) and 90.1% (grassland) of all follows in all habitats except riverine (59.6%). Although there were proportionally fewer feeding follows to total follows in grassland, the feeding rate within feeding follows was much greater in this habitat (Table 3.2). Feeding across habitats in relation to extent of habitats is addressed in the discussion (section 3.4).

Table 3.2 Variation in feeding across habitats. For example for Grassland: Percent of follows i.e., number in brackets in first data column (242 as a percent of 3836 = 6.4%); Percent feeding follows of all follows in habitat (218 as a percent of 242 = 90.1%); Percent feeding follows of all feeding follows (218 as a percent of 3072 = 7.1%); Percent feeding follows of all follows (218 as a percent of 3836 = 5.7%).

	Number of follows		Percent of feeding follows		
Habitat	**All follows (percent of follows)**	**Feeding follows**	**Of follows in habitat**	**Of all feeding follows**	**Of all follows**
Grassland	242 (6.4%)	218	90.1	7.1	5.7
Wooded grassland	1997 (52%)	1648	82.5	53.6	42.9
Open woodland	695 (18%)	565	81.3	18.4	14.7
Woodland	236 (6.2%)	201	85.2	6.5	5.2
Riverine	520 (13.6%)	310	59.6	10.1	8.1
Highway	146 (3.8)	130	89.0	4.2	3.4
Total	3836 (100%)	3072		99.9	80.0

3.3.2 Dietary profile (food source, type and parts)

Section 3.3.1 describes the observed patterns of feeding frequencies (measured as percentage of feeding follows), and feeding rate (measured as mean percentage feeding intervals in follows). This section describes the observed diet and classifies it as a food profile of: food source (plant, animal or exotic foods); food type (tree, forb, grass, shrub, vertebrate, and invertebrate); food part (fruit, leaf, seed, root, and exudates/sap); and Food package (defined by the size of food part, and number of processes involved before consumption; see appendix 2.6 and Chapter 2).

During this study baboons fed on 93 different plant species, of which 68 were native, 13 were anthropogenic/exotic foods originated from highway (ARO) and one was an introduced exotic (*Senna siamea*) (appendix 3.1). Plant species consumed included 34 tree species, at least 34 species of forbs, 11 species of shrubs and multiple species of grass. 13 forb species were only identified to genus level (appendix 3.1). Grasses were an important component of the overall diet, only 14 species could be identified (appendix 3.1). Animals and animal products (e.g. eggs, nests dung) were also an important component of the diet. Animals consumed were predominantly invertebrates and could not usually be identified to species but common (English) names were used where possible (e.g. spider, grasshopper, ant, beetle) (appendix 3.1). Anthropogenic (exotic) foods from the highway could usually only be identified by type (e.g. cooked porridge) or not identified (appendix 3.1).

Of the 93 plant species in the diet, three tree species; *Tamarindus indica*, *Acacia sieberiana* and *Kigelia africana*, and grass species (*Rottboellia cochinchinensis* and unknown grasses), were consumed in 52% of all feeding follows (appendix 3.2).

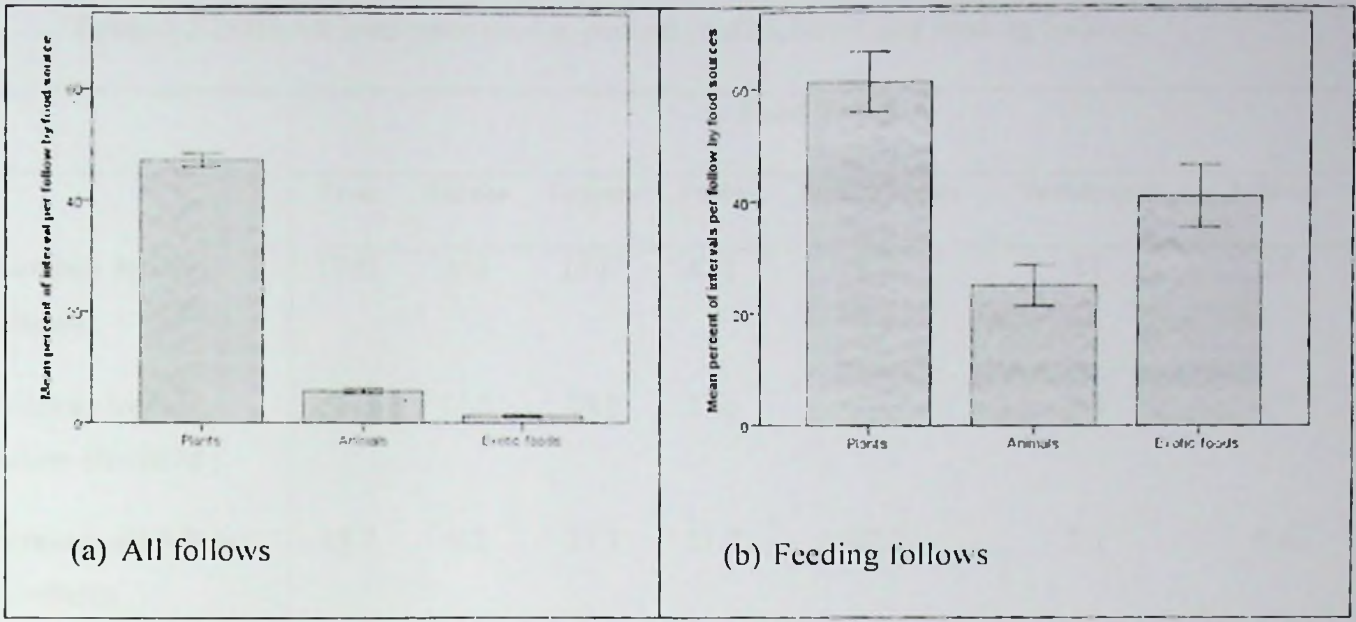
3.3.2.1 Food sources

The diet of yellow baboons was obtained from native plants (including mushroom and fungus), vertebrate and invertebrate animals, and anthropogenic (exotic) foods. Anthropogenic food was spilled cultivated plants and organic litter from vehicles.

Baboons fed on plants in 95.5% (2935) of 3074 feeding follows and 76.5% of all 3838 follows. Feeding on animals and animal products was observed in 29.7% of feeding follows and 23.8% of all follows. Exotic, anthropogenic, food was used in 4.0% of feeding follows and 3.2% of all follows.

Within follows, baboons often fed from more than one food source. They were recorded as feed on both plants and animals in 29.4 % (810 follows) of feeding follows. Plant feeding overlapped with feeding on exotic foods in 2.5% (76 follows) of feeding follows. Feeding from all three sources occurred in 0.68% (21 follows) feeding follows.

The mean percent of intervals feeding on a given food source was calculated using the number of feeding follows in which a given source was used. Figure 3.2 shows the mean percent of intervals for each source for all (total) follows (3.1a) and for the number of feeding follows in which a given source was used (3.1b). Figure 3.2a shows that plants were used with a mean of 47.3 % intervals per follow; animal were used in 5.7% of intervals and exotic foods were used in a mean of 1.3 % of intervals for all (Total) follows. Figures 3.2b shows that baboons were recorded feeding at proportionally higher rate on plants (mean of 61.4% intervals per feeding follow). The rate of feeding from exotic foods on the highway was higher than feeding rates on animals (Figure 3.2b), but overall baboons were recorded feeding on exotic foods in many fewer follows (Figure 3.2a).



(a) All follows

(b) Feeding follows

Figure 3.2 Mean percent of feeding intervals per follow for the three food sources (a) all follows; N= 3838 (b) Feeding follows per food source: Plants [2935]; Animals [913] and exotic Foods [122].

3.3.2.2 Food types use

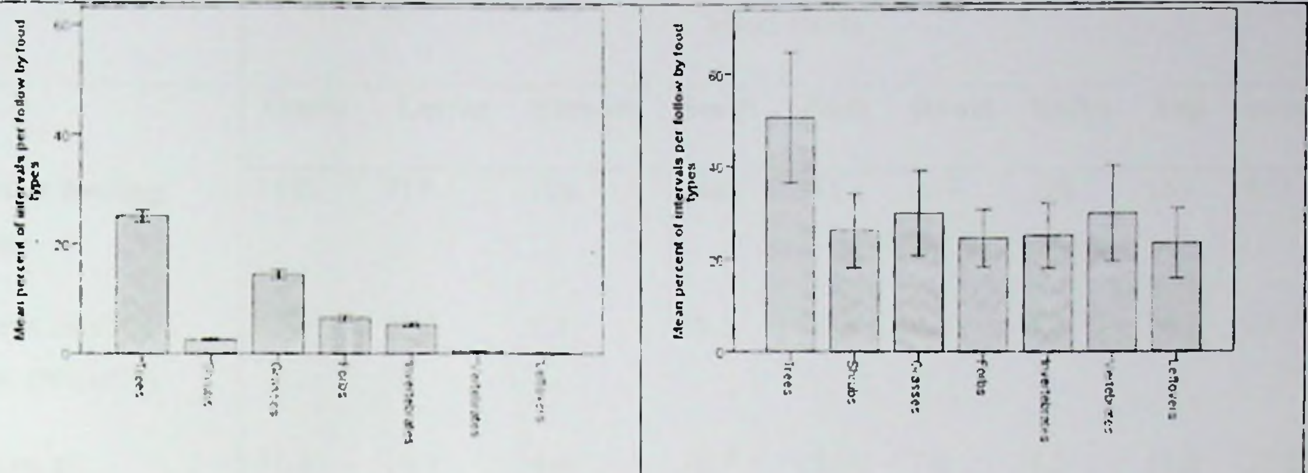
Food sources occur in a variety of types that are defined as food types in this study (section 3.2.2 and 3.3.2). Plant food sources are classified into 4 food types: trees, shrubs, grasses and forbs (forbs include lianas, vines and herbs). Food types from plant sources also included domestic cultivated plants of various types such as potatoes, oranges, rice, bananas and tomatoes from the highway. Animal food sources are classified into vertebrates and invertebrates and include products derived from animals such as eggs, egg cases and nests. Domestic foods leftover from the highway is classified as exotic food types.

Food type used was measured as percent of all follows and percent of feeding follows (Table 3.3). Food from trees was the most used food type comprising 58.3% of feeding follows. Grass as a type was used in 49% of feeding follows while: invertebrates and forbs showed a similar pattern of use at 27.7% and 27.0%, respectively, of feeding follows. Feeding on vertebrates (2.6% of feeding follows) and especially exotic food (0.7% of feeding follows was infrequent used) (Table 3.3).

Table 3.3 Different food types used as percent of all follows and feeding follows.

	Food Types						
	Trees	Shrubs	Grasses	Forbs	Invertebrates	Vertebrates	leftover
Number feeding follows	1793	353	1507	831	853	81	23
Percent feeding follow (N=3074)	58.3	11.5	49.0	27.0	27.7	2.6	0.7
Percent all follow (N=3838)	46.7	9.2	39.3	21.7	22.2	2.1	0.6

Figure 3.3 shows the mean interval rate of food type use for all follows (Figure 3.3a) and for food type specific feeding follows (Figure 3.3b). Figure 3.3b shows that trees, the most used type (Table 3.3) also had the highest mean interval rate use for type specific feeding follows. Similarly, grass and vertebrates have similar and relatively high mean interval rate but compared to proportion of feeding follows the rate is lower relative to that of trees. Exotic foods and vertebrates are rarely used and shrubs are somewhat used at lower rate overall, but when they were used, the mean interval rate use by the number of feeding follow for each; they were used at similar proportion with forbs and invertebrates (Figure 3.3b).



(a) All follows

(b) Feeding follows

Figure 3.3 Mean percent of feeding intervals per follow for food types (a) all follows (b) feeding follows per food type: trees [N=1793]; shrubs [N=353]; grasses [N=1507]; forbs [N=824]; invertebrates,=[N=851]; vertebrates [N=81] and exotic [N=23].

3.3.2.3 Food parts use

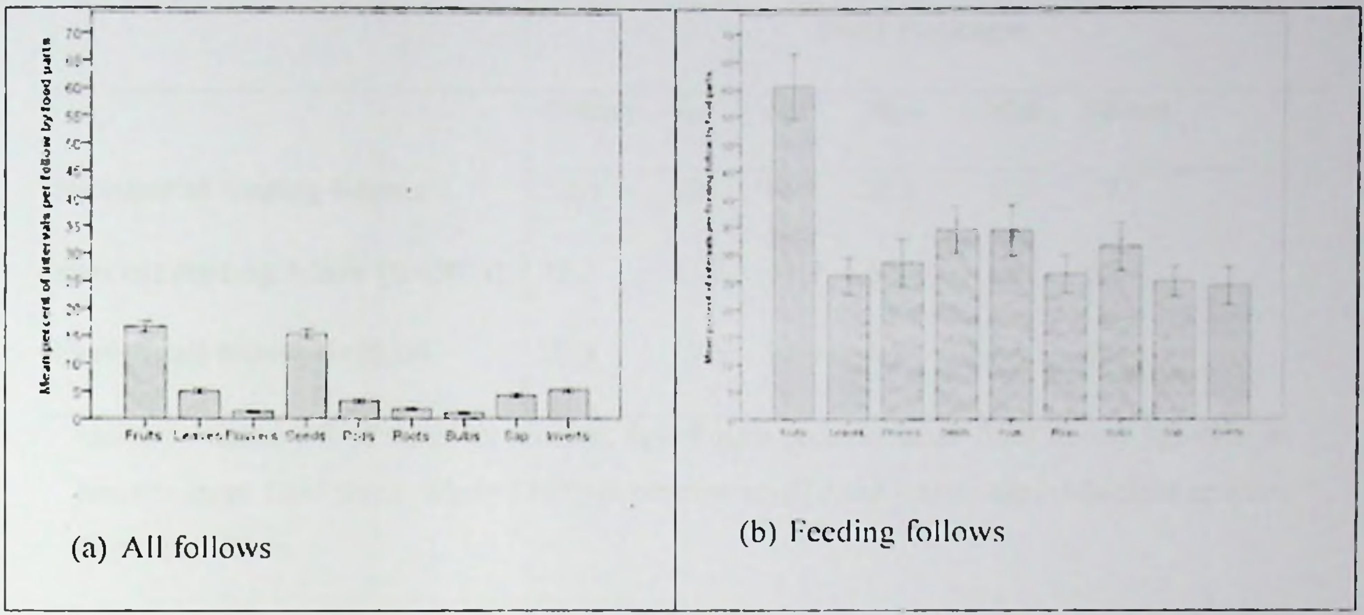
For herbivores, diet is frequently categorized by the plant parts eaten (Rothman et al., 2014) (e.g. Frugivorous, Folivorous). Plants are the primary source of food for baboons as observed in section 3.3.2. During this study 11 different plant parts were consumed (appendix 3.4). This section describes the overall use of the 8 most extensively used plant parts (fruits, leaves, roots, flowers, seeds, pods, bulbs and exudates/sap). Invertebrates were as frequently used as several plant food types (section 3.3.2.2) and are included with plant food parts for comparison. Table 3.4 shows that seeds and fruits are the food parts most often used on feeding follows while invertebrates, leaves and sap are used in about 20-30% of feeding follows.

Table 3.4 Food Part use as percent of all follows and feeding follows

	Food Parts								
	Fruits	**Leaves**	**Flowers**	**Seeds**	**Pods**	**Roots**	**Bulbs**	**Sap**	**Invert**
Number feeding follows	1193	717	178	1485	385	267	128	569	853
Percent feeding follow (N=3074)	38.8	23.3	5.8	48.3	12.5	8.7	4.2	18.5	27.7
Percent all follow(N=3838)	31.1	18.7	4.6	38.7	10.0	7.0	3.3	14.8	22.2

Note: Invert=Invertebrate

Figure 3.4 shows the mean intervals per follow different food parts were used over all follows (Figure 3.4a) and food part specific feeding follows (Figure 3.4b). For all follows (Figure 3.4a), fruits were used in a mean of 16.7% intervals per follow, seeds were used in a mean 15.4% of intervals. Other food parts were used in less than a mean 10% of intervals within follow for all follows. Figure 3.4b shows the mean intervals used per follow for food part specific feeding follows. This shows that when feeding on fruits the mean interval rate was high at 60% while for all other food parts the mean interval rate was lower and similar varying between 25-35%. Fruits were used on a high proportion of follows and used at a higher rate in those follows compared to other plant food parts and invertebrates (Figure 3.4b).



(a) All follows

(b) Feeding follows

Figure 3.4 Mean percent of feeding intervals per follow for food parts (a) all follows (b) feeding follows per food part: fruits [N=1193]; leaves [717]; flowers [178]; seeds [1485]; pods [385]; roots [267]; bulb [128]; sap [569] invertebrates [853].

3.3.2.4 Food packages consumed

Baboon foods can also be categorized into packages which are of different sizes can contain variable item or bites of food and require varying processing requirements. Food packages were defined by sizes and number of processes needed before consumption. Overall fifteen different categories of food packages were defined (appendix 2.6). In this section the use of six main food package categories unitary packages (include unitary small, large, mixed and clumped), single process small (Sps), single process large (Spl), multiple process small (Mps), multiple process large (Mpl) and mixed processes (appendix 2.6) are described.

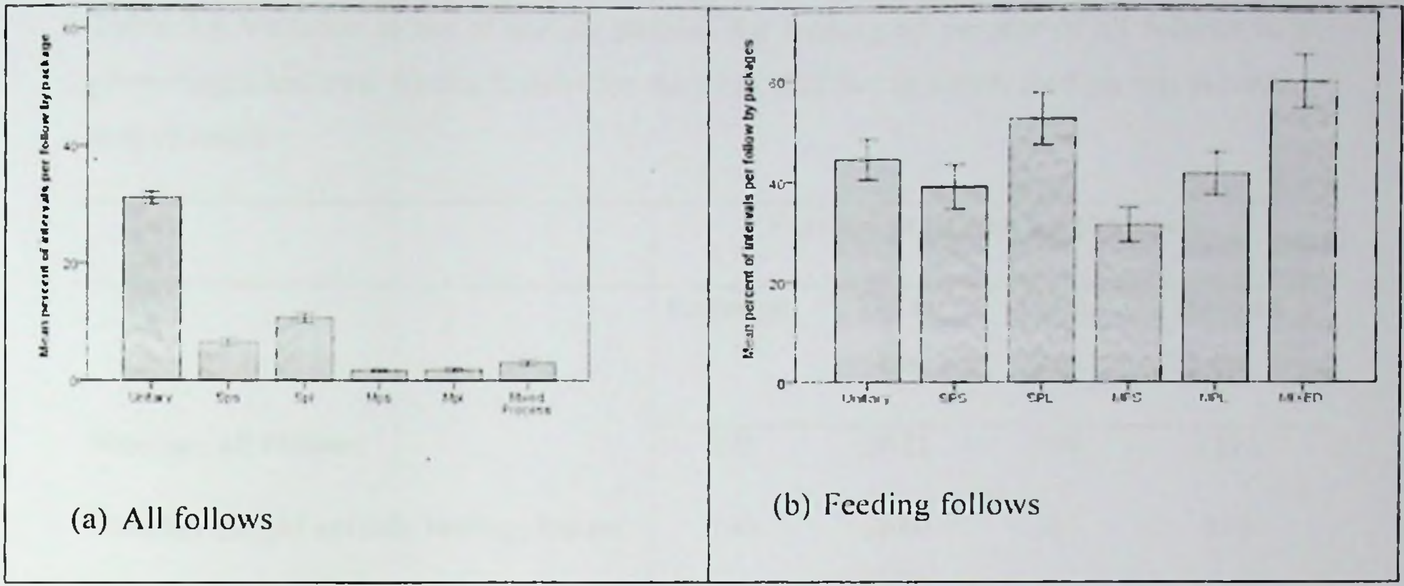
Table 3.5 shows the number of follows and percent of feeding follows and total follows in which these 6 food packages were used. Unitary packages were consumed in 76.1% of feeding follows and 60.9% of all follows. Food packages that require multiple processes and mixed processes before consumption were used in less than 10% of all follows and feeding follows (Table 3.5).

Table 3.5 Use of food packages as percent of all follows and feeding follows

	Food Packages					
	Unitary	**Sps**	**Spl**	**Mps**	**Mpl**	**Mixed**
Number of feeding follows	2338	681	957	201	170	192
Percent feeding follow (N=3074)	76.1	22.2	31.1	6.5	5.5	6.2
Percent all follow(N=3838)	60.9	17.7	24.9	5.2	4.4	5.0

Unitary= Unitary food items no process; Sps=Single process small food items; Spl=Single process large food items; Mps= Multiple process small food items; Mpl=Multiple process large food items.

For mean percent of intervals per follow of all follow unitary food packages (appendix 2.6) were used in a mean of 31.1% of intervals (Figure 3.5a). Larger packages requiring single process actions were used in a mean of 10.7% of intervals within follow (Figure 3.5a). Use of both small and large food packages that require multiple and mixed processes was rarely occurred, and had a mean of less than 10% of intervals per follow (Figure 3.5a). However, mean interval rate when a given package category was used on a feeding follow was similar across all package categories with the least used package category (Mixed Processes) having the highest rate (Figure 3.5b).



(a) All follows

(b) Feeding follows

Figure 3.5 Mean percent of feeding intervals per follow for food packages (a) all follows (b) feeding follows per food package: Unitary [N=2338]; Single process small items (Sps) [N=681]; Single process large item (N=Spl) [957]; Multiple process small item (Mps) [N=201]; Multiple process large item (Mpl) [N=170] and Mixed processes (mixed) [N=192].

3.3.3 Spacing behaviour/ spatial position

Age-sex differences can occur through differences in diet, and habitat use as profiled in preceding sections. This section describes proximate space use in both the vertical and horizontal plane. Details of the definitions and categories of space use behaviour rare provided in section 3.2.3.

3.3.3.1 Height category use

Feeding at different height levels was measured by percent of follows in which feeding was recorded at a given height. Table 3.6 shows that different height categories were used in different proportions of feeding follows and different proportions within follows. The ground level height category (0-1m above ground) was used most extensively. Baboons were recorded at ground level in 3022 (78.7%) of total follows. Tree canopy (above 2m) was used in 32% of total follows. The intermediate height (1-2m) was used in fewer overall follows (11.4%) and watercourses (Korongos) below ground height were used infrequently in 5% of overall follows.

Feeding within a given height category varied less across categories (Table 3.6). In all height categories, except for Canopy height (above 2m), baboons fed at that height in between 83.3% and 88.7% of height category feeding follows (Table 3.6). When using the canopy height category, feeding occurred in 66.9% of follows.

Table 3.6 Variation in use of vertical position for feeding by percent of all follows in a given height and total feeding follows for the study (follows in which feeding was recorded at least once)

	Vertical positions/height levels			
	Korongo	**Up to 1m**	**Up to 2m**	**Beyond 2m**
Number all follows	175	3022	436	1211
Number height specific feeding follow	146	2680	363	810
Percent height specific feeding follow	83.4	88.7	83.3	66.9
Percent total feeding follow (N=3074)	4.7	87.2	11.8	26.4

When feeding on a tree, baboons were not restricted to feeding at single height category within a follow, instead within a single feeding follow baboons often fed at different height categories. The extent of overlap (use of multiple heights within the same follow) is shown in Table 3.7.

Table 3.7 Percentage feeding at different vertical heights within single feeding follows.

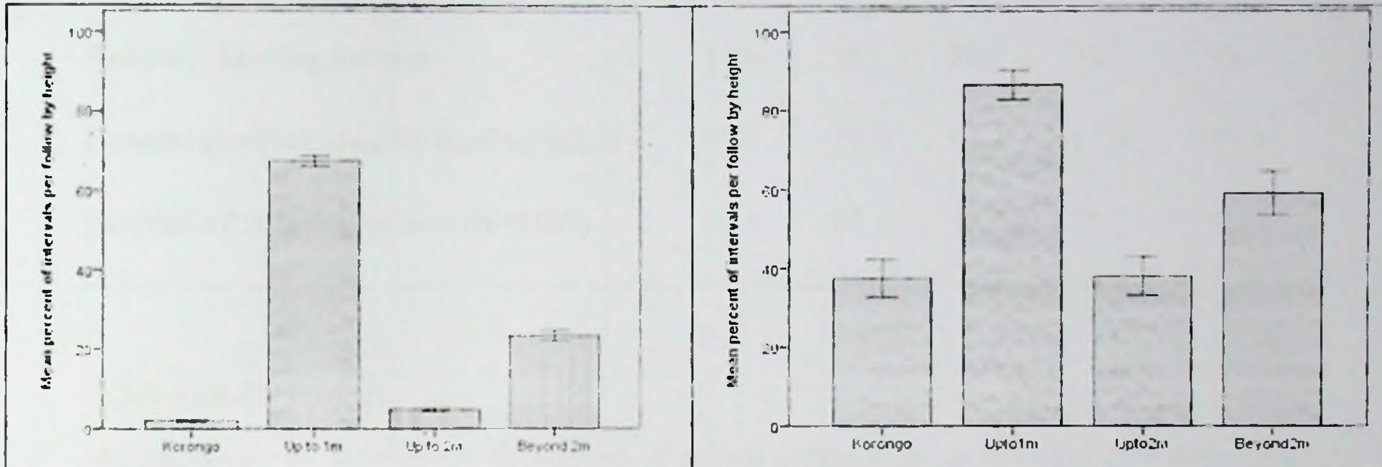
	Overlapped heights in single follow			
	< 1 and 2m	< 1 and >2	2m and >2	0m and <1m
Number of overlapped follows	324	460	97	139
Percent overlap by number of feeding follows in first height level	12.1	17.2	26.7	88.4

< 1= up to 1m (ground level); > 2=beyond 2m (canopy); 0= Korongo; 2= up to 2m

Figure 3.6 shows the mean number of intervals per follow in which height categories were used in all follows (Figure 3.6a) and height category feeding follows (Figure 3.6b). On average the ground category was used in 67.5% overall (Figure 3.6a). The canopy height category was used in a mean of 23.3% of intervals per follow. The intermediate height and

korongo categories were used at a mean interval rate of less than 5.0% (Figure 3.6a).

Within category specific feeding follows the mean interval rate of category use for ground was about 90% closely followed by use of canopy with about 60% mean interval rates. Korongo and intermediate height categories were very similar at about 40% mean intervals per category feeding follows (Figure 3.6b).



(a) All follows

(b) Feeding follows

Figure 3.6 Mean percent of feeding intervals per follow for vertical height categories: (a) all follows: Korongo [N=175]; Up to 1m [N=3022]; Up to 2m [N=436] and Beyond 2m [N=1211] (b) feeding follows per height category: Korongo [N=146]; Up to 1m [N=2680]; Up to 2m [N=363] and Beyond 2m [N=810].

3.3.3.2 Horizontal position relative to troop members

Horizontal positions were defined by the position of subject in relation to the centre of mass of the troop. Centre of Mass is defined as the centre of the weighted position of all individuals within the maximum troop width (Table 2.4). Positions were recorded at the beginning and end of follows. Positions were recorded in 2599 follows, of which 2107 follows (81%) were feeding follows.

In52.3% of 2107 feeding follows baboons were recorded feeding at the troop centre (Table 3.8). Very rarely (4.4% of total feeding follows) baboons were observed feeding away from the troop (Table 3.8). However, when baboons were in the front, back or away from troop, they were feeding in about 90% of the follows in these positions. When at the centre or at the edge of troop, feeding occurred in about 77% of follows (Table 3.8)

Table 3.8 Use of horizontal positions for feeding as proportion of all feeding follows and position specific feeding follows

	Horizontal Positions				
	Centre	Edge	Front	Behind	Away
Number all follows	1430	492	305	268	104
Number feeding follows	1101	383	284	246	93
Percent position specific feeding follows	77.0	77.8	93.1	91.8	89.4
Percent all feeding follows (N=2107)	52.3	18.2	13.5	11.7	4.4

3.3.4 Activity budget

As suggested by theories on occurrence of sexual segregation in sexually size dimorphic mammals, baboons may as well sexually segregate through variations in activity budgets (Ruckstuhl, 1998). Despite staying in permanent cohesive mixed-sex troops sexually size dimorphic yellow baboons could segregate through synchronization of their activities by size and/or sex (Ruckstuhl, 1998; Conradt and Roper. 2000). This section. describes patterns of diurnal activity focuses on the principle components of an activity budget; feeding, socializing, vigilance, resting and moving (Section 3.2.4; appendix 2.6).

Baboons like some other social animals can perform a number of activities concurrently but the pattern and proportion of concurrent behaviours will vary (Conway, 2009). For all follows; vigilance occurred in 81.5%, feeding in 80.2%. resting in 76.9%. moving in 72.1% and social behaviour in 29% of all follows (Figure 3.7).

Figure 3.7 shows the mean percent of interval per follow in which various activities occurred. This shows that feeding and moving were the highly performed activities, occurred at a mean of 70% intervals per follow while socializing and vigilance were least performed activities with mean occurrence of 45%-55% intervals per follow.

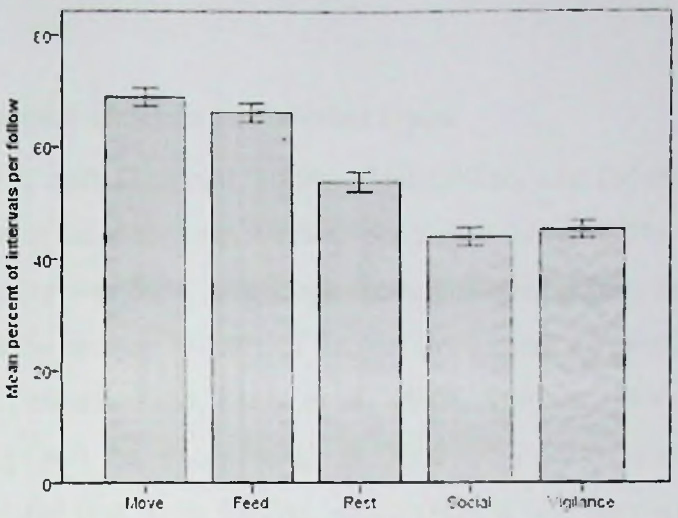


Figure 3.7 Mean percent of intervals per follows for six selected activities: Feeding [N=3074]; Moving [N=3616]; Resting [N=2970]; Socializing [N=1158]; Vigilance [N=3141] and other activities [N=768].

3.4 Discussion

3.4.1 Feeding in seasonal quarters and habitat types

Feeding occurred in at least 1 interval in 80% of all follows and for these feeding follows, the mean percentage of intervals with feeding per follow was 67.7%. For all follows the interval rate for feeding was 54%. Although methodologies differ, these proportions are consistent with the estimates of 70-80% of diurnal time spent on feeding and foraging by baboons (Post, 1981; Barton, 1989, Rhine et al., 1989; Altman, 1998). This study shows that overall feeding will be encountered in 80% of evenly distributed 16 minute observations periods and that when feeding is occurring it will be encountered in 70% of the observation period.

Baboons need to "exploit a wide array of plant foods to satisfy energetic and nutritional needs when faced with a shifting mosaic of possibilities" (Norton et al., 1987). In Mikumi, feeding and foraging rates and patterns reflect the seasonal and patchy conditions of resource and habitat. The Mikumi ecosystem is dominated by Miombo (*Brachystegia*) woodland. In the Viramba range, Miombo intermingles with patches of lowland and montane forests, thickets, riverine and grasslands and this is the seasonal feeding and foraging mosaic used by yellow baboons in Mikumi (Norton et al., 1987; Rhine et al., 1989). Within all seasons and habitat feeding was the most frequently occurring behaviour as would be expected for baboons and many other primates (Altmann, 1998). However, the feeding follow frequency and the interval rates of feeding within follows differed by season and habitat reflecting the changing ecological and resource conditions.

The higher records of feeding observed in this study are much associated with ecological influence on the diet and foraging behaviour of yellow baboons at Mikumi National Park reflecting Savannah vegetation. Savannah vegetation, unlike Tropical forest vegetation has more dramatic seasonality hence less consistence resource base, which potentially may affect baboons' dietary composition and feeding time (Newton-Fisher et al., 2006).

One key feature of this study is that sampling occurred across 2 ecological years and all seasonal quarters. Adaptation to seasonality with discrete prolonged dry seasons is an important trait of baboons (Barton, 1989). In the context of constraints of group living, all group members face the same seasonal variations in resource options. These options vary seasonally not just in abundance and availability (Clutton-Brock 1977), but also in degree and pattern of patches and the diversity of packages (strongly related to seasonal plant phenology (section 3.3.2.4). By sampling in all seasonal conditions across multiple ecological years the effect of constraints imposed on all age-sex classes can be accounted for.

The finding that, feeding follows were proportionally lower in the wet seasonal quarters (77% of total follows) than in the dry seasonal quarters (83% of total follows) fits with the work of Barton (1989). The study by Barton (1989) showed that, baboon feeds more during periods of low rainfall (dry seasons) than periods of higher rainfall (wet seasons). In this study, the higher proportion of feeding follows in dry seasonal quarters is associated with seasonal change in resources availability. In Mikumi periods dry seasons are accompanied by little rainfall especially in November (Table 2.1, chapter 2): in this period, corms, sedge bulbs and grasses (e.g. *Panicum spp*) are more abundant and/or accessible. All these foods are high-energy, high-protein and low-fiber (Pochron, 2000), but contain relatively lower biomass in dry season than during wet season (Barton, 1989). However, Barton (1989) points out that this pattern does not necessarily show less feeding in terms of nutrition or biomass ingested.

Nevertheless, the mean interval rate of feeding within follows was higher in the wet seasons than in the dry seasons (Figure 3.1b). This implies that, baboons fed in fewer follows in these seasonal quarters, but fed more within follows (i.e. spent more time feeding within a single follow). This is contrary to Post (1981) and Davidge (1978) who reported that, baboon spent more time feeding in dry seasons than in wet seasons. In this study, forage biomass and abundance is associated with higher mean interval rate of feeding within follow observed in wet season quarters. During this period, fruits which are more nutritious (Milton, 1993), easily harvested and processed packages are more abundant and used within wet seasons (particularly the late wet season). Vegetation monitoring in Mikumi shows seasonal plant phenology consistent with these patterns (ABRU unpubl). Thus, a large biomass may be positively associated with the time spent processing (handling time) and may have no direct relationship with caloric intake (Swedell et al., 2008). Clearly, changes in the spatial heterogeneity of resources (e.g., patches, packages, phenology and cover) can also result in variation in feeding patterns.

Another almost unique aspect of this study is the habitats and ecosystem of the MINAPA baboon population. Most research on baboon notably long-term research and especially feeding studies have been/or are of insular populations using marginal, atypical or disturbed habitats (Barton, 1989; Altmann, 1998). This is an artefact of anthropogenic reduction in typical habitats resulting in baboon populations largely remaining in those habitats that are less open to human use (e.g. swamps, rocky soil and steep slope topographies) or compatible with limited human use (rangeland, pastoral areas) (Samuel and Altmann, 1991; Hoffman and O'Riain, 2012). But the habitat and resource options available to baboons in MINAPA are extensive in area and diversity, largely uninfluenced by human activity. The exception to this is the highway that crosses the baboon range. It is located for engineering reasons in the alluvial area between hills and floodplain and this is also where the majority of baboons sleeping site trees are located.

Sleeping refugia for yellow baboons are groves and clumps of mature trees. In MINAPA baboons are not central place foragers moving from and returning to a limited number of sleeping sites (Rhine et al., 1989, pers. Obs). Thus habitats used represent actual choice options. Of the four extensive and easily available habitats (Grassland, Wooded grassland, Open woodland, Woodland) (Norton et al., 1987; Rhine et al., 1989), Wooded grassland was by far the most used habitat accounting for 52% of total follow locations. Riverine habitats which contain the majority of sleeping sites (Norton et al., 1987; Rhine et al., 1989, pers. Obs) are limited in extent and availability as they only occur within and along narrow watercourses (Korongos). Riverine was overall used in 13.6% of follow locations which more than Woodland and grassland which are extensive in the Viramba troop range. However, the pattern was different for proportion of feeding follow; woodland and grassland were used above mean proportion of feeding follows (at about 80%) compared to 59.6 % of feeding follow in Riverine habitat.

These findings are partially consistent with those of Cowlishaw (1996) and Barton et al (1992), who found that the use of habitats by baboon reflects location of sleeping sites and waterholes. The higher use of Riverine habitats observed in this study is highly associated with presence of sleeping sites and their allocation along narrow watercourse. The higher use of woodland and grassland during feeding is associated with their extensive proportion in Viramba range.

3.4.2 Dietary profile (food sources, types, parts and packages)

During this study the baboon diet consisted of a variety of plant parts from 93 species as well as many unidentified invertebrates (and products) and some animals (appendix 3.1). Norton et al (1987) reported over 190 plant species used over a period of 5 years and the overall baboon food list for Mikumi is now in excess of 220 plant species (ABRU database records). The 93 plant foods used during this study are mostly a subset of plants on these lists; about 45% of all recorded. The lower number of species recorded in this study compared to that of Norton et al (1987), may be accounted for by two main reasons; firstly is the study duration, while this study was conducted for two years, Norton et al, conducted their study for over more than 5 years. Secondly, there have been changes in both the environment and the size and structure of the baboon population (Chapter 2). For instance, in this study *Acacia sieberiana* was an important food species, one of three tree species that along with grasses accounted for feeding on over 50% of feeding follows (see below). But this tree was virtually absent from the diet observed by Norton et al (Norton pers. com). In fact, *Acacia sieberiana* was a rare tree in MINAPA prior to 1995 (ABRU database records: Norton pers.com), however the population has expanded in the last 20 years creating stands of this species where none existed.

The lower number of plant species used by baboons during this study is also likely to be associated with the demographic changes and trends presented in Chapter 2 (Section 2.3.1). There are fewer baboons than previously, troop sizes are smaller and troops are fewer in number. This in turn reduces the daily travel distance and patch depletion rate. Patch size and distribution is related to troop size as is daily range area, and travel time. Smaller troops, will have shorter daily travel distance and patch depletion rate: because of their troop size there will be more patches available hence taking more time to deprive a food patches, thus will have lower travel time and distance (Stevenson and Castellanos, 2000). In this study, members of both troops did not exceed 40 individual at any given time. With such small troop sizes patch stay can be longer and inter-individual competition will be reduced.

Findings from this study indicated that, plants were the major source of food but invertebrates were also important as has been reported for this population previously (Rhine et al., 1986). Foods were mostly obtained from trees and grasses although forbs and invertebrates were commonly used as well; moreover fruits were important food part consumed followed by seeds and pods. Many of the seeds used were from grasses, which partly explain the importance of grass as a food type. This is entirely consistence with authors who suggest that, baboons are eclectic omnivores showing preference for fruit (Barton, 1989; Milton, 1993; Rothman, 2014). Despite the availability and periodic use of large food packages with considerable edible biomass and requiring complex multiple levels of processing, baboons used small food packages that require little or no processing much more frequently. However, difference in definition of food package used in this study constrain comparing result in this study with findings in other studies on primates' food packages; for instance those in Altmann (2009).

Excluding the variety of unidentified grasses and invertebrates, baboons used a few species extensively. Twenty plant species (Appendix 3.2) accounted for about 77% of feeding follows of which three tree species along with grasses and invertebrates were the primary components of the diet. This finding mirrors the findings of Norton et al (1987), who identified 25 species as important plant species for baboons' diet in Mikumi. Moreover, the findings also reflect those of Post (1981) and Newton-Fisher and others (2006). Post reported yellow baboons in Amboseli National Park to have been observed feeding more commonly in 16 plant species, out of 30 plant species they were recorded to feed on: whereas Newton-Fisher and others reported olive baboons in Budongo forest to commonly feed from 21 plant species out of overall 51 plant species they were recorded feed on.

Furthermore, of the 20 commonly fed plant species, results shows that, 52% of feeding records baboons were recorded feeding on five plant species including three tree species; *Tamarindus indica, Kigelia africana* and *Acacia sieberiana*, as well as grass species: *Rottboellia* (appendix 3.2). Similar findings on baboon spending relatively more time consuming fewer plant species has been also reported by Post (1981) in Amboseli. In this study, the higher feeding record on five plant species is associated with the ability of those plant species being able to provide baboons with food most part of the year. For instance, it was observed that, at different times of the year, baboons fed on more than four different plant parts from the three tree species; the plant parts included: fruits, seeds, pods, flowers, exudates, bark and even stems. All these occur at different times of the year with different nutritional content, unlike most other plant species which could provide baboons with two to three food parts seasonally. Similar finding were also reported by Post (1981) that, fewer plant species which baboons spent more time feeding on in Amboseli; were consumed throughout the year and their availability showed minor fluctuation as compared to most other plant species. Focusing on a few species out of a higher number of food species in the diet seems typical of baboon populations regardless of differences in vegetation types, and this conform the reputation of yellow baboons as generalist feeders who carefully select their food (electric feeders) as described by Norton et al (1987).

Baboons were recorded feeding on fruits, seeds and invertebrates more often than other food parts; also to some extent they included leaves and tree sap/exudates. These findings, conform with the finding from other studies describing baboons as generalist omnivores who subsist mainly on fruits, leaves, seeds (Norton et al., 1987; Swedell, 2006; Swedell et al., 2008) and opportunistically on invertebrates (Altmann, 1974). The findings also coincide with findings from Post (1981) and Rothman et al (2014). Post argued that baboon fed mostly on fruits and flowers of trees, particularly Acacia spp, and grasses were fed at lower rate. Whereas, Rothman argued that, insects and other invertebrates form an important portion of primates diet, and they are incorporated in their diet as supplement to other diet especially food that could provide protein. In this study, the higher records of baboon feeding on fruits and seeds is much associated with abundance and availability of fruits and seeds in wet season, even though this study did not analyze for seasonal variability in food sources, it was much observed that, fruits and seeds especially from grasses were more abundant in wet season quarters than dry seasonal quarters. This also reflects the higher mean interval feeding rate per follow in wet seasons.

Additionally, the higher fruit consumption in wet season quarters has been also related to higher nutritional content and less toxicity of fruits during this period (Post, 1981; Milton, 1993). It has been reported that, ripe fruit serve as an important source of energy in primate species, while leave and insects serves as source of protein (Kamilar and Pokempner, 2008). However because of body size differences males and females differed in their fruit diet supplement (Kamilar and Pokempner, 2008).

Higher consumption of seeds was observed during dry season more especially in early dry, with also higher records of feeding on invertebrates. This is associated with availability of dry and burnt seeds, in addition to easy access to insect. In Mikumi, early dry period is the time for early burning as Park management tool to allow growth of new forage and control for late dry season fire. In addition to providing baboon with readymade "barbeque" from burnt invertebrates, the burning also opens area for higher vicinity for baboons. In that regard, baboons increase their daily range movement hence increase their rate of feeding on invertebrates and seeds. While Altmann and Altmann (1970), Swedell et al (2008) suggested baboons' feeding on invertebrates as opportunistic behaviour, the higher encounter of invertebrate feeding in this study (28% of feeding records) suggest that, in Mikumi more especially in dry season baboons do not feed on invertebrates opportunistically rather they seek them out. During this study baboons were moving longer distance searching for and catching invertebrates.

In addition to nutritional value and availability, higher consumption of fruits and invertebrates observed in this study is also associated with the nutritional reward. Fruits, seeds and invertebrates compared to leaves may involve many processes but the reward for such effort is high. Fruits especially when ripe, they are easily digestible and with high energy content; on other hand seeds and invertebrates are high in protein. Leaves are usually lower in sugar content, thus the nutritional reward is higher from fruits and seeds compared to leaves.

The other almost unique findings in this study are on the food packages consumed by baboons. Most studies on the feeding behaviour of baboons relate or define food packages in terms of actual nutritional content of the food (Altmann, 2009). However, in this study we referred food package in terms of its size and handling time before consumption. It was observed that, most of the food baboons consumed in Mikumi were food that do not require any processing before consumption (unitary packages), large food packages that require single process before consumption (SPL) and food packages that require mixed process (Mixed). Because of methodological discrepancy (especially on definition of food package), direct comparison of results from this study to those in other studies is difficult. However, when relating the findings on the size of food parts consumed to the findings from other studies, the findings in this study reflect findings from Swedell et al (2008) and Altmann (2009) who reported that, baboons most often feed on easily accessible foods such as seeds, leaves, flowers and even gum.

In this study, the higher feeding on unitary food packages is associated with baboon's higher feeding on seeds, leaves, invertebrates, exudates and flowers. All these are food packages that can be consumed without further processing, in addition to that they are also nutritionally rewarding as most of them are high-protein food except exudate which is high-energy food (has higher carbohydrates) (Milton, 1993). Higher consumption of large food packages that require single process before consumption is associated with consumption of fruits especially from *Kigelia africana* and *Diospyros kirkii*. These tree species produce large fruits from which baboons mainly feed on fruit flesh or seeds, thus for baboons to get the edible part of the fruits required to further process it before consumption. On other hand, higher consumption of food packages that require mixed process is much associated with higher consumption of fruits of *Tamarindus indica*. This finding may also reflect higher feeding on trees and shrubs and less on grasses. The correlation between food part consumption and package/process is important factor for assessing nature and extent of sexual segregation in baboon therefore will be discussed in detail in the next chapter.

3.4.3 Spacing behaviour

3.4.3.1 Vertical position

In this study baboons were observed feeding most frequently on the ground (up to 1m) and at the canopy (beyond 2m above ground) both during feeding and non-feeding follows (Figure 3.6). Despite of methodological discrepancy, this finding is consistent with that of Barton (1993 cited in Cowlishaw 1999) and that of Stacey (1986) that, baboons spent more time on the ground than in the tree. Moreover, these findings also conform to Altmann and Altmann (1970) description that, baboons are predominantly terrestrial primate move and feed frequently on the ground. However, terrestrial behaviour is not unique to baboons among primates. It has also been reported for other primates such white-faced capuchins (Gould et al., 1997), Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) (Li, 2007) and spider monkeys (Youlatos, 2002; Campbell et al., 2005). Terrestrial behaviour in primates has been reported to be influenced by various factors such as predation pressure (Campbell et al., 2005), resources distribution and habitat structure (Youlatos, 2002) and morphological difference such as body size (Dunbar and Badam, 2000).

The use of ground level (up to 1 m) by baboons as observed in this study is associated with habitat structure in Mikumi National park. Although, we did not analyze data for plant species distribution, data on the food type consumption by baboons (section 3.3.2.1) show that baboons fed more from grasses, forbs and invertebrates as compared to consumption of food sources from trees. As explained in section 3.4.1 above, Viramba range contains a larger proportion of grassland and wooded grassland comprised more with grasses, shrubs and forbs; thus provide baboons with more food. Fruits were the most fed plant parts, and were mostly obtained from trees. However, when available, they were easily and often obtained from the ground as fruits were dropped by birds or fallen. Tree species from which such fruits were consumed included; *Tamarindus indica*, *Kigelia africana* and *Acacia spp*. Additionally, when on the ground baboons have access to leaves and seeds from herbs and forbs which provide them with much needed protein. As primates usually prefer a high protein diet rather than a fibrous diet (Milton, 1979), leaves of herbs and forbs are preferred because they contain higher proportion of protein than leaves of most tree species (Li, 2007). Feeding on the ground enables baboons to use larger patches, and are able to space out when seeking new food patches hence reducing intra-group specific competition. Feeding within trees were individuals will be crowded into a limited canopy space and a limited number of branches increase competition (Cowlishaw, 1999).

The use of higher tree canopy (height beyond 2m) for feeding in this study is associated with fruit diet and vigilance behaviour in yellow baboons. This is consistent with observation on other primates such as spider monkeys (Youlatos, 2002 and Campbell et al., 2005). These studies associated the use of higher strata by spider monkeys with resource distribution, the same reason was also used by Xiang and others (2009) to explain the use of higher canopy by black-and –white snub-nosed monkeys (*Rhinopithecus bieti*). In this study the use of higher canopy by yellow baboons is associated with fruit consumption as reflected by the higher proportion of consumption from tree observed in the use of food type (section 3.3.2.2). Fruits consumed by baboons, were ripe fruits which more often were located at the tree canopy and poorly located at the middle part (height up to 2m) of the tree. The use of canopy by baboons was also associated with size of branches at this levels, although we did not analyze for tree size in this study, but from visual observation most of tree species had larger branches at higher canopy, these branches provides good support for baboons during vigilance. This is because lower heights usually have fewer branches and trunks as compared to canopies; hence primates more often avoid use of this stratum except for less behaviour such as socializing.

Moreover, the use of higher canopy is also associated with vigilance behaviour of yellow baboons, because of wooded grassland domination in the area, baboons spending most of the time feeding and moving on the ground may increase the risk of predation. This means, for baboons to safely move around in such environment need to increase their level of vigilance through scanning the area from higher canopies to increase visibility. This is because vigilance more often serves as a good technique of detecting predator before attack (Bednekoff, 2001; Smith et al., 2004). In addition to fruit diet and vigilance behaviour, the use of higher tree canopy may also explain the form of group living in baboons. Despite of the challenges associated with sexual body size dimorphism, group living has been explained as one of the anti-predatory mechanisms exercised by animals, in which animals potentially reduce the predation risk and time spent vigilant through dilution and/or detection effects (Lima, 1995 cited in Smith et al., 2004). This is more common in primates staying in mixed-species group as it increases predator detection through complementary vigilance (Rebassa et al., 2014). Given the possibility of high nutritional return from ripe fruit and strong braches to support baboons for vigilance, it is not surprisingly baboons had used the canopy more frequently compared to mid-canopy

3.4.3.2 Horizontal position

It was observed in this study that, while feeding on the ground, baboons fed more frequently at the centre of the troop and less behind the troop than at other positions. The centre of the troop was defined in reference to Altmann (1979) that "is the point where most members of the troop are found" (Table 2.4). This position could be clearly defined when the troop is resting and/or feeding on the ground rather than when the troop is moving or in the canopy. Findings from this study on the use of horizontal positions are consistent with the progression order hypothesis described by De Vore (1964 cited in Altmann, 1979, pp.46) that, when baboons are under the tree (presumably resting) seems to have no particular organization, but a clear order of organization appear when they start move out in open plain. Although the hypothesis did not describe the progression order in relation to age-sex classes, the way it was presented implied that majority of the troop was at the centre of the troop (described as "nucleus of the troop" in De Vore, 1964) with fewer individuals at the front and behind the troop. The progression order was later described as a by-product of what was known as "feeding concentric ring hypothesis" observed on feeding behaviour of Japanese macaques (*Macaca fuscata*); whereby feeding was more at the centre of the troop, with fewer individuals mainly subdominant and subordinates males at the periphery (Itani 1954 cited in Altmann, 1979). Similar phenomenon was reported by Rhine (1975) when describing the progression order of Amboseli baboons.

The higher records of baboons being at the centre of the troop as compared to other positions observed in this study is associated with overriding number of females in troops compared to that of adult males and sub adult males. In both troops V5 and V6, female population doubled that of adult males and was greater than that of sub adult males (appendices 2.3 and 2.4). However, despite of the lower observation of individuals at the front and behind the troop, the rate (proportion) of feeding at these positions were relatively higher (more than 90% of all follow) than at the centre of the troop (77% of all follows). The higher feeding rate per follow at the front and behind the troop is associated with presence of adult and sub adult males in the troop. Details of differences in spacing behaviour between age-sex classes will be discussed later in chapter 5. However, the higher feeding observation for adult males is associated with their willingness to trade-off their safety for foraging requirements as described by predation risk hypothesis (Table 1.1; Main et al., 1996). In this case feeding both at front and behind the troop is risky as individuals at these positions are at great chance of encountering any approaching predator. For subadult males the higher feeding observation in front of the troop is associated with their need to acquire skills from adult males as described by social preference hypothesis (Table 1.2: Bon 1991).

Knowledge on the terrestrial behaviour and use of stratum by primates is very important in clarifying their pattern of habitat use more especially that of diurnal primates, which is crucial information in understanding their social organization as it may elucidate age-sex class difference in the use of habitat (more discussion on this is provided in chapter 5). Such information is vital in understanding mechanisms used by yellow baboon to manage to stay in permanent mixed sex troop despite of body size dimorphism between sexes.

3.5 Summary of key findings

In the context of the aim of this study, the key findings of this Chapter are that:

- Trees, grasses and forbs were the main food types from plant sources; and invertebrates were the most important animal source used, while vertebrates made only a tiny contribution
- A wide range of plant parts were consumed with seeds, fruits and leaves being the mostly consumed parts, however exudates (sap) were also important.
- Food parts were consumed in variety packages, but unitary food package was the mostly consumed package.
- Subjects were observed most frequently on the ground (height up to 1m) regardless of feeding. The canopy (height beyond 2m) was also used extensively compared to mid-canopy and korongos. When on the ground subjects were most often at the centre of the troop mass and less frequently away from other troop members.
- Five activities were defined: Feed, Move, Rest, Social and Vigilance. Feeding and moving were the mostly performed activities. Plant sources predominated over animal or exotic sources.

This chapter has looked particularly at the diet of yellow baboons in new ways and, along with past work in MINAPA demonstrate that the resource options available to baboons are many and diverse. The diversity of resources provides baboons with multiple feeding and processing options, which may allow feeding differences for sexually size dimorphic baboons whilst staying in mixed-sex troops. This chapter also lays the foundation for the analysis by age-sex class in subsequent chapters by introduces key variables used to measure dietary profile, space use and activity.

Chapter 4: Dietary Profile

4.1 Introduction

4.1.1 Aim

This chapter focuses on addressing objective two of the study (Chapter 1, section 1.3.2). It tests the hypothesis that yellow baboons use subtle differences in their dietary profile as a mechanism for staying together in mixed-sex group despite differences in body size by comparing the diet of adult males, subadult males and adult females in relation to food:

- Sources
- Types
- Parts
- Packages

These different ways of looking at dietary profile were introduced in Chapter 3. Given that adult males are far larger than adult females and subadult males a pattern in dietary profile whereby adult females and subadult males are more similar to each other than to adult males would support this hypothesis.

4.1.2 Diets of non-human primates

Non-human primates eat a very wide variety of different species (Hohmann, 2009) but in general, large bodied primates are mostly folivorous (leaf eaters) whereas small and medium sized ones are mostly insectivorous (insect eaters) and frugivorous (fruit eaters) respectively (Rothman et al., 2014). This can be explained from the fact that leaves which are more abundant are lower in quality than insects, fruits, seeds and flowers (Milton, 1993).

Studies on dietary difference within individuals of the same species are rare, however a number of studies on feeding behaviour have considered dietary differences between species with different body size within the same genus (Stenland et al., 2003; Smith et al., 2004; Freed, 2006; Heymann, 2011). These studies have examined such relationship from niche partition point of view to allow association; such associations are referred to as mixed species or polyspecific association. Polyspecific associations are very common amongst Neotropical and African rain forests primates (Freed, 2006). The association can be composed of members from the same genus, for instance mixed group between

Cercopithecus mitis and *Cercopithecus ascanius* (Struhsaker and Leland, 1979), or members from different genus, like groups of *Saimiri sciureus* and *Cebus apella* or *Cebus albifrons* (Heymann, 2011). In both cases, the association is much more a result of complete overlap of home ranges (Heymann, 2011). The time spent in association by different groups varies based on the magnitude of costs and benefits obtained by members, influenced by portion of overlapped food resources and degree of body size dimorphism (Heymann, 2011). Both food resource overlap and degree of body size dimorphism are positively correlated with length of polyspecific association (Heymann, 2011).

The positive correlation between polyspecific associations and the degree of body size dimorphism between associating species is somewhat analogous to the idea of partitioning between large male baboons and smaller female and sub adult baboons. Because in polyspecific association, when species varies greatly in body size, they tend to have different diet, feeding behaviour and foraging techniques, which reduce within group competition for food (Main et al., 1996). For instance *Saguinus mystax* and *Saguinus fuscicolli* which strongly differ in body size spend most of their time in association as compared to less dimorphic *S. fuscicolli* and *S. imperator* which spend most of their time in single groups (Heymann, 2011). These patterns are consistent with the predictions for sexual segregation in sexually size dimorphic mammals. It should be noted however, that polyspecific primate associations are much more variable in occurrence, duration and cohesiveness than permanent baboon troops.

Large variation in diets within species has been documented across time, particularly seasons (Conklin-Brittain et al., 1998: Hohmann, 2003; Li, 2006) and spaces in different habitats (Lehman, 2004; Ménard et al., 2013; Dias et al., 2014). However inter-individual variation between members of the same species occupying the same habitat at the same time has less often been documented (Stensland et al., 2003; Reed and Bidner, 2004). This may be because these differences don't exist or it may be because diet has not been looked at an appropriate way or in sufficient detail. For example, most of the available literature on feeding behaviour of yellow baboons describes their extraordinary dietary diversity in terms of species eaten (Post, 1982; Norton *et al.*, 1987; Barton *et al.*, 1993), but never have explored the feeding options provided by such dietary profile.

4.2 Methods

This section provides information specific to this Chapter and supplements the information on the study area, data collection and analyses provided in Chapter 2. The categories used for analyses of Sources, Types, Parts and Packages are defined in Chapter 3. These were derived from data collected using a one-zero recording technique (Chapter 2. section 2.4.2).

For all analyses the follow was used as the unit of analyses but the data were considered at two different levels: Follow level and Interval level. The presentation of these two levels based on the general form of the word equations: **Response variable = Age-sex class + Subject ID** as described below using the Food Source category "Plant" as an example.

- Follow level: Presence versus absence of plant feeding in a follow. GEE analyses were performed according to the word equation: Plant feeding (present/absent) = age-sex class + subject ID (binary logistic model) (Equation A section 2.5.2).
- Interval level: Proportion of intervals plants eating recorded in a follow: GEE analyses were performed according to the word equation: Plant feeding (proportion of intervals) = age-sex class + subject ID (logistic model) (Equation B section 2.5.2).

For each of the dietary profile variables (sources, types, parts and packages) results were presented as described below:

Using Follow level: Feeding occurrence or non-occurrence (P/A) on any variable is presented as:

1. Table of proportion of variable (e.g. plant) feeding follow to number of feeding follows by age-sex class (e.g., Table 4.1)
2. Table of GEE results according to Word Equation A section 2.5.2 (e.g., Table 4.2)

Using Interval level: Proportion of feeding intervals dietary variable recorded within follow:

3. Error plot of mean percent of intervals per feeding follow by age-sex class (e.g., Figure 4.1)
4. Table of GEE results according to Word Equation B section 2.5.2 (e.g., Table 4.3)

4.3 Results

4 3.1 Food source use by age-sex classes

The overall pattern of food source use was presented in section 3.3.2.1 of Chapter 3. In this section, variation in food source use by age-sex class is analysed by percent of occurrence of feeding during follow (proportion of feeding follows over total follows) and by the extent of feeding within a follow (mean percent of interval with feeding per follow) for each age-sex class.

Due to demographic parameters there were more follows of adult females than of adult males and subadult males (appendix 2.1). This is reflected in total feeding follows for each age-sex category. Table 4.1 shows the total number of feeding follows and number of feeding follows by food source for each age-sex class. The percent of feeding follows for each food source and sex is given in brackets (Table 4.1).

Table 4.1 shows that the relative use of food sources by age-sex class is comparable to the overall profile described in chapter 3. All classes use plants as the principle food source and exotic foods are very rarely used. However, adult males use plants in proportionally fewer follows than the other classes and use exotics somewhat more. Adult males used plants in 91% of their 557 feeding follows while adult females used plants in 96.3% and subadult males used plants in 97% of their respective feeding follows.

Table 4.1 Proportion of food source use with overall number of feeding follows and food source specific feeding follows by age-sex category.

		Food sources (feeding proportion %)		
Age-sex classes	**Feeding follows**	**Plants**	**Animals**	**Exotics foods**
Adult Male	557	507 (91%)	180 (32.3%)	29 (5.2%)
Adult Female	1862	1793 (96.3%)	558 (30%)	69 (3.7%)
Sub Adult Male	655	635 (97%)	175 (26.7%)	24 (3.7%)
Total	3074	2935	913	122

The results of a GEE analysis show that age-sex class contributed significantly to variation in proportion of plant food source feeding follows (Table 4.2, test of model effects) but not for animal or exotic food source feeding follows. Adult females (AF) and subadult males (SAM) both fed significantly more from plants than adult males (AM) but did not differ from each other in the use of plants as source of food (Table 4.2, parameter estimates). Moreover, the three age-sex classes did not significantly differ from each other in the use of animals and exotic foods (Table 4.2, parameter estimates).

Table 4.2 Results of GEE analysis on food source use by age-sex classes (Word Equation A).

Test of Model Effects					**Parameter Estimates**					
					B-coefficient			**P-value**		
Response variable	**Wald Chi-Square**	**DF**	**N**	**P-value**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**	**AM vs AF**	**SAM vs AF**	**SAM VsAM**
Plants	12.146	2	3074	**0.002**	-0.053	0.007	0.059	**0.001**	0.426	**0.001**
Animals	2.383	2	3074	0.304	0.023	-0.033	-0.056	0.474	0.257	0.135
Exotics	3.761	2	3074	0.152	0.015	0.000	-0.005	0.064	0.962	0.128

Moreover, variation in use of food sources by age-sex classes was analysed by the extent (rate) of feeding on food source within a follow. This was presented as the mean interval rate of food source use per feeding follow by age-sex classes. Figure 4.1 shows that the mean percent of intervals per feeding follows in which plants were used is lowest in Adult Males and similarly higher in the other classes, as expected. The mean percent interval per follow of plant use for adult males is 52.3%, for adult females it is 59.7% and for subadult males it is 62.7%. Both Animal and Exotic sources were rarely fed, and both had lower mean percent of interval per feeding follow across all age-sex classes (Figure 4.1).

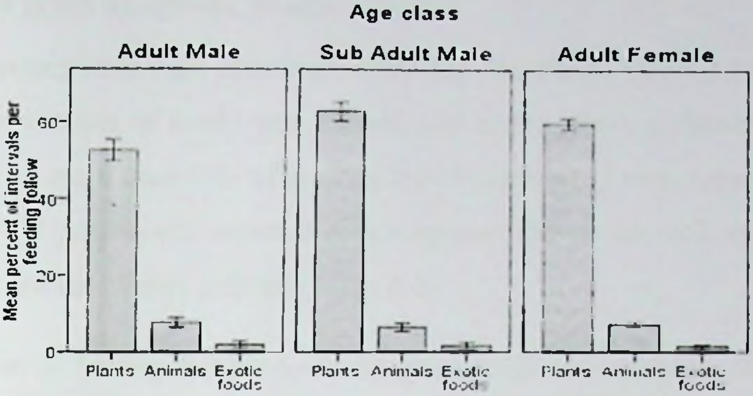


Figure 4.1 Mean percent of intervals per feeding follows by age-sex classes in use of food sources: Adult Males [N=557], Adult Females [N=1862] and Sub Adult Males [N=655].

Age-sex classes made a significant contribution to variation in number of intervals with feeding on plants within feeding follows (Table 4.3, test of model effects). There was no significant contribution from age sex classes to variation in number of intervals used per follow for animal or exotic food sources.

Adult males (AM) fed on plants in significantly less intervals per follow than both adult females (AF) and subadult males (SAM). there was no significant differences between Adult Females (AF) and Subadult males (SAM) males in plant use (Table 4.3, parameter estimates, P-value), although Subadult males used plant in more intervals than Adult Females (Table 4.3, parameter estimate, B- coefficient). There were no significant age-sex class differences for animal and exotic food sources use (Table 4.3, parameter estimate).

Table 4.3 Results of GEE analysis on number of intervals of food source use per follow by age-sex class (Word Equation B).

Test of Model Effects					Parameter Estimates					
					B-coefficient			P-value		
Response variable	Wald Chi-Square	DF	N	P-value	AM vs AF	SAM vs AF	SAM vs AM	AM vs AF	SAM vs AF	SAM vs AM
Plants	24.138	2	3074	**0.000**	-0.286	0.126	0.412	**0.000**	0.019	**0.000**
Animals	1.318	2	3074	0.517	0.085	-0.102	-0.187	0.549	0.408	0.262
Exotics	1.148	2	3074	0.563	0.282	0.117	-0.165	0.291	0.682	0.632

4.3.2 Use of food types by age-sex classes

This section analyses food type consumption by age-sex class. Table 3.3 and Table 4.4 show the variation in use of food types, overall, and across age-sex classes. Only 4 food types were used in more than 10% of feeding follows overall (Trees, Grasses, Forbs and Invertebrates. This pattern was repeated across age-sex classes as well although relative proportions between the classes differed (Table 4.4).

Table 4.4 Number of feeding follows by food type and age-sex category; With Proportion of food type specific feeding follows in brackets.

Age-sex Class	Feeding follows for various food types						
	Trees	Shrubs	Forbs	Grasses	Invert	Vert	Leftovers
Adult Males (557)	321 (57.6%)	40 (7.2%)	126 (22.6%)	231 (41.5%)	165 (29.6%)	18 (3.2%)	8 (01.4%)
Adult Females (1862)	1074 (57.7%)	233 (12.5%)	549 (29.5)	967 (52%)	525 (28.2%)	45 (02.4%)	10 (0.54%)
Sub Adult Males (665)	398 (59.9%)	80 (12%)	156 (23.5%]	309 (46.5%)	163 (24.5%)	18 (02.7%)	5 (0.75%)
Total	1793	353	831	1507	853	81	23

Differences in food type use by age-sex classes was tested on the number and proportion (percent) of feeding follows in which each food type was used. Age-sex class made a significant contribution to variation in number of feeding follows of three of the 8 food types; shrubs, forbs and grasses (Table 4.5, test of model effects). Adult males fed on shrubs and grasses in significantly fewer feeding follow than both adult females and sub Adult males. While there was no significant difference in number of feeding follow for use of forbs between adult males and subadult males, they both fed on this food types in significantly fewer feeding follows than adult females. There was no significance difference in number of feeding follow in use of shrubs between adult females and sub adult Males, but subadult males fed on grasses in significantly fewer feeding follows than adult females (Table 4.5, parameter estimates).

Table 4.5 Results of GEE analysis on food type feeding follows by age-sex classes (Word Equation A)

Test of Model Effects					Parameter Estimates					
					B-coefficient			P-value		
Response variable	**Wald Chi-Square**	**DF**	**N**	**P-value**	AM vs AF	SAM vs AF	SAM vsAM	AM vs AF	SAM vs AF	SAM vsAM
Trees	1.037	2	3074	0.595	0.000	0.031	0.031	0.984	0.321	0.379
Shrubs	16.774	2	3074	**0.000**	-0.053	-0.003	0.050	**0.000**	0.854	**0.008**
Forbs	8.891	2	3074	**0.012**	-0.062	-0.055	0.007	**0.043**	**0.009**	0.839
Grasses	22.274	2	3074	**0.000**	-0.105	-0.018	0.057	**0.000**	**0.009**	**0.026**
Inverts	2.053	2	3074	0.358	0.014	-0.033	-0.047	0.647	0.236	0.186
Verts	1.695	2	3074	0.429	0.008	0.003	-0.005	0.199	0.555	0.495
Leftovers	3.388	2	3074	0.184	0.009	0.002	-0.007	0.069	0.535	0.228

To test for differences in use of food types by age-sex classes within feeding follows, the mean interval rate within feeding follows of food type use was used. Figure 4.2 shows that there is considerable variation in the relative proportions of mean percent of interval of food type use across sexes. Adult males had lower mean percent intervals per feeding follows in use of shrubs, and grasses. However, they fed on forbs in relatively similar number of intervals per follow as subadult males (Figure 4.2).

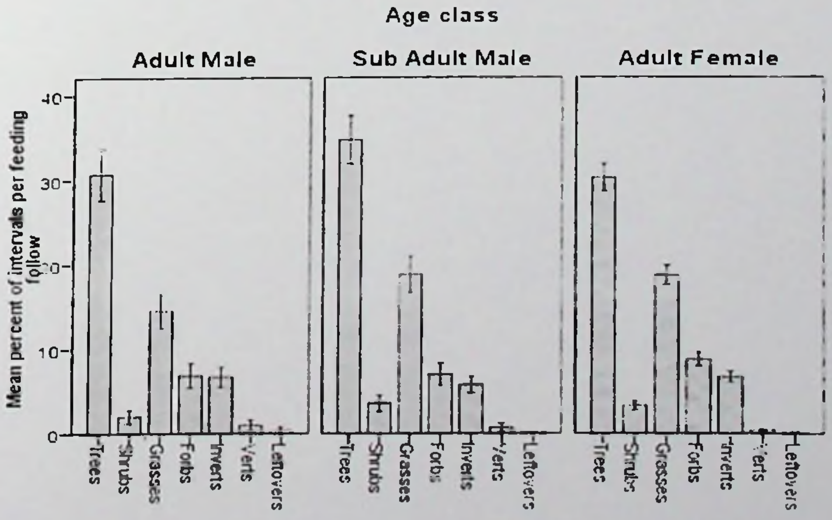


Figure 4.2 Mean percent of intervals per feeding follows by age-sex classes in use of food types: Adult Males [N=557], Adult Females [N=1862] and Sub Adult Males [N= 655].

Age-sex class contributed significantly to percent of intervals used per follow for grasses and forbs but for no other food type although it was marginally insignificant for trees and leftovers food types (Table 4.6 test of model effects). Adult males ate shrubs and grasses in significantly fewer intervals per follow than both adult females and subadult males. However, adult males fed on vertebrates and leftovers in significantly more intervals per follow than both adult females and subadult males. While adult females fed from trees in significantly fewer intervals per follow than subadult males, the two age-sex classes did not differ significantly in the use of other food types (Table 4.6 parameter estimates).

Table 4.6 Results of GEE analysis on number of food type intervals used per follow by age-sex class (Word Equation B).

Test of Model Effects					Parameter Estimates					
					B-coefficient			P-value		
Response variable	**Wald Chi-Square**	**DF**	**N**	**P-value**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**
Trees	5.594	2	3074	0.061	0.024	0.207	0.183	0.791	**0.019**	0.089
Shrubs	4.662	2	3074	0.097	-0.515	0.081	0.596	**0.045**	0.633	**0.036**
Forbs	4.020	2	3074	0.134	-0.264	-0.213	0.051	0.147	0.109	0.805
Grasses	18.105	2	3074	**0.000**	-0.301	-0.005	0.296	**0.000**	0.945	**0.001**
Inverts	1.695	2	3074	0.429	0.003	-0.163	-0.166	0.982	0.208	0.312
Verts	8.091	2	3074	**0.018**	0.830	0.522	-0.308	**0.009**	0.095	0.428
Leftovers	5.642	2	3074	0.060	1.321	0.158	-1.164	**0.024**	0.793	0.069

Inverts= invertebrates; Verts= vertebrates

4.3.3 Food part use by age-sex classes

The use of food parts (plant parts plus invertebrates) varied within age-sex classes in the same pattern as the baseline overall use (Chapter 3 Section 3.3.2.3). Table 4.7 shows that for all classes the largest proportions of feeding follows were for Seeds followed by Fruits. For Adult Females and Sub Adult Males Seeds and Fruits were used in more than 85% of their feeding follows, while in Adult Males the two food types were used in 83.3% of their feeding follows (Table 4.7). Invertebrates, Leaves, and Exudates were the remaining food parts used in about 14-30% of feeding follows in all classes.

Table 4.7 Number of feeding follows by food part and age-sex category with Proportion of food part specific feeding follows in brackets.

Age-sex Class	Feeding follows for various food parts								
	Bulb	Fruits	Leaves	Flowers	Seeds	Pods	Roots	Sap	Invert
Adult Males (557)	18 (3.2%)	217 (39.0)	99 (17.8)	21 (3.8)	247 (44.3)	47 (8.4)	32 (5.7)	77 (13.8)	165 (29.6%)
Adult Females (1862)	87 (4.7%)	721 (38.7)	471 (25.3)	134 (7.2)	927 (49.8)	262 (14.1)	177 (9.5)	354 (19.0)	525 (28.2%)
Sub Adult Males (655)	23 (3.5%)	255 (38.9)	147 (22.4)	23 (3.5)	311 (47.5)	76 (11.6)	58 (8.9)	138 (21.1)	163 (24.9%)
Total	128	1193	717	178	1485	385	267	569	853

Age-sex class significantly contributed to variation in number of feeding follows used for all food parts except Fruits, Seeds, sap (exudates) and Bulbs. However the age-sex contribution to number of feeding follows with Seed use approached significance (Table 4.8, test of model effects). Adult males ate pods, roots and exudates in significantly fewer feeding follows than both adult females and subadult males. While there was no significance difference between adult and subadult males in number of follows in which they fed on leaves and seeds, adult males fed on these food parts in significantly fewer follows than adult females. Both adult males and subadult males fed on flower in significantly fewer follows than adult females. There was no significant difference in all age-sex categories in number of follows in which they fed on fruits, bulbs and invertebrates (Table 4.8, parameter effects).

Table 4.8 GEE analysis results, number food part feeding follows by age-sex classes (Word Equation A).

Test of Model Effects					Parameter Estimates					
					B-coefficient			P-value		
Response variable	Wald Chi-Square	DF	N	P-value	AM vs AF	SAM vs AF	SAM vs AM	AM vs AF	SAM vs AF	SAM vs AM
Fruits	0.019	2	3074	0.990	0.002	0.002	0.000	0.906	0.931	0.993
Leaves	13.556	2	3074	**0.001**	-0.075	-0.029	0.047	**0.000**	0.246	0.088
Flowers	18.442	2	3074	**0.000**	-0.034	-0.037	-0.003	**0.000**	**0.001**	0.824
Seeds	5.477	2	3074	0.065	-0.054	-0.023	0.031	**0.028**	0.147	0.208
Pods	26.064	2	3074	**0.000**	-0.056	-0.026	0.032	**0.000**	0.073	**0.034**
Roots	12.681	2	3074	**0.002**	-0.038	-0.007	0.031	**0.000**	0.635	**0.045**
Bulb	3.221	2	3074	0.200	-0.014	-0.012	0.003	0.111	0.222	0.803
Exudates	10.552	2	3074	**0.005**	-0.052	0.021	0.072	**0.003**	0.525	**0.032**
Inverts	2.053	2	3074	0.358	0.014	-0.033	-0.047	0.647	0.236	0.186

Figure 4.3 shows the variation between age-sex classes in food part mean intervals used per follow. Again patterns are similar to the overall baseline (XREF C3. Figure 3.4a). Fruits and Seeds the most used parts on feeding follows are also used at a higher mean rate. Exudates show some variability in relation to other parts (Figure 4.3).

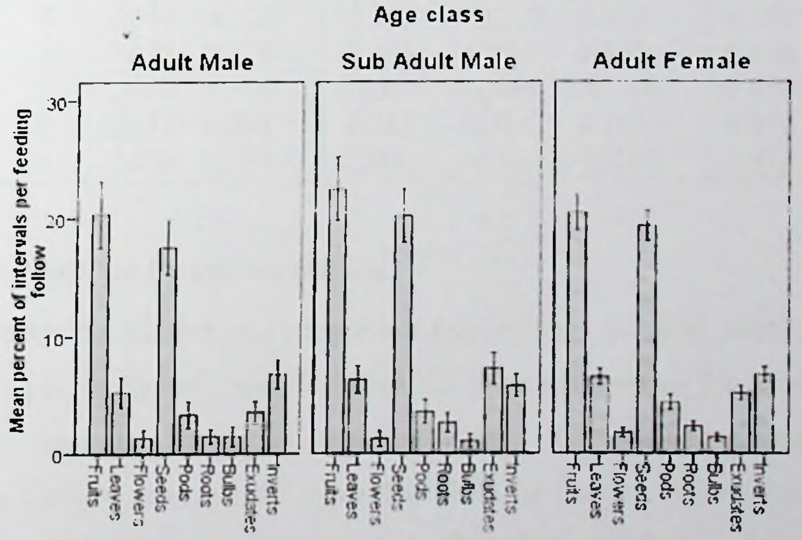


Figure 4.3 Mean percent of intervals per feeding follows by age-sex classes in use of food parts: Adult Males [N= 557], Adult Females [N= 1862] and Sub Adult Males [N= 655].

Age-sex class contributed significantly to variation in food part interval per feeding follow for one part, exudates (Table 4.9 test of model effects). Adult males fed on exudates in significantly fewer intervals within follow than both adult females and subadult males. Although, age-sex class made no significant contribution in variation in intervals per feeding follow in use of roots (Table 4.9, test of model effects), adult males fed on roots in significantly fewer intervals within follow than both adult females and subadult males (Table 4.9 parameter estimates).

Table 4.9 Results of GEE analysis on use of food parts in intervals per feeding follow by age-sex classes (Word Equation B).

Test of Model effects					Parameter Estimates					
					B-coefficient			**P-value**		
Response variable	**Wald Chi-Square**	**DF**	**N**	**P-value**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**
Fruits	1.627	2	3074	0.443	-0.004	0.120	0.124	0.970	0.215	0.306
Leaves	2.289	2	3074	0.319	-0.226	-0.034	0.193	0.131	0.783	0.272
Flowers	2.079	2	3074	0.354	-0.277	-0.358	-0.082	0.340	0.223	0.829
Seeds	2.914	2	3074	0.233	-0.118	0.054	0.173	0.216	0.409	0.089
Pods	3.461	2	3074	0.177	-0.282	-0.219	0.063	0.180	0.142	0.792
Roots	5.312	2	3074	0.070	-0.456	0.139	0.595	**0.036**	0.450	**0.028**
Bulb	0.501	2	3074	0.778	0.053	-0.264	-0.318	0.890	0.500	0.540
Exudates	12.612	2	3074	**0.002**	-0.388	0.365	0.753	**0.020**	**0.023**	**0.000**
Inverts	1.695	2	3074	0.429	0.003	-0.163	-0.166	0.982	0.208	0.312

4.3.4. Food package use by age-sex classes.

Table 4.10 shows the number and proportion (percentage) of food package by feeding follows for all age-sex classes. For all classes, the great majority of food package use was of Unitary, as well as, Single process-small (Sps), and Single process-large (Spl). Proportionally, Unitary accounts for more than 70% of feeding follow for each age-sex classes and Sps and Spl accounts for more than 50% of feeding follows for Adult Females and Sub Adult Males, and about 46% of feeding follows for Adult Males (Table 4.10).

Table 4.10 Number of feeding follows by food package and age-sex category with proportion food package specific feeding follows in brackets.

		Clumped food package categories					
Age-sex Classes	**Number of feeding follows**	**Unitary**	**Sps**	**Spl**	**Mps**	**Mpl**	**Mixed**
Adult Males	557	404 (72.5%)	102 (18.3%)	155 (27.8%)	25 (4.5%)	25 (4.5%)	31 (5.6%)
Adult Females	1862	1452 (78.0%)	424 (22.8%)	592 (31.8%)	127 (6.8%)	112 (6.0%)	118 (6.3%)
Sub Adult Males	655	482 (73.6%)	155 (23.7%)	210 (32.1%)	49 (7.5%)	33 (5.0%)	43 (6.6%)
Total	3074	2338	681	957	201	170	192

Age-sex class was a significant contributor to variation in number of feeding follows for Unitary, Single process-small (Sps) and Multiple process-small (Mps) food packages (Table 4.11, test of model effects). Adult males fed on single process-small food item and multiple process-small food items in significantly fewer follows than both adult females and subadult males. While adult males and subadult males did not differ significantly in use of unitary food packages, they both fed on this food package in significantly fewer follows than adult females (Table 4.11, parameter estimates).

Table 4.11 GEE analysis results in use of food package per feeding follows by age-sex classes (Word Equation A).

Test of Model effects					**Parameter Estimates**					
					B-coefficient			**P-value**		
Response variable	**Wald Chi-Square**	**DF**	**N**	**P-value**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**
Unitary	11.371	2	3074	**0.003**	-0.054	-0.044	0.011	**0.029**	**0.003**	0.691
Sps	9.641	2	3074	**0.008**	-0.045	0.009	0.054	**0.007**	0.587	**0.005**
Spl	3.563	2	3074	0.168	-0.040	0.003	0.042	0.076	0.878	0.083
Mps	10.099	2	3074	**0.006**	-0.023	0.007	0.030	**0.003**	0.520	**0.020**
Mpl	2.657	2	3074	0.265	-0.015	-0.010	0.005	0.137	0.303	0.648
Mixed	0.792	2	3074	0.673	-0.008	0.002	0.010	0.417	0.874	0.511

Figure 4.4 shows variation in food package mean interval rate of use per follow across age sex classes. The pattern observed in Figure 4.4 for all age-sex classes is similar to that found in Table 4.10 and that described in Figure 3.5a in chapter 3.

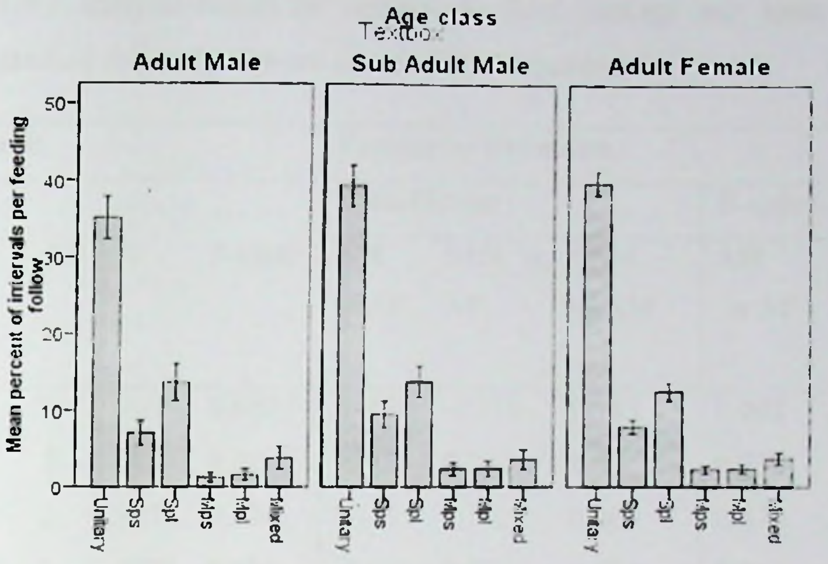


Figure 4.4 Mean percent of intervals per feeding follows by age-sex classes in use of food package: Adult Males [N= 557], Adult Females [N= 1862] and Sub Adult Males [N=655].

Age-sex class significantly affected variation in Unitary and multiple process small food item (Mps) packages (Table 4.12, test of model effects). Adult males fed on unitary and multiple process small food (Mps) packages in significantly fewer intervals within follow than both adult females and subadult males. While subadult males fed on single process small item in significantly more intervals within follow than adult males, adult females did not significantly differ with both adult males and subadult males in number of intervals within follow in which they fed on this food package (Table 4.12 parameter estimates).

Table 4.12 GEE analysis results on variation in food package use mean number of intervals per feeding follow by age-sex classes (Word Equation B).

Test of Model effects					Parameter Estimates					
					B-coefficient			P-value		
Response variable	Wald Chi-Square	DF	N	P-value	AM vs AF	SAM vs AF	SAM vs AM	AM vs AF	SAM vs AF	SAM vs AM
Unitary	9.963	2	3074	**0.007**	-0.198	-0.016	0.183	**0.002**	0.778	**0.010**
Sps	5.072	2	3074	0.079	-0.121	0.200	0.321	0.218	0.117	**0.025**
Spl	1.965	2	3074	0.374	0.103	0.112	0.009	0.325	0.237	0.940
Mps	7.031	2	3074	**0.030**	-0.622	0.022	0.644	**0.011**	0.887	**0.013**
Mpl	3.187	2	3074	0.203	-0.405	0.002	0.408	0.078	0.992	0.197
Mixed	0.023	2	3074	0.983	0.015	-0.027	-0.042	0.939	0.914	0.880

4.4 Discussion

4.4.1 Food source consumption

The expectation of different nutritional requirements in animals of different body sizes (forage selection hypothesis-Table 1.1) led to the question: Do baboons of different sizes use food resources differently? Because of sexual body size dimorphism in baboons (adult males with 21.8kg is almost as twice heavier as adult females with 11kg, Cawthon, 2006), this study hypothesized that, adult male and female baboons will differ in their nutritional requirements hence their strategies for food choices. The prediction is that, adult females and sub adult males show similarity in their feeding behaviour because of similar body size and differ from adult males. We tested food sources, types, parts and packages use by age-sex class. This discussion focuses on the results from GEE analyses of number of intervals per follow by age-sex class for each of these food (diet) categories. For the age-sex classes, these analyses provide information on use within feeding follows and the rate as frequency of intervals per follow (C3 section 3.2.5).

Results on food source use (C3 section 3.2.5) were found to be consistent with the general prediction. Adult males fed on plants in significantly fewer feeding follows than either adult females or subadult males while adult females did not differ from sub adult males. Although strict interpretation of P value indicates there was no significant difference between age-sex classes in use of animals and exotic foods within feeding follows (Table 4.3, parameter estimate); the coefficient values suggest that, sub adult males are more similar to adult females, as they both fed in animals and exotic foods in less intervals per follow than adult males (Table 4.3, parameter estimate). These findings seems to be similar to that of Rose (1994), who reported similar pattern on the feeding ecology of white- faced capuchin, where by adult males fed more on invertebrates and vertebrates and less on plant food sources than adult females.

Probably, because of methodological difference in recording plant species consumed by baboons, the findings on food sources consumed in this study were inconsistent with that of Rhine and Westlund (1978), who reported no difference in the rate of food intake by adult males and female baboons.

These significant differences in feeding on plants are consistent with the general prediction that there will be age-sex class feeding differences related to size. Smaller bodied individuals loose energy fast through heat evaporation because of their large body size to surface areas ratio, thus will have higher metabolic rate. Larger bodied individuals on the other hand, have smaller body size to surface ratio will have lower rate of energy loss but will require higher basal metabolic rate for basic body function (Klieber's law). Therefore, smaller bodied animals are expected to feed on higher quality plant food, while larger bodied animals are expected to feed on lower quality plant food.

Large males are eating plants less often and at a lower rate than the smaller sized animals but do not differ in feeding on animals or exotic food from highways. Males could still be acquiring more energy from the plants or animals they eat (differences between food types, parts and packages) and/or how they eat them compared to the other classes. For instance, males (larger bodied) can process fiber more efficiently than adult females and sub adult males (smaller bodied individuals) (Pérez-Barbería et al., 2008). Although larger males spent less time per follow feeding on plants, and more time per follow feeding on exotic foods and animals than smaller adult females and subadult males, time spent feeding and other measures of overall feeding are not necessarily good indicators of nutritional intake (Chiver, 1998), though they can be used as the measure for foraging efforts of subjects (Rothman et al., 2011).

The higher proportion of plant feeding observed for adult females and sub adult males in this study could be related to the allometric relationship of body size to post canine tooth (cheek tooth) occlusal area, that chewing surface (occlusal area) should match food biomass required by animals to meet their metabolic needs (Pilbeam and Gould, 1974; Kay, 1975). Because larger bodied individual (adult males) feeds on lower quality diet, they need to have larger cheek teeth to increase surface area for chewing lower quality diet (Kay, 1975). This is less advantageous or costly when feeding on smaller parts like grass seeds, because the food biomass obtained from single bite of these foods is smaller compared to their large chewing surface (because chewing surface is isometric to body mass) (Ungar, 2014). However, it is advantageous when they feed on large plant parts such as leaves or fruits, because a single bite of such food can provide them with food biomass isometric to their chewing surface (i.e. cheek teeth occlusal area). Nonetheless, since adult males feed on lower quality diet which requires them to spend more time processing the food (chewing) to meet their metabolic needs, they spent less time (fewer intervals within follow) feeding on plant sources compared to adult females and subadult males who feeds on higher quality diet and spent less time chewing because their bite size scaling one-to one with their body size (Gordon and Illius, 1987) and their chewing surface area (Ungar, 2014).

Alternatively, the reproductive demands on females and the demands of continuing growth and maturation on subadult males, may lead to higher energetic needs in these classes. The significantly higher rate of plant feeding in sub adult males compared to adult females is consistent with this second alternative. However, these alternatives are not mutually exclusive and are considered further below.

The insignificant results between age-sex classes in consumption of animals were contrary to the predictions. Because of smaller sized bodies, adult females and subadult males were expected to have higher proportion of animal consumption than larger males as protein supplement for their plant diet because smaller bodied animals are less efficient in processing fibres (Pérez-Barbería et al., 2008), which is higher in plants (Kay, 1984; Milton, 1993). However, these findings are consistence with that reported by Rhine and others (1986), on feeding behaviour of yellow baboon in Mikumi, and that reported by Fragaszy and Boinski (1995) and Isbell (1998), on different studies of insectivory on pata monkeys (*Erythrocebus patas*). All these studies reported on insignificant difference in animal consumption especially invertebrates between age and sex classes on primates. Lack of significant differences in animal feeding between age-sex classes in this study is likely associated with the opportunistic and seasonal pattern of animal feeding. In Mikumi baboons were feeding on animals whenever encountered. Searching for animals, almost exclusively invertebrates occurred during moving foraging when baboons were widely dispersed and was highly seasonal as observed by Rhine and others (1986), who observed that most invertebrate feeding occurred during dry seasons, consistent with findings from this study, that invertebrates were highly fed during early dry and burning seasons (section 3.4.2, chapter 3).

Opportunistic availability may also explain the lack of significant differences in consumption of exotic foods. However in this study, consumption of exotic foods in fewer intervals within follow by adult females and sub adult males is associated with male dominance over other age-sex classes probably because of their large body size. Findings related to these has been reported by Altmann and Muruthi (1988) in Amboseli baboons, that dominant animals often supplant lower ranking individuals from garbage pit or other human prepared food when found them.

Implication of these findings is that, adult males differed from the other classes by feeding less overall and this difference was mostly caused by adult males feeding on plants in fewer intervals per follow than adult females and subadult males. These findings support the expectation that age-sex classes in yellow baboons establish subtle difference in their feeding behaviour more especially on plants, and this difference could be used to maintain stable mixed-sex troop as hypothesized earlier in the chapter.

4.4.2 Food types consumption

Section 3.3.2.2 of chapter 3, describes different food types used by baboons in this study. The different age-sex classes were also expected to differ in use of food types as outlined above and in section 4.1. Adult females and sub adult males were expected to show similarity in use of food types and vary from adult males.

Only feeding on two food types, grass and vertebrates were found to differ significantly in number of intervals per feeding follow by age sex class. Age-sex class made marginal contribution to variation in number of intervals per feeding follow for consumption from trees and leftovers. Adult males feed on grasses in significantly fewer intervals per feeding follow than either adult females or subadult males. Similar findings were observed for feeding on shrubs. However, while significant result for feeding on grasses is consistent with the predicted direction of difference, feeding on shrubs is not. It suggests that the observed lower proportion on plant feeding interval by adult males is the result of eating less grass. This is consistent with the predicted direction of difference. It suggests that the lower plant feeding interval rate is the result of eating less grass. This is also consistent with the suggested consequences of bite size as explained above in section 4.4.1. A principle food part of grasses is seeds that are eaten off of burned ground individually or through a harvest process called slide where the entire grass seed head is pulled through the mouth to remove the edible seeds. Large males find it more difficult to locate and pick-up small individuals grass seeds and appear less able to efficiently slide grass seed heads through their larger teeth.

The higher proportion of feeding on grasses observed in adult female might be associated with feeding on grass seeds, the food part which contains more protein than fruit and fewer fibres than leaves. The higher protein demand of adult females is associated with extra reproductive costs during pregnancy and lactation. During pregnancy or lactation nonhuman female primates may require up to approximately 25% more protein than non-reproductive females (Silk, 1987). This study however, did not analyze data for the relationship between female reproductive status and foraging behaviour. This question will be the focus of for further analysis.

For subadult males, the observed higher proportion in number of feeding intervals per follow in shrubs and grasses may be associated with their preference for easier to extract foods like grass seed. Moreover, the higher proportion of grass feeding may further be associated with subadult males demand for protein needed for growing muscles and tissues. For example Johnson and Bock (2004) reported that juvenile male chacma baboon spent more time feeding on easier to extract foods than adult males and females.

Seasonality in plant productivity (especially fruits and leaves), phenology and the dominance of grass in the biomass of baboon habitats, presents baboons with variety of food type options of differing nutritional qualities that can be consumed in different seasons (Clutton-Brock, 1977; Norton et al., 1987; Milton, 1993; Diego, 2003). The higher proportion of feeding on grasses by adult females and sub adult males may be associated with the acquisition of nutrients from the variety of food parts produced by grasses across seasons. Young grass leaves are eaten regularly in the early and mid-wet seasons, grass seed heads are available through the late wet and into the late dry season (depending on the timing and locations of fire). In the late dry season and early wet seasons corms and fallen seeds are available especially in burned areas. (Table 2.1, Hawkins, 1999)

Adult males used vertebrate foods significantly more than adult females but not subadult males. Similarly findings were also observed on feeding on leftovers. Opportunistic availability of these foods and dominance behaviour of large males over adult females and subadult males is the probable explanation for these results. This is consistent with the findings of Rhine et al (1986) who noted that adult females often harvested larger vertebrate prey but lost it to aggressive males. In addition, the allometric ratio of body size to canine size of adult males (Galbany et al., 2015) provide a better tool for males to be able to pull flesh off larger prey. Furthermore, the findings are consistent with the report by Rhine et al (1986) that, adult males obtained their animal source from vertebrates while adult females and subadult males obtained it primarily from invertebrates. However, feeding on invertebrates was insignificantly different between age-sex classes; (see section 4.4.3 on discussion of food parts used).

Variation in feeding from trees was marginally insignificant at the model level (p=0.61), but at parameter level, subadult males fed from trees in significantly more intervals per follow that adult females, but marginally insignificant from adult males. This is associated with the significant parameter effect of subadult males using canopy and more often hence feeding on more tree products in intervals than adult females and adult males, who spent more feeding time on the ground or mid-canopy heights. This will be considered further below (chapter 5) in the discussion of vertical spatial positioning.

There were significant differences between age-sex classes in the use of some food types especially shrubs and grasses. Other significance differences were in consumption from other food types such as trees, vertebrates and leftover, however the relation to prediction for age-sex classes is unclear. This implies that, baboons express characteristics of sexual segregation through their choices of food types, but the difference is subtle.

4.4.3 Food parts consumption

The feeding strategies of animals with differed body size are expected to differ in response to their difference in energetic demand influenced by differences in body size The varied nutritional contents of different food parts is well established and the relationship of body size and digestive systems to the differing costs and nutritional benefits of food parts well demonstrated both across and within species (Milton, 1981; Rothman, et al., 2014; Pérez-Barbería et al., 2008). The distinction between the need for and the ability to use high verses low quality plant parts is one of the predicted drivers of sexual segregation. We expected differences in plant part use to reflect the different needs of the sexes as driven by the metabolic demands of body size, reproductive demands and maturation. Therefore, adult females and sub adult males are predicted to have higher proportion of feeding intervals per follow on seeds, fruits and exudates/sap but less proportion of intervals in feeding on leaves.

Generally, the results from this study showed no significant difference in consumption of food parts except for exudates, and this difference was not as predicted (i.e. similarity in consumption between adult females and subadult males). The results on exudates. (B-coefficient; Table 4.9) indicates that, the consumption of exudates is more influenced by sex (i.e. adult males and subadult males consume more than adult female) rather than size. These findings are contrary to the suggestion that, because of their limited availability, exudate/gum is common food and manageable by small bodied primates (Kay, 1975 cited in Isbell et al., 2013). Although not directly related, the finding from this study that baboon consumed exudates are consistent with that from Hausfater and Bearce (1976) who also observed yellow baboons feeding on exudates in Amboseli.

The higher consumption of exudates by subadult males are related with higher energy demand for continue growing. Exudates usually contain gums, saps, resins and latexes (Kumar et al., 2009; Porter et al., 2009), which are rich in carbohydrates and can easily provide energy compared to leaves and fruits (Isbell et al., 2013). Exudates also contain small quantities of protein that can be metabolized to provide more energy (Bearder and Martin, 1980; Garber, 1984; Lambert, 1998). In addition, exudates also contain some minerals such as calcium, potassium and magnesium which are important requirements for growth (Garber, 1984).

Similarly, the higher consumption of exudates by adult males is also associated with higher energy demand by adult male for maintenance of their large body size. Feeding on exudates is challenging to non gummivory primates because exudates contains gums consists primarily with beta-linked polysaccharides which make them difficult to digest for primate species that lack specialized anatomical adaptation for gummivory (Garber. 1984: Isbell et al., 2013). Because of large body size, adult male baboons are believed to have ability to slow down digestion process by retaining the food in the digestive system for longer time to allow enough time for microbial fermentation (Isbell. 1998: Lambert. 2002; Isbell et al., 2013) similar anatomical adaption to other non-specialized gummivory primates such as pata monkeys (*Erythrocebus patas*) (Isbell, 1998): lesser bushbabies (*Galago senegalensis*) (Bearder and Martin, 1980) and tamarins spp (Heymann and Smith. 1999).

In this study baboon found to consume exudates mostly from *Acacia spp*; however. they used exudates from other tree species such as *Sterculia spp*. *Kigelia africana*. *Ficus spp*. *Sclerocarya caffra* and others (appendix 3.4, chapter 3). These findings especially feeding on exudates from *Acacia spp* are consistent with those from Bearder and Martin (1980) on lesser bushbabies; Isbell (1998) on pata monkeys and Hausfater and Bearce (1976) on baboons. All these studies reported on primates feeding on exudates from different species of *Acacia* trees. Consumption of exudates from other tree species in addition to *Acacia* spp observed in this study is likely to be related to the fact that, nutritional composition of exudates varied between different tree species or even subspecies (Bearder and Martin. 1980). Hausfater and Bearce (1976) reported baboons feeding on exudates from two different species of *Acacia* (i.e. *A. tortilis* and *A. xanthophloea*), but usually fed on exudates from *A. xanthophloea* that contain more carbohydrates.

Use of root approached significance (p=0.070) at the model level. However. parameter estimates results showed that, there were significant differences between age-sex classes in consumption of roots (Table 4.9). The direction of difference suggests age rather than sex influences consumption of roots (similarity between adult females and subadult males). The direction of difference was expected to favour large bodied adult males because the fibrous nature of roots, harvesting and processing requirement demands individual to spent excess energy to harvest them from the ground and time to process, all these expose individuals to potential risk of predation and are costly in time and energy The observed pattern of root consumption is associated more with the food sources from which roots were harvested. Although was not analyzed, field observations suggests that most of the roots consumed by baboons were harvested from grasses and shrubs. Roots from these food types were relatively small in size hence contain less fibres, easy to harvest and were easy to process (usually single process or of unitary package); characteristics that made it easy for adult females and subadult males to use them. For adult males these characteristics would probably mean spending more time harvesting and processing but lower energetic rewards. Further analysis on the package characteristics of roots from different species may help clarify this question.

No other plant food parts including fruits and seeds, and animal food including invertebrates showed significance differences in interval use by age-sex classes in GEE analysis both at model level and p-value parameter estimates (Table 4.9). The lack of differences between age-sex classes in consumption of fruits support the suggestions of Johnson et al., (2012); Milton (1993) and Agetsuma (2001) that, because of readily available structural carbohydrates, low fibres and low toxins fruits have been considered as primary source of energy to primates regardless of difference in age-sex classes.

The consumption of fruits by adult males in this study is also associated with their frequent use of vertical positions at mid canopy to canopy level (detailed discussion in chapter 5). Adult males were observed to use tree canopies more than adult females. This may have provided them with opportunity to feed fruits at higher canopy levels which may be less fibrous and toxic than that at lower heights (Smith et al., 2004). The interval rates of feeding on fruits by adult females observed is likely to be associated with presence of lactating and pregnant females in the troop. Pregnant and lactating females usually increase their time spent feeding on fruits to cope with metabolic costs of gestation and lactation as fruits contain easy and readily available carbohydrate an important source of energy (Agetsuma, 2001). For sub adult males, the proportion of feeding on fruits is related to energy requirement associated with increasing body size (growth) (Milton, 1993). Because energy requirement per unit body weight is negatively correlated with increase in body weight, sub adult males rely more on higher quality diet to maximize their energy intake to couple with metabolic costs of their growing bodies (Agetsuma, 2001; Sakada et al., 2011). These findings correlate with the general explanation on food choice of sexually body size dimorphic primates that, typically they select food with high energy and protein (Barton and Whiten, 1994; Conklin-Brittain et al., 1998).

Feeding behaviour of primates suggest that, regardless of sexual body size dimorphism both adult males and females feed on fruits as the primary source of readily available energy but differ in the choice of their supplementary diet (Kay, 1984). Males (large bodied individuals) tend to supplement their fruit diet with leaves which are more abundant and they can easily extract available protein, whereas females (smaller individuals) tend to supplement their fruit diet with insects (Kay, 1984; Leigh, 1994). Findings on food parts consumption in this study were contrary to this general statement, as there was insignificant difference between age-sex classes on consumption of both leaves and invertebrates. However, the B-coefficient on parameter estimate suggests that, adult males fed on invertebrates in relatively more intervals per follow than both adult females and subadult males (Table 4.9). The number of intervals per follow adult males fed on invertebrates is associated with their seasonal availability, harvesting and processing technique and size preference. In Mikumi invertebrates especially insects were seasonally available particularly in dry season during early burning, also reported by Rhine et al (1986). During this season, most of the occurring invertebrates were arthropods and molluscs. Because nutritionally arthropods are higher in protein and fats compared to leaves and fruits (Rothman et al., 2014), for larger bodied animals it is profitable to consume them when available in large quantity. The size, harvesting and processing of snails (molluscs), favour their consumption by adult males more than adult females and subadult males. Snails require extensive processing including thrashing and puncturing by to open the shell before ingestion, this was easy to adult males as they used their strong and large canine contrary to adult females and subadult males. On other hand, invertebrate consumption by adult females and subadult males was associated with their feeding more on invertebrate products such as larvae embedded on tree trunks or branches rather than competing with males of capturing insects and snails. Similar findings have been also reported by Fedigan (1993) on sex difference in insectivory by Cebus monkeys.

Generally, baboons showed no significant difference between age-sex classes in the use of different food parts except for exudates at test of model effect level (Table 4.9). Similarly, they showed no significant difference between age-sex classes in consumption of all food parts except for root, which showed significance influence of size on its consumption; and exudates which showed influence of no particular direction. However, results on parameter estimate B-coefficient suggest variation in food parts consumption in the predicted direction especially in consumption of fruits and seeds. While there was age-sex variation in consumption of food parts, this variation cannot be directly linked with body size or sex difference. Instead the variations are subtle and can be linked with differences in harvesting and processing techniques between age-sex classes. Such differences enable may enable maintenance of permanent mixed sex troop.

4.4.4 Use of food packages

Previous sections addressed variation between age-sex classes in consumption of food sources, types and parts. These elements of the dietary profile are associated in one way or another with the value of the component in terms of energetic and nutritional content (Foltin, 1994). Expected differences between age-sex classes are based on the predicted relative value of these dietary components to the different classes. Foods packages differ from this model somewhat in the predicted differences between age-sex classes are determined by the cost to benefit ratio of obtaining, retaining and processing a package in relation to the overall biomass obtainable from that package (Altmann, 2009). Adult females and sub adult males were expected to have higher proportion of intervals in follows in which they used smaller packages that require little or no processing and could be consumed rapidly. Adult males were expected to use large packages with a high biomass return and more time consuming or demanding processing. These predictions were based on the idea that large males had the strength and dominance to acquire and retain such large packages as well as the strength, teeth and gape to extract the edible biomass.

The results were consistent with predictions. Age-sex classes significantly explained the variance in interval use per follow of multi-process small packages. Adult Females and Sub Adult males used these packages in significantly more intervals per follow then Adult males. There was no difference between adult females and Subadult males. However, smaller food items that require multiple processes (Mps) were not used on many follows. The vast majority of packages were unitary. These are small easily consumed items requiring no processing at all. Age-sex class significantly explained the variance in the interval use per follow of unitary packages (Table 4.12). As predicted adult females and sub adult males feed on unitary packages in significantly more intervals per follow than adult males.

This observation is mainly associated with two factors: allometric relationship of body size and nutritional requirements of animals and relationship between body size and predation risks. The body size of animals tends to affect their energy requirement per unit body weight and metabolic rate (Jarman-Bell principle; Jurmain et al., 2009, pp.134). Larger animals have smaller ration body size to surface area to body size, thus require fewer calories per unit weight compared to smaller animals. Similar observation has been made on the relationship between body size and metabolic rate (BMR) (Kleiber's law). Because of this, smaller animals including primates will require energy rich diet compared to larger animals (Bell, 1971; Jarman, 1974). It has been proposed that, the nutritional quality of diet decreases as the size of food item increases more particulary on fruits (Fleming, 1991): in that regard, the higher frequency of adult females and subadult males feeding on unitary package is associated with nutritional quality of this food package due to package size as influenced by animal's body size.

The higher frequency of feeding on unitary packages by adult females and subadult males is also associated with predation risks. Response of primates to predation risk depends among other factors on their body size (Jurmain et al., 2009, pp. 135): however, smaller bodied primates are more susceptible to predation risks than larger bodied primates (predation risk hypothesis). Thus, feeding on unitary packages allows adult females and subadult males to reduce the time spent on proceeding food hence reduce the risks of exposing themselves to predation.

4.5 Summary of key findings

In the context of the aim of this study, the key findings of this Chapter are that:

- There was subtle difference between age-sex classes in terms of food sources, types, part and package used.
- Age-sex difference was observed in plant sources but not on animal and exotic foods. Adult males fed on plants in relatively fewer intervals within follow than adult females and subadult males.
- Age-sex classes differences was observed in some food types, the direction of difference was as predicted on consumption of shrubs and grasses. Another significant difference between age-sex classes was observed on consumption of trees, vertebrates and leftovers, but the difference was not on the direction of prediction.
- There was no significant difference between age-sex classes in consumption of food parts except for consumption of exudates; however the direction of difference was not as predicted. Adult females and subadult males consumed roots in relatively more intervals within follow than adult males; however the difference was marginally significant.
- Age-sex classes significantly differed in consumption of unitary food packages and

consumption of small multiple process food packages. As was predicted, adult females and subadult male consumption food items under these packages in more intervals within follow than adult males.

There were significant differences between age-sex classes in some aspects of dietary profile that are consistent with characteristics of sexual segregation. Most of the differences were subtle and consistent with the hypothesis that yellow baboons exhibit "non-classic" sexual segregation through subtle differences in their dietary profile to stay in stable permanent mixed-sex troop despite of sexual body size dimorphism.

Chapter 5 Use of Space

5.1 Introduction

5.1.1 Aim

The aim of this chapter is to address object 3 of this study (Chapter 1, section 1.3.2). It tests the hypothesis that yellow baboons use subtle differences in their use of space, in relation to their environment and in relation to each other, as a mechanism for staying together in mixed-sex groups despite differences in body size by comparing of adult males, Subadult males and adult females in terms of:

- Distance from ground (Height)
- Position in the troop (Position)

These ways of looking at space use were introduced in Chapter 3.

Space use by individuals within and away from the vicinity of other members of the same group is an important component of group cohesion and dynamics. For instance, use of different vertical stratification in habitat allows sister species to coexist at local scale (Terborgh, 1983). For most social animals with differing body sizes, coexistence at local scale is challenging due to the struggle of balancing between troop association or dispersion as driven by their different nutritional requirements in relation to predation risk and feeding competition (Cowlishaw, 1999; Grassi, 2000). To overcome these problems, individuals may opt to disperse (maintain a distance from each other) as the means for reducing intraspecific competition. Different sexes of the same species may feed at different height levels and/or occupy different horizontal position particularly during feeding (e.g. rain forest primates, Gartlan and Struhsaker, 1972; desert baboons, Cowlishaw, 1999; gray bamboo lemur, Grassi, 2000). On other hand, individuals may choose to stay close to each other (associate/aggregate) and form large group as strategy for reducing predation risk through increased predator detection ("many eyes" hypothesis; Robinette and Ha, 2001), or through dilution/confusion (Lima, 1998 in Robinette and Ha, 2001). Knowledge of spacing behaviour between individuals is important in understanding group cohesion in animals as it relates to costs and benefits of group living.

5.1.2 Use of space in non-human primates

For primates, in addition to reduction of competition and predation risks, spacing behaviour within and between species can be influenced by other factors, such as quality of the diet, distribution of resources, dominance rank and the role of individuals in the community (Smith et al., 2004; Xiang et al., 2009; Houle et al., 2014). For instance, it has been reported that, fruits which are highly energetic and serve as the primarily source of energy to primates, are usually at higher density in the higher canopy and mid canopies than lower strata (Houle et al., 2014). This may trigger competition between individuals leading to dominant individuals monopolizing upper canopies while subordinates occupy lower strata (Houle et al., 2014). Reproductive roles of males and females in the community may determine their space use more especially during resting and when moving. Because of their investments for access to partners and protection against predators when resting male primates are likely to use vertical strata more than females to increase their ability to detect potential predators and intruders (Smith et al., 2004).

During movement on the ground (horizontal position), primates more especially baboons has been reported to move in a particular order with individuals of different sex and rank occupying different positions, typically adult males move in front of the troop followed by lower ranking males and older juvenile males, other members of the troop move or rest in the periphery, while pregnant, oestrous and lactating adult females with their infants occupy the centre of the troop; the rear of the troop is the reflection on the front with more adult males (Altmann, 1979; Rhine and Westlund, 1981; Collins, 1984;Rasmussen, 1986).

5.2 Methods

This section provides information specific to this Chapter and supplements the information on the study area, data collection and analyses provided in Chapter 2.

The categories used for height variables were defined in Chapter 3. Height data were recorded using an instantaneous recording technique (Chapter 2, section 2.4.2).

The categories defined for vertical height were: 0m = below ground/in Korongo. (Korongo literally mean ditch/trench in Swahili and refers to seasonal water course); up to 1m above ground =ground; up to 2m above ground = intermediate/ lower canopy; and beyond 2m above ground=canopy (Table 2.5).

The categories defined for the horizontal height spatial variables were: centre of the troop, troop periphery, front of the troop, behind the troop and away from troop (detailed definition in Table 2.4).

For all analyses on vertical height positions, the follow was used as the unit of analyses but the data were considered at two different levels. These are described below using the Height category "Korongo" as an example.

- Whether or not Korongo was recorded at least once during follow. GEE analyses were performed according to the word equation: Korongo (yes/no) = age-sex class + subject ID (binary logistic model); Word Equation A.
- Proportion of intervals Korongo was recorded in a follow: GEE analyses were performed according to the word equation: Korongo (proportion of intervals) = age-sex class + subject ID (logistic model); Word Equation B.

For all analyses on horizontal positions, the follow was used as the unit of analyses and are described below using the Position category "Centre" as an example.

- Whether or not Centre was recorded as Position at start of follow. GEE analyses were performed according to the word equation: Centre (yes/no) = age-sex class + subject ID (binary logistic model): Word Equation A.

5.4 Results

5.4.1 Vertical positioning (height levels)

As specified above, vertical height positions used were grouped into four different categories: 0m above ground (In watercourse or gully = Korongo); up to 1m above ground (ground level), 1m to 2m above ground (intermediate) and beyond 2m above ground (canopy level) (Chapter2, Table 2.5).

Table 5.1 shows the number and proportion of feeding follows in which each age-sex class used the various height categories. Ground level was used most frequently on feeding follows by all classes and the canopy level was the second most used by all. Proportionally Sub Adult Males used the Ground Level less frequently than Adult Males and Females and used the Canopy level more than the other classes. Subadult males also used Korongos in a smaller proportion of feeding follows. Adult Males used the intermediate level in proportionally fewer feeding follows than Adult Females and Subadult males. Adult Male use of ground level was proportionally lower than that of Adult Females.

Table 5.1 Number of feeding follows by vertical height position and age-sex category. With (Proportion of vertical height specific feeding follows)

Age-sex class	**Feeding follows**	**Height Categories**			
		Korongo	**Up to 1m**	**Up to 2m**	**Beyond 2m**
Adult Males	557	29 (5.2%)	473 (84.9%)	52 (9.3%)	144 (25.9%)
Adult Females	1862	94 (5.0%)	1666 (89.5%)	228 (12.2%)	431 (23.1%)
Sub Adult Males	655	23 (3.5%)	541 (82.6%)	83 (12.7%)	235 (35.9%)
Total	3074	146	2980	363	810

Age-sex class significantly contributed to the number of feeding follows in which the height categories were used (Table 5.2, test of model effects). While adult males and sub adult males did not differ significantly in number of follows they were recorded feeding at ground level, they both fed at this height in significantly fewer follows than adult females. Adult males fed at height up to 2m (lower canopy) in significantly fewer follows than adult females, and the difference with subadult males was marginally significant, while there was no significant difference between adult females and subadult males in number of follows they were recorded feeding at lower canopy heights. Adult males and females did not significantly differ in number of follow they were feeding at height beyond 2m, but they both feed at this height in significantly fewer follows than subadult males (Table 5.2. parameter estimates).

Table 5.2 Result of GEE analysis on variation in use of height levels by number of feeding follow by age-sex classes (Word Equation A).

	Test of Model Effects				**Parameter Estimates**					
					B-coefficient			**P-value**		
Response variable	**Wald Chi-Square**	**DF**	**N**	**P-value**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**
Korongo	1.847	2	3074	0.397	0.002	-0.015	-0.017	0.880	0.215	0.211
Up to 1m	16.851	2	3074	**0.000**	-0.046	-0.069	-0.023	**0.002**	**0.001**	0.296
Up to 2m	5.062	2	3074	0.080	-0.029	0.004	0.033	**0.045**	0.792	0.058
Beyond 2m	24.749	2	3074	**0.000**	0.027	0.127	0.100	0.324	**0.000**	**0.001**

Figure 5.1 shows the mean interval use per feeding follow of height categories by age-sex classes. The use of height categories within follow by age-sex classes relates to the patterns described above (Table 5.1). Subadult males used the ground level less but used canopy level more than adult males and females.

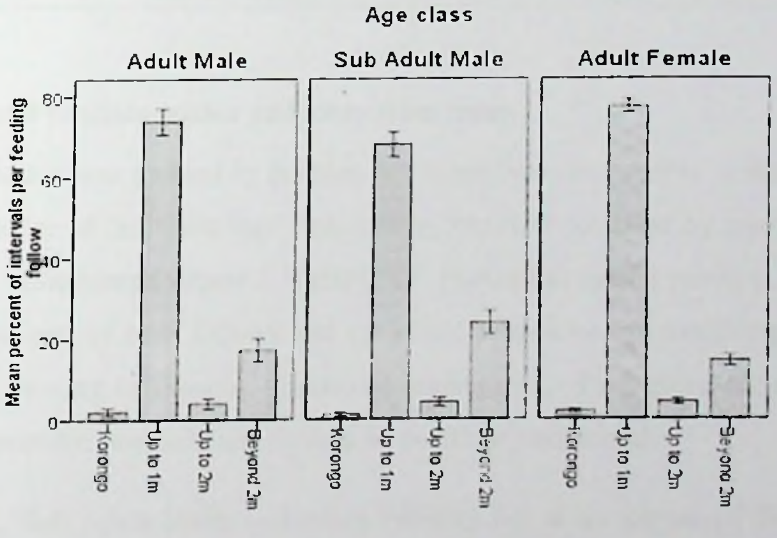


Figure 5.1 Use of height category: Mean percent intervals use per feeding follows by age-sex class classes: Adult Males [N=557], Adult Females [N= 1862] and Sub Adult Males [N= 655]; Error bar= standard error of mean.

Age-sex classes significantly affected variance in number of intervals per follows in which baboons were recorded feeding on the ground and canopy levels (Table 5.3. test of model effects). Sub adult males fed on the ground (height up to 1m) in significantly fewer intervals per follow than both adult males and females. Although adult males fed at this height in relatively fewer intervals per follow than adult females (B-coefficient). the difference between them was marginally insignificant (P= 0.078). Similarly. subadult males differ significantly from adult males and females by feeding at the canopy (beyond 2m) in more intervals per follow than both adult males and females. Between adult males and females the variation was marginally insignificant (Table 5.3 parameter estimates).

Table 5.3 Results of GEE analysis for number of intervals per feeding follow at different height levels by age-sex classes (Word Equation B).

	Test of Model Effects				**Parameter Estimates**					
					B-coefficient			**P-value**		
Response variable	**Wald Chi-Square**	**DF**	**N**	**P-value**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**
Korongo	2.055	2	3074	0.358	0.089	-0.538	-0.627	0.668	0.214	0.152
Up to 1m	16.731	2	3074	**0.000**	-0.185	-0.462	-0.277	0.078	**0.000**	**0.015**
Up to 2m	0.494	2	3074	0.781	-0.117	0.009	0.126	0.502	0.970	0.617
Beyond 2m	19.974	2	3074	**0.000**	-0.220	0.595	0.375	0.068	**0.000**	**0.006**

5.4.2 Horizontal position within and away from troop

Horizontal position was defined by position of subject baboons relative to the centre of the troop. The centre of the troop was measured by position occupied by majority of troop members (see definitions Chapter 2, Table 2.4). Horizontal spatial position was recorded at the start and end of each follows and could not always be estimated especially when troop was not moving or showing directional orientations. Thus there are fewer feeding follows with recorded positions and no data on positions on intervals.

Proportionally. Sub Adult Males and Adult Females fed at the centre of the troop more than Adult Males; whereas Adult Males fed behind the troop more than Adult Females and Sub Adult Males (Table 5.4). Adult Males fed at troop peripheries in similar proportion with Adult Females, whereas they fed in front of the troop in similar proportion with Sub Adult Males (Table 5.4).

Table 5.4 Number of feeding follows by horizontal position and age-sex category. With (Proportion of position specific feeding follows)

Age-sex class	Feeding follows	Horizontal position categories				
		Centre	Periphery	Behind	In front	Away
Adult Males	378	178 (47.1%)	68 (18.0%)	75 (19.8%)	30 (7.9%)	27 (7.1%)
Adult Females	1278	667 (52.2%)	245 (19.2%)	138 (10.8%)	176 (13.8%)	53 (4.1%)
Sub Adult Males	451	256 (54.4%)	70 (14.9%)	71 (15.1%)	41 (8.7%)	13 (2.8%)
Total	2107	1101	383	284	247	93

There were significant effects of age-class on number follows in which start position was at centre, behind, in front, and away of/from troop (Table 5.5. test of model effects). Adult Males were significantly more often at back of troop and less often at front of troop than Adult Females. They were significantly less often at troop centre and more often away from troop compared to Subadult males. Adult Male number start positions away from troop were very close to significance compared to females. Sub Adult Males like Adult Males were significantly less often in front and more often in back than Adult Females (Table 5.5, parameter estimates).

Table 5.5 Result of GEE analysis variation in number of feeding follows at different horizontal positions by age-sex classes (Word Equation A).

	Test of Model Effects				Parameter Estimates					
					B-coefficient			P-value		
Response variable	**Wald Chi-Square**	**DF**	**N**	**P-value**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**
Centre	7.032	2	2107	**0.030**	-0.051	0.046	0.097	0.143	0.189	**0.008**
Periphery	3.080	2	2107	0.214	-0.011	-0.036	-0.025	0.585	0.081	0.261
Behind	18.128	2	2107	**0.000**	-0.058	-0.047	0.012	**0.000**	**0.008**	0.450
In front	14.740	2	2107	**0.001**	0.090	0.049	-0.041	**0.001**	**0.028**	0.211
Away	6.483	2	2107	**0.039**	0.030	-0.013	-0.043	**0.053**	0.215	**0.011**

5.5 Discussion

The focus of this chapter was to assess spacing behaviour of baboons and relate it with sex difference in body size. We assessed whether baboons of different age-sex classes differ in their use of vertical heights levels during feeding and whether spatial position within the troop differed on the horizontal plane when feeding. We expected differences in spatial position during feeding on both vertical and horizontal plane that would support the predicted within group segregation on the bases of age-sex classes. That is, similarity between adult females and subadult males in the use of both vertical and horizontal plane would indicate sexual segregation by size. As with the dietary profile this discussion uses results from GEE analysis of intervals per follow.

5.5.1 Use of vertical position (height levels)

Results from statistical analysis at the level of model effects indicates that, age-sex classes significantly contributed in the variation in number of intervals per follow in feeding on the ground (up to 1m) and at the canopy (beyond 2m). Patterns of variation indicate that, the significance difference was between subadult males and adult males as well between subadult males and adult females (P-value, parameter estimates). However, the direction of difference between age-sex classes in the use of these vertical height levels indicates that, both adult males and subadult males fed on the ground and at the canopy in relatively fewer intervals per follow than adult females (B-coefficient, parameter estimate). The finding that, age-sex classes significantly contributed in the variation of number of intervals per follow in use of ground and canopy height levels is consistence with that of Cowlishaw (1999) who reported to find significant effect of sex among other factors can influence spacing behaviour of desert baboon (*Papio cynocephalus ursinus*). However, the finding that, adult males fed on the ground in relatively fewer intervals per follow than adult females in inconsistent with finding from Fleagle (1999 cited in Xiang, 2009) who suggested that, because anatomy in primates, larger bodied individual usually are associated with living on the ground. Similarly, the finding that, adult males fed at the canopy in relatively fewer number of intervals per follow are inconsistent with that of Houle et al (2014), who reported that, larger bodied and dominant individual usually monopolize higher canopies because of higher fruit density at this height, leaving smaller bodied individuals and subordinate occupying lower canopies.

The use of higher vertical heights in more number of intervals per follow for feeding expressed by adult females and sub adult males observed in this study is associated with their body sizes. With their small bodies, adult females and subadult males are lighter than larger bodied males, therefore can be supported by small branches at higher vertical height when feeding. Higher nutritional demand influenced by their smaller body size is also associated with the observed higher rate of feeding at higher canopy by adult females and subadult males. As reported by Houle et al (2014). fruits which are higher in carbohydrates a nutrient rich in readily available energy for primates (Milton, 1993), are more abundant and at high density in upper canopies, moreover it is believed that fruit at this height are less toxic with little fibres (Milton, 1993; Houle et al., 2014). Such characteristics of fruits as primary source of energy to primates is believed may have an influence on the pattern of use of higher canopy for feeding by baboon of different age-sex classes as observed in this study.

Moreover, in addition to resource distribution, the use of higher canopy by adult female may also be associated with reduction of predation risks. As it has been observed and documented that the chief predator of baboons are leopard, cheetah and lion, all these are ground predator (Cowlishaw, 1994; Diego, 2003; pers. Obs). thus baboons especially adult females and juvenile males will avoid frequently feeding and/or on the ground particularly when they are in habitat that limit their visibility. This finding can also be associated with the fewer number of intervals per follow in which adult males were recorded feeding at higher canopy. Given their investment in access to mating partner (Trivers, 1972) and additional role of protecting the troop, adult males are predicted to use higher canopy for increasing visibility towards potential invading males and predators, van Schaik et al (1983) showed that, males may tend to increase their detection ability especially for ground predators by using higher canopies (higher height levels). In that regard when adult males are at higher canopies they are more vigilant and may reduce their feeding rate. The lower rate of feeding (fewer number of interval per follow) and potentially vigilance role of adult male at higher canopies may also be associated with the finding that adult males had more number of follow at this height than adult female (Table 5.2). Similar situation has been reported on white-faced capuchin (Rose and Fedigan, 1995), in tamarins (Smith et al., 2004) and in desert baboon (Cowlishaw, 1999).

Both adult males and females significantly differ from subadult males by feeding in more intervals per follow when they are on the ground (height up to 1m): whereas, between themselves there was no significant difference, although adult females fed in more intervals per follow at this height level than adult males. Abundance of variety of food types consumed by baboons at the ground level (i.e. up to 1m) is associated with their higher feeding rate per follow when on the ground. Table 4.4 showed that, apart from trees, baboon especially adult females fed a lot from grasses, forbs and invertebrates, all these are food types which are more abundant at the height level less than 2m above ground. The higher feeding rate by adult males at this height level is much associated with their consorting behaviour and friendship with adult females to increase their chances for accessing mating partner. In several occasions, when consorting adult males had been observed feed when adult female feed and feed on the same food as adult females. Similar situation has been also reported on chacma baboons (Palombit et al., 1997; Palombit, 2000).

The results on the use of vertical height categories by baboon of different age-sex classes for feeding, indicates that spacing behaviour in vertical height by baboon is not influenced by age and/or sex as expected in the prediction for occurrence of sexual segregation in baboons. For that reason, baboons' feeding in various levels of vertical strata may be influenced by reduction of predation risk hence stay close to each other when in tree. Such explanation has been also provided by Cowlishaw (1999), Xiang et al., 2009 and Youlatos (2000) that reduction of predation risk is one of the reasons for primates to form cohesion of mixed-sex troop, similar explanation has been reported as reason for group formation in ungulates (Conradt, 1998; 2000).

5.5.2 Use of horizontal position

In addition to use of vertical heights in spacing behaviour of baboons, we also assessed whether baboons of different age-sex classes differ in their use of horizontal position within and away from vicinity of other troop members during feeding. This form of spatial positioning can only be measured when troops are showing some form of directional behaviour which can be define a front and rear to overall troop positions.

Because horizontal position could only be assessed in relation to directionality, there are fewer follows and no interval data. Using variation proportion of feeding follows starting at a given position, there were significant differences in number of follow by age sex for all horizontal position except the periphery at the level of model effect (Table 5.5). Adult males and subadult males were significantly at the front of the troop more often than adult females. Similarly, adult females were at the back of the troop significantly more often than both adult males and subadult males. Subadult males were significantly at the centre and away from the troop more often compared to adult males. Although adult females did not significantly differ from adult males being at the centre of the troop at the start of follow (p-value), result indicates that, adult females were at the centre of the troop in more follows than adult males (B-coefficient). To some extent these findings especially the occupancy of front position by adult males and centre by adult females and subadult males were consistence with that from Rhine and Westlund (1981). Rhine (1986) in their different studies in progression order of yellow baboons, and Collin (1984) in the study of spacing behaviour of olive baboons. In all these studies, it was reported that, when moving and/or feeding baboon move in an order of protective ring whereby large bold adult males tend to provide outer protective ring to centrally located vulnerable individuals, young juveniles and lactating females.

The findings that adult females and sub adult males were recorded as being feeding more at the centre of the troop more than adult males is associated with avoidance of predation risk influenced by their body size. Both adult females and sub adult males because of their small body size are vulnerable to predation as they are easier target to predators, because adult males would usually retaliate to predator attack (Cowlishaw, 1994). In that regard, as the strategy to reduce predation risk especially in daytime, smaller bodied individuals especially adult females and young juvenile will tend to feed and/or move in areas safe from predators (i.e. centre of the troop) (predation risk hypothesis) (Hay et al., 2008; Ruckstuhl and Neuhaus, 2002); with protection of adult males in front of the troop.

Moreover, both insignificant result between adult males and adult females at the centre of the troop, and adult males occupancy in front of the troop are consistence with progression order hypothesis (De Vore, 1964 cited in Altmann, 1979), which express that "when the troop moves out onto the open plains, a clear order of progression appears. Out in front of the troop move the boldest troop members-the less dominant adult males and the older juvenile males, following them at the troop's periphery are; pregnant and oestrus adult females and juveniles. Next, in the centres, comes the nucleus of dominant adult males, females with infants, and young juveniles. The rear of the troop is a mirror image of its front, with adults and older juveniles following the nucleus and more adult males at the end". The dominance of centre position during feeding by adult females and adult males observed in this study are much associated with their reproduction investments. Adult female invest in more in post-reproductive activities hence will tend to feed and move in safe from predator, while adult males invest primarily in access to mating partner hence will tend to forge friendship with prospective female partner (Trivers, 1972; Palombit, 1997), this in turn will make adult males and females to be together at the same place most of the time as long as the place is safe for adult females and infants.

In addition to being associated with occupancy of adult females and males at the centre of the troop as well as significance dominance of adult males in front of the troop; progression order as described by Altmann (1979) is also associated with sub adult males being recorded as feeding in front of the troop more than adult females. As stated the progression order ".....Out in front of the troop move the boldest troop members-the less dominant adult males and the older juvenile males...": the presence of subadult males/older juvenile in front of the troop with less dominant bolder males is associated with the intention of subadult males to learn the role of protecting the troop (Social preference hypothesis- Bon, 1991). In addition to that, although subadult males are more or less similar in size as adult females, they are considered to have less fear intensity compared to adult female, hence less nervous, therefore can retaliate to predator attack as do adult males (Rhine, 1975; Schmitt and Di Fiore, 2015).

Although data were not analyzed for female reproductive status, reduction of predation risk and probably protection of infants from infanticide is probably associated with the unexpected insignificant findings between adult females and adult males feeding away from the troop. Adult females care for their safety and that of their infants; this may lead them to choose to feed where adult males as their strategy to reduced risk of predation and attacks to their infants from intruders or males who are fighting to gain access to females. Such spacing behaviour has been reported in gorilla that, feeding position of females was affected by position of males, as they may tend to feed where males feed or positioned (Remis, 1999 cited in Remis, 2000).

Furthermore, adult females were find to be behind the troop at the start of follow more often than both adult males and females most often when the troop in feeding while moving. This is unexpected result and is shifting from the explanation of progression order (Altmann, 1979). This abnormal behaviour of female being behind the troop can be associated with age or physical injury, although no analysis related to these to variables was conducted. Physical injuries being a reason for some individual baboons to be dragged behind the troop has been also reported by Rhine (1975) on yellow baboons in Mikumi National Park. In addition to this, human presence (researcher) amongst the troop of baboons may have influenced adult females to comfortably feed behind the troop without fear for predation as would have been expected in troops without human interference; however, probably this is the area need further studies.

As it was for spacing behaviour in vertical height categories, spacing behaviour of yellow baboons when on the ground (horizontal position) at model effect level indicates that age-sex classes significantly influence spacing behaviour of baboon at the start of the follow in all horizontal position except for periphery. These findings may designate presence of sexual segregation in baboon in relation to horizontal position. However, results on the direction of differences between age-sex classes suggest no particular pattern as predicted. In that regard, the findings on horizontal position do not support the hypothesis.

5.6 Summary of key findings

In the context of the aim of this study, the key findings of this Chapter are that:

- Age-sex classes were significantly different in the use of ground (height up to 1m) and canopy (beyond 2m). Both adult males and females used ground level in significantly more intervals per feeding follow, in contrary they used higher canopy in significantly fewer intervals than subadult males. However, the difference was marginally insignificant between them.

- Adult females were at the centre of the troop more often than adult males, and less often than subadult males. However, the difference was not significant between adult females and other age-sex classes. Similarly, adult males were at the centre of the troop significantly less often than subadult males.

- Unexpectedly, both adult and subadult males were significantly less often behind the troop than adult females. However, in line with expectation they were significantly more often in front of the troop as compared to adult females.

- In line with expectation, adult females and subadult males were significantly less often away from the troop than adult males.

While there are differences between age-sex classes in use of space in the ways measured, the pattern of differences provides no evidence that differential use of space is a potential mechanism explaining how baboons of different body sizes stay together in a group.

Chapter 6 Activity Budgets

6.1 Introduction

6.1.1 Aim

This chapter focuses on addressing objective four of the study (Chapter 1, section 1.3.2). It tests the hypothesis that yellow baboons use subtle differences in their activity budgets as a mechanism for staying together in mixed-sex group despite differences in body size by comparing four different aspects of activity budgets between adult males, Subadult males and adult females. Given that adult males are far larger than both adult females and Subadult males a pattern of activity whereby adult females and Subadult males are more similar to each other to adult males would support this hypothesis. Four aspects of activity are considered in this chapter:

- The allocation of time to different activities.
- The number of activities performed together
- The occurrence of selected pairs of behaviour together.

6.1.2 Activity budgets in non-human primates

Activity budget of an animal can be simply defined as assessment of performance of activity, it either determines how long or frequent the activity has been performed or even both (Downing, 2013). For social animals living in groups, activity budget is very important as it can either lead into group cohesion (Neuhaus and Ruckstuhl, 2004) or group segregation/splitting (Conradt and Roper, 2000, Neuhaus and Ruckstuhl, 2004). Group cohesion can be achieved through synchronization of activities by group members (King and Cowlishaw, 2009; Bousquet and Sumpter, 2011). If the groups are composed of members of different size, age and sex classes, the individual costs of activity synchronization can be high due to differences in nutritional requirements and information about environment (Sueur et al., 2011). Such differences may lead to differences in time allocated for performing various activities between classes (Conradt and Roper, 2000). Hence group members develop different time allocation strategies to maximize personal benefit while living in a group (Conradt and Roper, 2000). If these differing strategies conflicts, it can cause group instability and eventually fission (Conradt and Roper, 2000).

Studies on activity budgets of non-human primates indicate that variation in activity budget is influenced by group parameters such as group size (Isbell and Young, 1993; Teichroeb et al., 2003). For instance in large troops, there is reduction in foraging efficiency and time devoted by individuals for assessing predation risk through vigilance (Terborgh and Janson, 1986). Moreover, larger groups have longer daily travel range and spend more time feeding and moving than smaller groups (Steenbeck and van Schaik, 2001). Activity budgets are also affected by environmental factors such as availability and distribution of food (Watts, 1988). Availability and distribution of food may affect activity budget in the time needed for feeding and moving. For instance, groups with home ranges contain abundant food sources of high quality; can reduce time spent for feeding and moving (Watts, 1988; Altmann and Muruthi, 1988).

In order to maintain group cohesion, all members in a mixed-sex group of sexually body size dimorphic animals must balance their individual nutritional needs in order to synchronize their activities in such a way that, all members in the group remains in proximity to one another engaging in compatible activities at the same time (Conradt and Roper, 2000; Duranton and Gaunet, 2016). The need for synchronous compatible behaviours is likely to be one explanation of why few inter-individual activity differences within group have been found (Barton, 1989; Hawkins, 1999). Another explanation may lie in the way activity budgets are typically measured. for example using instantaneous sampling which restricts how behaviour can be recorded in a single follow because predetermined time limits for data collection can lead to bias against short duration behaviours (Struhsaker, 1975 cited in Struhsaker, 2010). This is particularly relevant in non-human primates which mostly are highly social animals (live in mixed sex troops), and heterogeneous feeders with multiple feeding options (diet variability). Variability in diet provides non-human primates with multiple foraging and processing techniques to reduce intra specific competition. Higher social interaction and multiple options for food processing allow non-human primates to perform more than a single activity simultaneously particulary during feeding and /or foraging. Unlike for example ungulates which are homogenous feeders only browsing or grazing on grasses (no food processing required) with less intra specific competition and social interaction. This allows them to frequently perform single behaviours at a time particularly when feeding (section 1.2.5; Norton et al., 1987; Pollard and Blumstein, 2008; Dunbar et al., 2009). However, less often ungulate can perform multiple activities at a time usually this occurs when they are resting.

However, the efficiency of behavioural synchronization depends on the ability of members within group to share information about their activities (Conradt and Roper. 2000: Michelena et al., 2006). Higher degree of behaviour synchronization is expected in groups where members can establish high visual contact (Michelena et al., 2006) and with strong social bonds attained through social interaction (Palombit. 2000: Lehmann et al., 2007: Grueter et al., 2015), as well as in single sex groups (Michelena et al., 2006). Lower degree of behaviour synchronization is expected in groups composed on members of different age, and size due to differences in nutritional requirements (Michelena et al.. 2006).

6.2 Methods

This section provides information specific to this chapter and supplements the information on the study area. data collection and analyses provided in Chapter 2.

Six activity budget categories are considered in this chapter: Move. Feed. Rest, Social. Vigilance and Other. Analyses and discussion focuses primarily on the first five. These were derived from data collected using a one-zero recording technique (section 3.2.4 and appendix 2.6) and used in the following way:

- Percentage of intervals in a follow that these categories were recorded was used to measure the allocation of time to different activities. GEE analyses were performed according to the word equation: Proportion of intervals activity recorded = age-sex class + subject ID (Word Equation B).
- The number of these categories recorded in a single follow was used to measure the number of activities performed together: GEE analyses were performed according to the word equation: Number of activities = age-sex class + subject ID (Word Equation A).
- The number of follows in which both categories occurred in the same interval was used to measure the occurrence of certain pairs of behaviour together: GEE analyses were performed according to the word equation: Proportion of follows both activities occurred = age-sex class + subject ID (Word Equation B).

6.3 Results

6.3.1 Allocation of time to different activities

Proportionally, there was slight difference between age-sex classes in time allocated for similar activity as measured by mean percent of intervals within follow (Figure 6.1). All age-sex classes allocated most time to moving, however adult males then allocated most time to resting rather than feeding whereas for both adult females and subadult males did the reverse (Figure 6.1). Moreover, all three age-sex classes allocated least time to social behaviour.

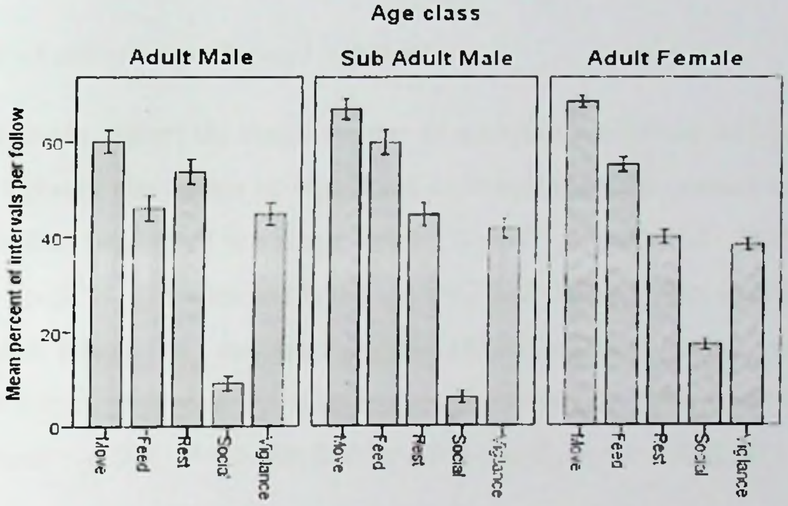


Figure 6.1 Time allocated for different activities as measured by mean percent of intervals per follow by age-sex classes: Adult Males, [N=755]; Adult Females, [N=2308]; Sub Adult Males, [N=775].

Age-sex class contributed significantly to the amount of variation in allocation of time to different activities (Table 6.1, test of model effects). Adult males allocate less time to movement than both adult females and subadult males. Moreover, Adult males allocated less time on feeding and socializing and more time on being vigilant than adult females. Subadult males allocated more time in feeding and resting and less time on socializing than adult females. The time allocated by subadult males to vigilance was nearly significance compared to that of adult females. Similarly, sub adult males allocate less time in resting and socializing and more time in feeding than adult males (Table 6.1, parameter estimates).

Table 6.1 Results of GEE analysis on time allocated to different activities by age-sex classes (Word Equation A).

Test of Model effects					**Parameter Estimates**					
					B-coefficient			**P-value**		
Response variable	**Wald Chi-Square**	**DF**	**N**	**P-value**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**
Move	62.964	2	3838	**0.000**	-0.364	-0.071	0.294	**0.000**	0.293	**0.000**
Feed	51.287	2	3838	**0.000**	-0.366	0.195	0.561	**0.000**	**0.002**	**0.000**
Rest	60.947	2	3838	**0.000**	0.562	0.197	-0.366	**0.000**	**0.010**	**0.000**
Social	69.992	2	3838	**0.000**	-0.714	-1.155	-0.441	**0.000**	**0.000**	**0.025**
Vigilance	13.783	2	3838	**0.001**	0.269	0.144	-0.125	**0.000**	0.055	0.168

6.3.2 Number of activities performed together

For all three age-sex classes the modal number of activities performed within follows was 4 and overall age-sex class made no significant contribution in the amount of variation in number of activities performed in a single follow (Wald $X^2_2 = 4.843$. N= 3838. P = 0.089). However, this result is borderline and both Figure 6.2 and the parameter estimates analyses suggest that adult female (AF) and subadult males (SAM) are more similar to each other in this respect, and do slightly more activities in a single follow than adult males (AM) (AM v AF: B-coefficient = -0.078, P = 0.029; SAM v AF B-coefficient = -0.012, P = 0.649).

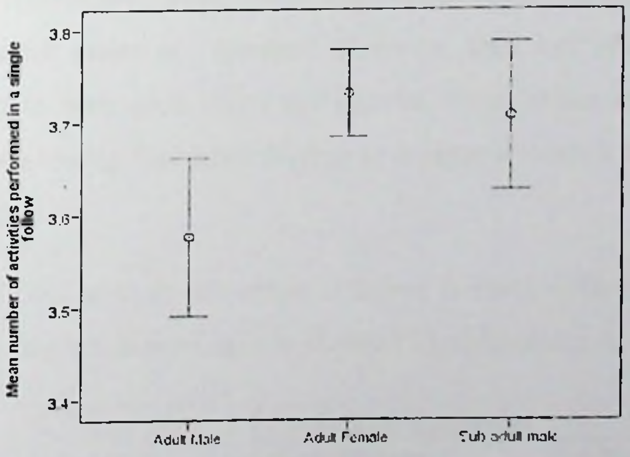


Figure 6.2 Mean number of activities performed in a single follow; N number of follow: Adult Males [755], Adult Females [2308] and Sub Adult Males [775].

6.3.3 Occurrence of pairs of activities together

The four activities that were mostly recorded as being performed by individuals of all age-sex classes were feeding, moving, resting and vigilance (section 6.3.1). Looking at selected pairwise combinations of these, resting and vigilance were the most common for adult males in a single follow (69.7%; Table 6.2) whereas both adult females and subadult males combined Vigilance more with feeding rather than Resting (67.1% and 72.1% respectively: Table 6.2).

Table 6.2 Percent occurrence of different sets of two activities performed in a single follow by age-sex classes

Age-sex class (number of follows per age-sex classes)	Percent of follows in which two different activities were performed together in a single follow				
	Feed-Move	**Feed-Rest**	**Feed-Vigil.**	**Rest-Vigil.**	**Rest-Social**
Adult Males (756)	57.7	58.7	62.7	69.7	18.7
Adult Females (2305)	67.9	57.0	67.1	62.0	29.7
Sub Adult Males (774)	67.1	64.6	72.1	67.1	13.2

Vigil. = vigilance

Age-sex class contributed significantly to the amount of variation in occurrence of all pairwise combinations of behaviour (Table 6.3, Test of model effect). Adult males less often feed and move at the same time compared to both adult females and subadult males. Subadult males more often feed while resting and become more vigilant while feeding as compared to both adult males and females. However, they less often socialize while resting as compared to both adult males and females. Adult males more often become vigilant when they are resting than when feeding as compared to adult females (Table 6.3, parameter estimates).

Table 6.3 Results of GEE analysis on number of follow in which different sets of activities were performed in a single follow by age-sex classes (Word Equation A).

Test of Model effects					**Parameter Estimates**					
					B-coefficient			**P-value**		
Response variable	**Wald Chi-Square**	**DF**	**N**	**P-value**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**	**AM vs AF**	**SAM vs AF**	**SAM vs AM**
Feed-move	21.025	2	3835	**0.000**	-0.115	0.014	0.130	**0.000**	0.552	**0.000**
Feed-rest	13.927	2	3835	**0.001**	0.017	0.068	0.051	0.416	**0.000**	**0.022**
Feed-vig	20.575	2	3835	**0.000**	-0.040	0.046	0.086	**0.014**	**0.011**	**0.000**
Rest-vig	16.997	2	3835	**0.000**	0.086	0.055	-0.031	**0.000**	**0.018**	0.222
Rest-soc	29.063	2	3835	**0.000**	-0.053	-0.180	-0.127	0.113	**0.000**	**0.001**

6.4 Discussion

6.4.1 Time allocated to different activities

The focus of this chapter was to assess activity budget of yellow baboons and relate this to age-sex difference in body size. We assessed whether baboons of different age-sex classes differ in allocation of time for different activities, number of activities performed in a single follow and types of activities that can be performed at the same time. We expected differences in activity budget that would support predicted within group segregation on the basis of age-sex classes. As with previous chapters, this discussion uses the interval rate per follow results from GEE analyses.

Result indicated that, overall age-sex classes have significant influence on allocation of time for different activities. However, adult males allocate more time into resting and vigilance compared to both adult females and subadult males, which in turn allocate more time for movement and feeding. Moreover, although adult males allocate slightly more time for socializing than subadult males, however time allocated for socializing by both adult and subadult males was little as compared to that of adult females. Generally, the findings that adult male allocate more time for resting, while adult females and subadult males allocate more time to feeding and moving are consistent with the prediction for the theory of allometric relationship between body size and metabolic rate (i.e. large bodied animal have lower metabolic rate hence spent more time resting while digesting the food) (Conradt, 1998; Ruckstuhl, 1998; Ruckstuhl and Neuhaus, 2002; Michelena et al., 2006; Barberia-Perez et al., 2007). Small bodied animal have higher metabolic rate hence higher energy demand, thus will frequently feed and move around searching for food (Jarman, 1974; Conradt and Roper, 2000).

More time allocated to feeding and moving by adult females and sub adult males realized in this study is associated with need of high quality resources influenced by nutritional requirement of small bodied animals, and for reproductive females energetic cost for gestation and lactation. Smaller animals require more energy per unit of body mass as compared to larger bodied animals, thus require proportionally higher energy intake to maintain energy balance (Kleiber's law). Baboons like most other primates particularly cercopithecines are caeca-colic fermenters, and their nutritional and energy demand is well associated with passage rate, retention time and digestibility (Demment, 1983; Watanuki and Nakayama, 1993; Marques and Marques, 1994; Sakada et al., 2011). Gut capacity is linearly related to body size, therefore larger bodied animals can retain foods with gut for longer time as compared to smaller bodied animals, hence increase digestibility of foods (Demment, 1983). Thus digestibility potential is lower in smaller bodied animals than in larger ones; as response to this, smaller animals will feed on rapidly digesting foods as we have already discussed in chapter 4, both adult females and sub adult males feed more on fruits and seeds which contain readily available carbohydrates hence provided enough need energy (Milton, 1993). In Mikumi such foods are rare and usually seasonal (Norton et al., 1987; Rhine and Westlund, 1978), thus adult female and subadult males move more frequently searching for such food from one patch to another.

However, difference in time allocated into movement did not affect troop cohesion which would have been caused by males being left behind; instead baboon managed to stay together because in addition to long distance walking, movement was also defined by individual walking between patches. While adult females and subadult males moved a lot between patches during feeding most often adult males were resting. However, this does not mean that adult males were left behind while adult females and subadult males were feeding; this is because feeding movements were within the vicinity of other troop members. Nonetheless, when the troop was moving to and/or from a particular destination for instance moving towards water point or moving away from sleeping site, all members were moving as a troop and no individual was left behind in the previous point, in that regard troop members stayed together.

In addition to moving from one patch to another, searching for higher nutritious food, smaller animals also feed more frequently as response to inefficient digestibility caused by lower retention rate and higher passage rate (Demment, 1983). Relationship between diet, passage rate, retention time and digestibility is also related to more time allocated for resting by adult males. Although, this was observed in ungulates, similar observations have been also reported in howler monkeys (*Alouatta* spp) (Marques and Marques, 1994); Japanese monkeys (*Macaca fuscata*) (Watanuki and Nakayama, 1993); yellow baboon (Altmann and Muruthi, 1988) and in gelada monkeys (*Theropithecus gelada*) (Radek et al., 2014).

Although data on female reproductive states was not analysed in this study, more time allocated for feeding by adult females in this study is likely to be associated with variation in energy need across female reproductive states. For adult females time allocated to feeding has been also related to agonistic ranking, the number of children they had (parity) in relation to consortship behaviour (Rasmussen, 1985) and costs of reproduction (Silk, 1987, Muruthi, 1988). When not in consort, higher ranking females spent more time feeding than lower ranking females; and the proportion decrease when in consort (Rasmussen, 1985). Moreover during consortship, feeding time for females that have never give birth is proportionally higher than those who had given birth once or more increase (Rasmussen, 1985). In addition to this, females also increase their time for feeding more especially for protein intake during gestation and lactation as response to reproductive costs of conception (Silk, 1987; Muruthi, 1988).

More results of time allocated for different behaviours/activities indicate that, adult males significantly differed from adult females by allocating more time for vigilance. Similarly, results (B-coefficient) indicates that, adult males allocate more time for vigilance than subadult males although the difference was not significant as predicted. These findings are consistence with those in Van Schaik and Noordwijk (1989), who reported that adult males of two species of capuchin monkeys *(Cebus albifrons* and *C. apella)* were more vigilant than adult females. More similar findings were also reported in Cowlishaw (1998), that adult male desert baboons were more vigilant than adult females. However, findings from this study are inconsistent with that in Diego (2003) who found that there was no significance difference between sexes in level of vigilance in baboons.

In animal species, vigilance is reported to primarily serve two main functions; anti-predatory defence and social monitoring (Smith et al., 2004; Gaynor and Cords, 2012). However, it has been always a problem to distinguishing the function or target of vigilance in most animal species particularly primates as the target is always not clear because vigilance may also serve in searching for food (Pays and Jarman, 2008), group defence (Van Schaik and Noordwijk, 1989), mate defence (Gould et al., 1997) and infanticide avoidance (Steenbeek et al. 1999; Palombit, 2000). Nonetheless, anti-predatory defence has been considered to predominate vigilance in most animal species and as a general rule, it is expected to decrease among individuals in larger groups (Hirsch, 2002; Smith et al., 2004; Pays and Jarman, 2008). However, this is contrary in primates especially highly social species which normally experience regular threats from other group members, in such species vigilance may increase in larger troops to monitor conspecifics rather than or in addition to predators (Hirsch, 2002). Thus, both anti-predatory defence and social monitoring may play as primary function or target of vigilance in such primate species.

A number of variables can be used to express the target or function of vigilance behaviour in primates. For instance, proximity between conspecifics (number of nearest neighbour); individual level of vigilance tends to increase with increase in number of nearest neighbour because of increased competition over food and resources (Hirsch, 2002; Gaynor and Cords, 2012). This is believed to be a clear evidence of conspecific monitoring, and social monitoring considered primarily function or target of vigilance (Cowlishaw, 1998). Similarly, individual level of vigilance increase with lower neighbour density, in this case vigilance is considered primarily anti-predatory in function because individuals with lower numbers of neighbours undergo a higher threat of predation (van Schaik and van Noordwijk 1989; Cowlishaw 1998).

As it has been stated above for most primate species it is difficult with certainty to place the primary function of vigilance as anti-predatory defense or social monitoring, because depending on the environment the two function of vigilance behaviour are not mutually exclusive. In that regard, the allocation of more time on vigilance by adult males as compared to adult females observed in this study is associated with both anti-predatory defense and social monitoring functions. In primates, the anti-predatory behaviour and social monitoring function of vigilance has been associated with increase in troop size particularly number of neighbours.

For social monitoring function, vigilance level increase with increase in number of neighbours (Hirsch, 2002). Baboons are known as gregarious animals live in multi-male, multi-females troop with only few females fertile and accessible at a given time. Because of this, there is continuous struggle between males within the troop to win competition for access to mating partners (Trivers, 1972). Therefore, males particulary dominants ones continuously monitor activities and presence of conspecifics within the troop, consequently increase the time spent being vigilant. The presence of several males in both studied troops (there were always more than 3 adult males in V5, Appendix 2.3 and more than 6 adult males in V6, Appendix 2.4), and only few fertile females at a given time is much associated with adult males allocating more time in vigilance than adult females and subadult males. Because there were no less than 24 individuals in both troops at any given time, the increase in time allocated for vigilance by adult males despite of troop size is much associated with adult males being scanning and monitoring the activities of conspecifics in the troop especially when the troop is on the ground, near the ground or in open woodland habitats (Hirsch, 2002). In that regard, social monitoring for conspecific is considered was the primary function of vigilance. Similar situation has been also reported in capuchin monkeys (Van Schaik and Noordwijk, 1989; Rose and Fedigan, 1995), and is referred to as mate guarding (Gould et al., 1997). In relation to mate guarding, increased time for scanning by adult males is also associated with dominance behaviour of adult males over adult females. It has been reported that, in primate species dominance influence vigilance behaviour particularly in cercopithecines and cebines, whereby males become more vigilant than females by increasing frequency and time spent in vigilance (Boinski, 1988; Van Schaik and Noordwijk, 1989; Rose and Fedigan, 1995).

Similarly the observation that, adult male allocate more time to vigilance than adult females and subadult males is also associated with anti-predatory function of vigilance. Unlike the social monitoring function of vigilance explained above; the anti-predatory behaviour of vigilance in this study is much associated with the use of horizontal and vertical positioning of adult males. In the previous chapter (chapter 5) adult males were reported to prefer feeding at tree canopies and mid-canopy heights, and horizontally they showed preference in feeding in front of the troop and at troop peripheries. This spatial positioning of adult males (i.e. at canopies, in front of troop and troop peripheries) is associated with anti-predatory function of vigilance behaviour of primates. This argument can further be supported by allocation of less time for feeding by adult males as indicated earlier in this chapter. The observed higher frequency of adult males using higher canopy and mid-canopy is related to the fact that, by using the higher canopies adult males expand the area of visibility and increase their chances for detecting potential predators in the wider horizon. This may also explain why adult males feed and forage less but spent more time in vigilance when they are at the canopies.

Similarly the record of adult males mostly frequently being in front of the troop and at troop peripheries during progression or when feeding is associated with the defensive role of adult males in the community (Smith et al., 2004). As it has been described in the progression order (section 5.5.2) and by Collin (1984) that "when moving and/or feeding baboon move in an order of protective ring whereby large bold adult males tend to provide outer protective ring to centrally located vulnerable individuals, young juveniles and lactating females". Thus, by being in the periphery and in front of the troop, one of the strategy for adult males play their protective role to other troop members, they allocate more time to vigilance through increased level of scanning their surrounding environment. Moreover, addition to all these, the fact that adult dominant male tolerated the presence of other adult and subadult males in the troop indicated that increased time for vigilance was also for anti-predatory behaviour as it has been reported that dominant males may tolerate the presence of additional subordinate males in the troop in return for assistance in predator detection (Gould et al., 1997). This may be supported by the finding that there was no significance difference in vigilance level between adult and subadult males. Increase in vigilance by adult males as related to their position in the troop and feeding behaviour has been also reported by Van Schaik and Noordwijk (1989) in capuchin monkeys, but contrary to the findings from Hirsch (2002) on brown capuchin monkeys in Iguazu, Argentina, who found low level of vigilance at higher canopies.

Although difference in vigilance between males and females has been described in other several mammalian taxa, males have been reported to be more vigilant than females in a broad variety of primate species including: squirrel monkeys (Boinski, 1988), capuchin monkeys (Van Schaik and Noordwijk, 1989), tamarins (Smith et al., 2004), vervet monkeys (Gaynor and Cords, 2012) and langur (Steenbeek et al. 1999) to name the few.

The overall results in time allocation for different activities indicate the significance influence of age-sex class to all activities. Although this may suggest presence of sexual segregation within troops of baboon, only pattern of difference on movement was consistence with predicted direction indicating size influence of movement. Conversely, pattern of difference in vigilance indicate direction of difference suggesting the influence of sex rather than size, although not as predicted.

6.4.2 Number of activities

In addition to time allocated for performance of various behaviours, we also assessed for the difference in occurrence of multiple at the same time between age-sex classes. As it was other assessment, we expected differences in number of activities that would support predicted within group segregation on the basis of age-sex classes.

Results indicated that adult females performed significantly more activities in a single follow than adult males. Similarly, subadult males performed more activities in a single follow than adult males, although the difference between them was not significant (section 6.3.1.1). A direct comparison of these findings to those in other studies on baboon's activities budget is constrained by methodological differences. However, despite of this methodological difference the facts that other studies also documented on baboons, ability to perform multiple activities at the same time (Post, 1981; Silk, 1987; Conway, 2009; Shanee and Shanee, 2011; Radek et al., 2014) reflect the findings in this study. The ability of baboon to perform multiple activities at the same time can be associated with resource availability and distribution as well as level of predation risk and mate guarding for males. This is supported from the fact that, two of the following behaviours: feeding, moving and vigilance were among activities that were mostly performed at the same time (section 6.3.2; Figure 6.1).

The finding that adult females and sub adult males were feeding and moving more frequently in a single follow than adult males can be associated with allometric relation of body size and energy requirement. Because of their smaller bodies they have higher energy requirement per body unit (Klieber's law), but they have lower retention rate and higher passage rate thus lower digestive efficiency (Bell, 1971; Jarman, 1974, Demment, 1983). To compensate for lower digestive efficiency, smaller bodied animals have to feed on higher quality, easy digestible food that can provide quick energy (Jarman-Bell principle). Since higher quality food are often less abundant and in case of Mikumi are seasonal, adult females and subadult males have to move more and feed in a single follow more frequently than adult males hence they move more often in a single follow; while adult males because of lower metabolic rate rest more often in a single follow, thus reduce the chance of engaging in other activities. Furthermore, social bonds between adult females and interaction adult females and their infants are associated for their performance of more activities in a single follow, as in addition to other activities they will socialize more frequently.

The overall borderline significance in number of activities performed in a single follow between age-sex classes, and insignificant results in the same variable between adult males and subadult males suggests that, size and/or sex of baboon may have little influence on variation in number of activities performed. Instead, the observed difference might have been in addition to size and /or sex by other ecological factors such as resource distribution and habitat quality. These factors have been reported in other studies to have influence on behaviour performed of baboon (Barton, 1996; Cowlishaw, 1997; Zhou et al., 2007).

6.4.3 Combinations of activities

Again methodological differences constrain directly comparing findings in this study with those in other studies on activity budget and feeding behaviour of baboon. However, the observation that adult females and subadult males showed more overlap in feeding and moving reflect findings in several studies (e.g., Davidge 1978; Hill et al., 2003). The higher occurrence of feeding and moving at the same time realised by adult females and subadult males can be associated with allometric relation of body size and energy requirement as explained above by Kleiber's law. In addition to this, feeding on high quality diet made small bodied animals more selective on diet, hence frequently move between patches searching for food that fulfill their nutritional requirements (forage selection hypothesis: Main and Coblentz, 1996; Ruckstuhl and Neuhaus, 2000; Post et al., 2001; Ruckstuhl, 2007).

Although is study did not analyse the influence of female reproductive status in activity budget, but the higher occurrence of feeding in a single follow realised by adult females is also associated with the cost of reproduction such as carrying the pregnancy and lactation thereafter, thus females will increase their feeding budget to address these additional protein requirements (Silk, 1987).

The higher rate of overlap between resting and vigilance observed in adult males is associated more by lower metabolic requirements and higher retention rate of animals with large bodies (Demment, 1983). With lower metabolic requirement, large bodied adult males feed on lower quality, higher in fiber and abundant diet; this will require them to spend more time resting and digesting (Demment, 1983). The higher frequency of vigilance is associated with their protective role in the community and reproductive investment, most often scanning for potential predators and invading males. The higher vigilance behaviour of adult males has been also reported in Bednekoff (2001), Palombit et al (1997) and Gould et al (1997), all these studies associated this behaviour with males' expectation of increasing chances for getting access to females, and Bednekoff referring them as sentinel animals.

Most of the findings in this chapter were not consistent with the predicted pattern of activity that activity budget will be influenced by size and therefore adult female will be similar to subadult males in their pattern of activity budget and differ from that of adult males. However, results showed patterns of activity budget that suggest influence of both sex and size in all variables for measuring activity budget variation, i.e. time allocation for various activities, number of activities and combination of activities. In that regard, finding on activity budget support the hypothesis that yellow baboons manage to stay in in stable permanent mixed-sex troop despite of sexual body size dimorphism through subtle differences in their diurnal activity budget.

6.5 Summaries of key findings

In the context of the aim of this study, the key findings of this Chapter are that:

- Age-sex classes significantly differed in the time allocated for various activities. Adult males move less frequently than both adult females and subadult males as predicted.
- Overall age-sex classes did not indicate a clear pattern of difference in time allocated for feeding, resting and socializing. However, adult males allocated less time for feeding and socializing than adult females; but more time on resting and vigilance than both adult females and subadult males.
- Adult males performed slightly fewer different activities in a single follow than Adult Females and Subadult Males.
- Adult females and subadult males feed and move within a single follow (combined activities) most frequently than adult males; while males (both adult and subadult) combine vigilance with resting within a single follow more frequently than adult females.

While there are differences between age-sex classes in activity budget that would suggest the influence of size and/or sex on activity budgets, the pattern of differences provides little evidence that observed subtle differences between age-sex classes is a potential mechanism explaining how baboons of different body sizes stay together in a group.

Chapter 7 General Discussion

7.1 Introduction

This chapter integrates the most relevant outcomes and results obtained from the tests of the expectations derived from the conceptual framework (Chapter 1). The implication of each test of these predictions from the conceptual framework and how these results are related to the study question are detailed in discussion sections of each chapter. This chapter presents an overview of the key findings, integrates these into an overall conclusion and discusses the need and direction for further analysis and study.

7.2 Sexual segregation but not as we know it?

Baboons are social animals whose adult females and males exhibit strong body size difference (Altmann et al., 1993). Ideas on social organization of animals with differing body size that have developed from studies on ungulates suggest that, males and females of animals with differing body size live separately outside breeding seasons. This pattern is referred to as sexual segregation (Conradt, 1998; Ruckstuhl and Neuhaus, 2000; 2002; Ruckstuhl, 2007). Classic sexual segregation is defined as "differential use of space (and often habitat or forage) by sexes outside the mating system" (Bowyer, 2004, pp. 1040; Ruckstuhl, 2007, pp. 245). However, a consensus on what is or is not sexual segregation remains lacking (Ruckstuhl and Neuhaus, 2000; Bowyers et al., 2002). In mammals, sexual segregation occurs either as social segregation (section1.2.2.2) or as habitat segregation (section1.2.2.1) (Conradt, 1998; Ruckstuhl and Neuhaus, 2000; 2002; Ruckstuhl, 2007; Hay et al., 2008). Recently it has been also reported that, sexual segregation may also result from sex differences in activity budget and patterns of movement (Ruckstuhl, 1998); and in temperate regions, it may also occur as the result of sex difference in weather sensitivity (Conradt et al., 2000; Bowyer, 2004). A number of hypotheses have been developed to explain the selective pressures leading to sexual segregation. Among these are: predation risk/reproductive strategy hypothesis, scramble competition hypothesis, forage selection hypothesis, activity budget hypothesis and social preference hypothesis (Ruckstuhl, 2007). Social segregation is described by several of these hypotheses and has received considerable attention among behavioural ecologists.

Habitat segregation has been suggested to occur as the consequence of sexually size dimorphic male and females by several hypotheses. These includes: sex differences in reproduction investments and risk taking (predation risk/reproductive strategy hypothesis); differences in retention rate and /or passage rate and digestion efficient due to difference in body size between sexes (forage selection hypothesis) and sex difference in tolerance to lower forage biomass due to allometric relationship of body size to bite size (scramble competition hypothesis). These hypotheses have been collectively classified as habitat segregation hypotheses (Table 1.1).

Similarly, hypotheses for social segregation address differences in activity budget, social preference and social associations of sexually size dimorphic male and female mammals (Bon and Campan, 1996; Ruckstuhl, 2007). Sexually size dimorphic mammals are predicted to live in different social groups (same sex groups), when size/sex differences in time allocation for various activities and/or movement pattern occurs (activity budget hypothesis) (Ruckstuhl, 2007). Socialisation, passive learning and similar needs may lead to associations of individuals of the same or similar age/sex class. This would lead to animals to living in different social groups (social preference hypothesis). Both the activity budget hypothesis and the social preference hypothesis will result in social segregation, and are therefore classified as social segregation hypotheses (Table 2.2).

The general prediction from these five hypotheses is that, the degree of sexual segregation increases with increase in sexual body size and/or mass dimorphism (Ruckstuhl and Neuhaus, 2000). Habitat segregation is predicted to occur or be more pronounced in extremely sexually size dimorphic species (Ruckstuhl and Neuhaus, 2000). Social segregation hypotheses predict incompatibility of activity budgets between individuals of different age-sex classes, thus sexual segregation should be greater in species with strong sexual size dimorphism and diverse group composition (Conradt, 1998; Ruckstuhl and Neuhaus, 2000; Ruckstuhl, 2007). Broadly, sexual segregation in any form is more likely and is expected in species with sexual size dimorphism and should be uncommon or absent in species with slight size dimorphism and in monomorphic species (Ruckstuhl and Neuhaus, 2000; Section 1.2.2.3, Figure 1.1).

All five general hypotheses of sexual segregation in mammals were developed and tested in ungulates (Table 1.1; Table 1.2). Like ungulates, yellow baboons are sexually size dimorphic mammals, with adult males being as twice heavy as adult females (Cawthon, 2006; Table 1.3). Because of this sexual size difference, yellow baboons like ungulates; would expected to show strong sexual segregation based on the predictions of sexual segregation hypotheses. But contrary to these predictions, yellow baboons stay in permanent stable mixed-sex troops without apparently exhibiting the characteristics related to sexual segregation as typically defined. Apart from yellow baboons, other diurnal primate species live in permanent mixed sex groups that coordinate locations and activities despite exhibiting pronounced sex size dimorphism (Watts, 2005). Moreover, sexual segregation occurs in some species such as temperate bats (*Myotis daubentonii*) (Altringham et al., 2005) and in Iberian noctule bats (*Nyctalus noctule*) (Popa-Lisseanu et al., 2009) in absence of sexual size dimorphism. The lack of classic sexual segregation in highly social group-living diurnal primates with clear and pronounced sex/size dimorphism presents a problem for the existing theoretical structure.

The hypotheses developed to predict and explain strict segregation between sexually dimorphic animals are based on studies from ungulates. Ungulates are homogenous feeders only browsing or grazing. Such feeding and foraging adaptations limit alternative feeding options available to different age/sex classes. Thus competition between sexes will be heightened and due the nutritional and energy demands related to body size differences result in different social groups or the use of occupy different habitats. Species like yellow baboons are not faced with such problem to the same degree constraints. They can feed from a wide variety of both plant and animal species (Post, 1982, Norton et al., 1987; Barton et al., 1993). This dietary breadth provides a range of dietary options (Altmann, 2009). These multiple feeding options include varied food packages and processing techniques as well as varied food types and parts. Through this yellow baboons not only fulfil nutritional requirements of animals with differed body size living in mixed-group but also reduce resource intra specific competition. This then can lead to sexual segregation within permanent mixed sex troops.

Feeding behaviour of yellow baboons has been described in a number of studies in Mikumi (Rhine and Westlund, 1978; Post, 1981; Rhine et al., 1986; Rhine et al., 1989). Most of these studies have not considered adult sex differences in feeding. When sex differences have been addressed, sampling has tended to focus on time spent feeding and intake rate. Few meaningful differences between sexes in adult baboons have been documented. None of these studies have attempted to find age and size (age-sex) differences in feeding behaviour related to troop living except to test for effects of intra sex feeding competition within troops.

Sexual segregation has been explained to occur either as social segregation or habitat segregation (Main et al., 1996; Conradt, 1998; Ruckstuhl, 1998; 2007; Ruckstuhl and Neuhaus, 2002). Group cohesion in contrary, has been explained to be possible through activity synchronization between members within the troop (Conradt and Roper, 2000;

Ruckstuhl, 2007). So the inherent conceptual conflict is between the asynchrony of sexual segregation and the synchrony of permanent groups. However, this study make clear that sexual segregation may occur through subtle asynchronies in feeding activity and spatial positioning while maintaining the synchronies of groups (Chapter 4-6). Additionally, assumptions of cohesive stable mixed-sex troop may not always be met (Chapter 6 section 6.3.4).

The eclectic omnivory of yellow baboons is shown in Chapter 3. Chapter 3 describes the diversity of feeding options available to baboons and the pattern in which these options are used overall. Baboons can and do feed on differing food sources, a multiplicity of plant and animal species from multiple types of plant. Importantly they feed on many different parts of plants often from the same plant species. Despite a large number of species used, the overall diet was dominated by few tree species, a large range of grass species and invertebrates. Seeds (frequently grass seed heads) and fruit were predominate in the diet. Invertebrates, leaves and exudates were also important. Baboons used different food packages but the most common package was the simplest to harvest and consume requiring little processing while containing limited biomass. Chapter 3 also showed that space use by baboons was 3-dimensional with both ground level and canopy levels being used extensively.

Chapter 4 supports the prediction that adult males, adult females and sub adult males subtly differ in their feeding behaviour. These differences were generally in line with expectation; adult females and subadult males showed similar patterns that differed from adult males more especially in use of food sources, types, parts and packages. There were meaningful differences between age sex class for the dietary components plants, grasses, exudates and packages. Grass use varied in line with expectations; no differences between adult females and subadult but these classes used grasses significantly more than adult males. Exudate was the only food part that showed a significant difference by age-sex class and this was opposite to expectations, with males using significantly more exudate then the other classes and adult females using more the subadult males. The competitive acquisition of this resource by males over other classes is suggested as the reason for this pattern. The higher rate of use on various food items within follows by adult males and sub adult males may indicate their foraging efforts accord with literature that associate this with nutritional requirement influenced by their body sizes (Clutton-Brock, 1977; Gordon and Illius, 1987; Milton, 1993; Rothman et al., 2014).

Finally, food packages use differs in line with expectations, with adult females and subadult males using significantly more unitary food package and small single process food items than adult males. Most of food items associated with such packages (i.e. unitary and single process packages) were small food items which represent low processing cost which can be consumed rapidly and repeatedly, however had lower protein but higher fibre contents hence considered had low energy return (Barton and Whiten, 1994). Such food packages were appropriate for smaller bodied primates (adult females and subadult males) in trade off of their nutritional and energy demand for their safety (predation risk hypothesis: Main and Coblentz, 1990; Main et al., 1996; Ruckstuhl and Neuhaus, 2002; Hay et al., 2008).

The dietary profile of yellow baboons described by this study (Chapter 3) indicates that, unlike other sexually size dimorphic mammals such as ungulates, yellow baboons could segregate by age and sex within permanent mixed-sex troops. Sexual segregation in baboons can occur through subtle differences between age-sex classes in the use of differing components of amount of the diet. Variation in use of food source, species, types, parts and packages by differing age-sex classes would allow within group diet segregation. This was measured and tested as diet components consumed within a given time (measured by mean percent intervals per feeding follow)(chapter 4). Smaller sized individuals (adult females and subadult males) fed significantly more from plant sources, particularly on roots and seeds and from grasses and shrubs compared to large sized individuals (adult males). Such subtle differences in feeding behaviour can allow individuals to fulfil their nutritional and energy needs while within mixed-sex troop.

Chapter 5 demonstrated age-sex classes differences in spacing behaviour especially during feeding; however the differences are less in line with expectations. Proportionally all age-sex classes use ground and canopy height more for feeding than other vertical height categories. However, adult males and females used ground level in significantly more intervals within follow than sub adult males. Moreover, adult males fed in higher canopy in significantly fewer intervals within follow than subadult males and this was marginally insignificant with adult females. Lighter body weight due to smaller body size (Gebo and Chapman, 1995), higher nutritional content, lower level of toxin and tannin in fruits at higher height (Houle et al., 2014) have been associated with the more use of higher height levels by smaller bodied animals than larger bodied animals. Food abundance at ground level and safety of infant have been associated with the more use of ground level by adult females than subadult males, whereas males' consorting behaviour has been accredited for the insignificant difference with adult females in the use of ground level for feeding

(Palombit et al., 1997).

When feeding on the ground, adult females and sub adult males feed more at the centre of the troop than adult males, while the difference between adult males and females being at the centre mass of troop was insignificant, it was very significant between adult males and subadult males. Reduction of predation risk and need to feed and move in safe places are associated with higher proportion and rate in use of centre of the troop by adult females and sub adult males. This accord with the progression order hypothesis (Rhine, 1975; Altmann, 1979) and spacing behaviour as explained by Collin (1984). Moreover, male investment in access to mating partners, hence forging "friendships" with prospective partners may explain the insignificant difference in use of centre of troop mass between adult males and females (Trivers, 1972; Palombit et al., 1997). The fact that, adult females and subadult males were significantly less often away from the troop as compared to adult males in line with expectation. Reduction of predation risks and need to forage in safe place is associated with this pattern (Collin, 1984). Similarly, as was for the expectation of this study, adult males being more often in front is associated with their protection role in the community as explained by the progression order hypothesis (Altmann, 1979).

Lastly, chapter 6 showed that there were subtle differences in activity budget between members of differed body size. The chapter showed that in line with prediction, adult females and subadult males allocated significantly more time to move than adult males; while adult males did not differ from subadult males in time allocated to vigilance, they significantly allocated more time to this behaviour than adult female. Overall results from this chapter indicated that, there was no sex or size related significant direction of difference in time allocated for feeding, resting and socializing. However, within follows adult females and sub adult males allocated more time to feeding, while adult males allocated more time to resting. This suggest that, the observed significance age-sex difference in time allocated for these activities are influenced by other ecological and /or physiological variables rather than age, sex and size differences. Furthermore, within follows adult males allocated more time to resting and vigilance while adult females and sub adult males allocated more time to move and feed. In a single follow all age-sex classes most frequently were feeding, moving, resting and being vigilance, however adult females and sub adult males performed more activities in a single follow than adult males. Selection of higher quality diet influenced by nutritional requirement of smaller bodied animals (forage selection hypothesis) is associated with more time allocated to feeding and moving and performance of more activities in a single follow by adult females and sub adult males (Muruthi, 1988; Conway, 2009; Radek, 2014). Additionally, reproductive costs (need of more protein for lactating and pregnant females) (Silk, 1987; Muruthi, 1988) and dominance position (rank) (Rasmussen, 1986) is associated with increased time for feeding observed in adult females. More time allocated to resting by adult males is associated with lower metabolic rate (Kleiber's' law) and digestion efficient associated with allometric relationship of body size and retention rate of larger bodied animals (Jarman-Bell principle: Mysterud, 2000). Thus larger bodied animals will spent more time resting while digesting the food (Conradt, 1998; Ruckstuhl, 1998; Ruckstuhl and Neuhaus, 2002; Michelena et al., 2006; Barberia-Perez et al., 2007). More time allocated to vigilance by adult males has been also reported in other studies of primates (van Schaik and Noordwijk, 1989; Cowlishaw, 1998; Smith et al., 2004), and is associated with protective role of males against potential predators (anti-predatory role) and/or social role as scanning around for potential invading males.

7.3 Limitations and further research

This study was designed to measure the occurrence of the many multiple components of feeding and foraging behaviour as well as the overall activity budget. It was also designed to sample multiple subjects as evenly as possible over all temporal periods evenly and repeatedly. This approach necessitates simple sampling measures such as 1/0 and instant sampling. It relies on many repeated short samples (follows). Consequently, this study did not measure time spent in behaviour directly or the number of bouts or bout rates directly. The relative rate of use and frequency of encounter per unit time can, however, indirectly indicate time spent in behaviour such as feeding, and can be used as a good measure for foraging and feeding effort (Rothman et al., 2014).

Evaluating nutritional intake and measuring abundance and availability of food was also not possible in this study and may not be possible in the extensive complex environments of Mikumi (Clutton-Brock, 1977; Chivers, 1998). Thus food intake for any dietary component could not be evaluated in terms of nutritional intake relative to age-sex class and body size (Clutton-Brock, 1977; Gordon and Illius, 1987; Milton, 1993; Rothman et al., 2011).

This study did not consider variation in behaviour in relation to female reproductive status. Reproductive constraints on adult females (Silk, 1987) and need of additional energy for maturing subadult males might be explain the general failure to find meaningful differences in feeding between the sexes classes in yellow baboons (e.g. Barton 1989. Rhine et al., 1986; Rhine et al., 1989). These two age-sex classes remain similar in size or most of the male subadult phase, thus we predicted that adult females would have similar energetic demands as subadult males, hence would be expected to address their similar needs in similar ways and which would differ from adult males.

The relationship between adult female reproductive condition and variation in food intake could be investigated in the future (Silk, 1987; Agetsuma. 2001). Similarly behavioural variation within and between seasons and between age sex classes were not assessed in this study analysis, but could be.

The choice of Subadult males as a comparator with adult females to assess body size effects should be further assessed in terms of growth rate and energetic requirements in relation to females. Other factors such as food patch type and size and intraspecific competition within and between age-sex classes should also be considered and incorporate into a more complete model of how segregation by size and sex can and perhaps must operate in cohesive permanent mixed sex groups of sexually dimorphic animals.

The analyses of this study were designed to confirm the feasibility and likelihood of within group sexual segregation in yellow baboons. It was also intended to illuminate avenues for more detailed tests for sexual segregation within permanent groups some of which are discussed above.

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APPENDICES

Appendix 2.1 Number of subjects followed each month in the two troops (Viramba 5 and 6) from mid-August, 2010 to November 2012.

		Viramba 5				Viramba 6			
Year	Months	Adult female	Adult males	Sub adult males	Troop size	Adult female	Adult males	Sub adult males	Troop size
2010	Aug	9	4	6	38	15	8	5	43
	Sept	9	4	6	37	17	7	5	42
	Oct	9	4	6	37	18	7	6	46
	Nov	9	5	6	38	18	7	5	44
	Dec	9	5	6	35	18	8	4	44
2011	Jan	9	4	6	33	19	8	3	43
	Feb	9	4	6	34	19	8	3	43
	Mar	9	6	6	35	19	8	3	43
	Apr	9	4	6	34	18	6	3	41
	May	9	5	6	34	19	6	3	43
	Jun	9	5	6	34	18	5	3	42
	Jul	9	5	6	36	18	5	3	42
	Aug	9	6	7	36	18	5	3	42
	Sep	9	5	6	36	18	5	3	42
	Oct	-	-	-	-	-	-	-	-
	Nov	-	-	-	-	-	-	-	-
	Dec	8	5	6	35	16	4	3	43
	Jan	8	5	6	39	16	4	3	43
2012	Feb	8	5	5	37	16	4	3	42
	Mar	7	5	4	35	17	4	1	42

	Apr	7	4	2	32	17	4	4	41
	May	6	3	4	31	16	6	4	40
	Jun	6	4	4	32	16	6	4	39
	Jul	7	3	4	31	14	7	4	39
	Aug	7	4	4	30	14	7	4	38
	Sep	8	4	5	25	13	6	4	35
	Oct	-	-	-	-	-	-	-	-
	Nov	8	3	4	24	14	7	4	37

Appendix 2.2 List of all individuals in Viramba 5 as of 1st July 2012: data were collected on Adult Males, Females and Sub Adult Males only.

ID= Individual identification number; **AGE/SEX CLASS**= see Table 2.3 for code number; **BIRTH/TRANSFER**= year and date (Julian calendar) in which individual was born or migrated to troop (e.g. for Uliza: 97325 means she was born in 1997, on 325 day of the year), T= Transfer; **MINUTES OF DATA**= Time in minutes individual was followed for data collection. * = Individual was not in the troop by the end of study (November 2012): **= Individual was promoted to Adult female before the end of study. **Total time** (Minutes for data collection; **Adult Females** = 11,888 min: **Adult Males**= 4,960 min: **Sub Adult Males**= 6, 352 min.

AGE GROUP	ID	AGE/SEX CLASS	BIRTH/ TRANSFER	MOTHER	MINUTES OF DATA
ADULT FEMALE					
*Kitovu	79	3	91105	Ubavu	336
*Uliza	98	3	97325 (1st obs. 331)	Swali	1536
*Johari	99	3	98258	Kitovu	528
Dadisi	302	3	99065 (1st obs. 79)	Siafu	1552
Manyoya	305	3	00052	Kitovu	1712
Chelewa	312	3	02232	Kitovu	1600
Zumaridi	317	2	04226	Johari	1536
*Pili pili hoho	319	2	05162	Kitovu	784
Kangaruu	320	2	05204	Dar	1568
ADULT MALE					
Skauti	198	6	T. 09 (09145)	-	976
Steve	277	6	1st T. 08007; 2nd T.12148 (V6)	-	768
Tukio	278	10	T. 08 (08019)	-	1360
*Mkono II	288	7		-	768
*Rangi	293	6		-	32

*Njano	294	6		-	400
*Endesha	296	6		-	48
*Ramisi	297	6		-	592
*Sababu	299	6		-	16
Subadult males					
*Hoja	194	5	03347	Uliza	192
*Baraka	196	5	04046	Heshima	432
*Dafina	401	5	04197	Dadisi	592
Shujaa	404	4	05072	Shuku	1472
Makaroni	408	4	05225	Malaika	1376
Ufaransa	410	4	06206	Johari	1056
Ujerumani	411	4	06213	Kitovu	1232
LARGE JUVENILE FEMALE					
**Chutama	332	2	08032	Chelewa	352
**Utafiti/Fanya	333	2	08083	Uliza	128
**Uhuru	335	2	08084	Johari	256
Lilian	340		08156	Mwenzi	
Uzima	342		08320	Mwanamifu	
Kulia	344		09017	Dadisi	
LARGE JUVENILE MALE					
Garrett	422		08160	Shuku	
Bunifu	424		08235	Kirefu	
Darwini	425		09133	Kitovu	
Udzungwa	426		09201	Uliza	
Jumamosi	427		09234	Johari	
Chema	431		09314	Chelewa	

SMALL JUVENILE FEMALE					
Macheo	351		11143	Manyoya	
SMALL JUVENILE MALE					
Kanganya	448		11163	Kangaruu	
INFANT FEMALE					
Cheza	357		11209	Chelewa	
Zuhuru	359		12005	Zumaridi	
INFANT MALE					
Ulipaji	449		11190	Uliza	
Dandia	453		11263	Dadisi	

Appendix 2.3 List of all individuals in Viramba 6 as of 1st July 2012: data were collected on Adult Males, Females and Sub Adult Males only.

ID= Individual identification number; **AGE/SEX CLASS**= see Table 2.3 for code number: **BIRTH/TRANSFER**= year and date (Julian calendar) in which individual was born or migrated to troop (e.g. for Uliza: 97325 means she was born in 1997, on 325 day of the year), T= Transfer; **MINUTES OF DATA**= Time in minutes individual was followed for data collection. * = Individual was not in the troop by the end of study (November 2012); **= Individual was promoted to Adult female before the end of study. **Total time** (Minutes for data collection: **Adult Females** = 25,066 min: **Adult Males**= 8,032 min: **Sub Adult Males**= 5,290 min.

AGE GROUP	ID	AGE/SEX CLASS	BIRTH/ TRANSFER	MOTHER	MINUTES OF DATA
ADULT FEMALE					
*Hayupo	81	3	93043	Rahisi	896
Kirefu	86	3	94030	Kikubwa	1584
Kuongeza	89	3	T.94294	Kuvimba	1536
Kucheko	90	3	T.94294	Kuvimba	1408
*Shuku/Sifuri	91	3	94236	Swali	154
Huruma	92	3	95188	Heshima	1840
Dar	95	3	96336	Kikubwa	1760
Amka	301	3	98355	Kuongeza	1760
*Malaika	303	3	99300 (1st obs 305)	Kuvimba	96
Upende	306	3	00062	Heshima	1600
Kibeti	310	3	01365 (1st obs. 024)	Kirefu	1824
Mwenzi	311	3	02166	Heshima	1056
*Shiriki	313	2	02287	Shuku	176
Angaza	318	02-Mar	04249	Amka	1648
Kiputo	323	2	06074	Kirefu	1648
Italia	325	2	06195	Upende	1552
Tamu	328	1	06254	Kuchecko	1520

Hitaji	330	2	07171	Hayupo	1664
*Bonde la Ufa	331	3			528
Uduvi	337	1	08104	Kibeti	800
ADULT MALE					
*Pumba	267	10	T.05 (Jun 24)	-	32
Karanga	269	10	T. 05 (Aug 5)	-	1616
Evander	275	10	T. 07 (07364)	-	1856
*Tutu	283	7	T. 09053	-	16
*Dereva	286	6	T. 09250	-	16
*Epiana	290	6		-	48
Korosho	291	7	T. 10 (10189)	-	1728
*Pekecha	292	6		-	240
Nyasi	295	7	T. 10259	-	1648
Ungana	501	6	T. 12085	-	96
Wasita	502	6	T. 12085	-	368
Nungunungu	503	6	T. 12180		128
*July	504	6	12193 (Jul 11)	-	240
Subadult males MALE					
Tekenya	197	5	04071	Kucheeko	1856
*Utulivu	400	4	04192	Huruma	918
(Kimbia) Mpunguo 2	414	10	07	-	560
(Elewa) Makende 2	416	10	07	-	656
*Baruti	436	6		-	756

Bendera	440	7	T. 10225		544
LARGE JUVENILE FEMALE					
**Alfajiri	327		06235	Amka	16
LARGE JUVENILE MALE					
Hodi	430		09279	Huruma	
SMALL JUVENILE FEMALE					
Akili	347		10042	Amka	
Samiani	348		10093	Shriki	
Barizi	350		T.10225	Bonde La Ufa	
SMALL JUVENILE MALE					
Harakati	439		10253	Hayupo	
Dahari	446		11116	Dar	
Kiroja	447		11126	Kirefu	
INFANT FEMALE					
Amsha	355		11237	Amka	
Kitoto	358		11270	Kiputo	
Huba	360		12034	Hitaji	
Itibari			12155	Italia	
INFANT MALE					
Upeo	451		11248	Upende	
Kumbatia	457		12040	Kuongeza	

Appendix 2.4 An example of daily animal follow rota for V5.

WEEK DAY	7:00-9:30	9:30-12:00	12:00-14:30	14:30-17:00
1	Ramisi	Kitovu	Uliza	Pili pili Hoho
	Tukio	Endesha	Mkono II	Chelewa
	Steve	Makaroni	Dafina	Skauti
	Kangaruu	Manyoya	Johari	Baraka
	Dadisi	Shujaa	Hoja	Zumaridi
2	Kitovu	Ramisi	Pili pili Hoho	Hoja
	Dafina	Uliza	Tukio	Mkono II
	Manyoya	Zumaridi	Dadisi	Steve
	Chelewa	Johari	Baraka	Kangaruu
	Makaroni	Skauti	Shujaa	Endesha
3	Shujaa	Dafina	Steve	Uliza
	Hoja	Dadisi	Zumaridi	Ramisi
	Johari	Baraka	Kitovu	Manyoya
	Endesha	Mkono II	Skauti	Tukio
	Pili pili Hoho	Chelewa	Kangaruu	Makaroni
4	Uliza	Pili pili Hoho	Ramisi	Kitovu
	Baraka	Steve	Manyoya	Shujaa
	Zumaridi	Hoja	Chelewa	Dafina
	Mkono II	Kangaruu	Makaroni	Johari
	Skauti	Tukio	Endesha	Dadisi

Appendix 2.5 Data sheet used for collection of behavioural observations.

SUBJECT:	ID:	AGE/SEX:	CYCLE:	CONSORT:	DATE:	TIME:
LOC: /	HABITAT: /	POSITION: /	WEATHER: /			

SEARCH								
Investigate								
Locate								
Harvest								
Abandon								
Acquire								
Process1								
Remove								
Process 2								
Examine								
Reject								
Intake								
Intake chew								
Carry								
Supplanted/abandon								
Disguise								
Take over								
Pouch fill								
Pouch process								
pouch chew								
Patch shift								
Shift								
Move								
Visual TROOP								
Visual AWAY								
SENTRY								
Rest/Inactive								
AGO + or -								
AFF + or -								
SEXUAL + or -								
Groom + or -								
Self-groom/scratch								
Groom Intake								
Drink								
OTHER								
POUCH USE								
COVER								
# NEIGHBOUR								
CLOSE NEIGHBOUR								
# ASSOCIATE								
MISS DATA								
HEIGHT								
PATCH								
Beh.on inst.missed								

FOOD LIST

No.	Part	Package	Burnt	Species
1				
2				
3				
4				
5				
6				
7				
8				
9				
10				
11				
12				
13				
14				
15				
16				

Appendix 2.6 Protocol used with data sheet in Appendix 2.4.

RECORD AT START OF FOLLOW:	
SUBJECT	Name of focal baboon (with TROOP V5 or V6 in brackets)
ID	ID number of focal baboon
AGE/SEX	1 nulliparous female (no infant yet), 2 Premaporous female (given known birth once), 3 multiparous female (more than 1 birth), 4 natal male aged 5 to 7 years. 5 natal male over 7 years. 6 recent transfer male (less than 1 year in troop). 7 transfer male 1-2 years in troop. 8 transfer male 2-3 years in troop. 9 transfer male 3-4 years in troop. 10 transfer male over 4 years in troop.
CYCLE	1 flat before menstruating. 2 menstruating 3 flat after menstruating. 4 going up. 5 full swell. 6 going down, 7 pregnant. 8 lactating
CONSORT	ID number of companion if the focal subject is consorting with another troop member
DATE	Julian date and normal date
TIME	Use 24 hour clock
RECORD AT START AND END OF FOLLOW:	
LOC	Grid map location at the start of follow and at the end , e.g. 011430 to 011432.
HABITAT	1 grassland. 2 wooded grassland, 3 open grassland. 4 woodland, 5 closed-canopy woodland, 6 riverine thicket, 7 riverine forest, 8 waterhole, 9 korongo. 10 highway
POSITION	1 Centre of the troop, 2 Troop peripheries 3 In front of troop. 4 behind the troop, 5 away from. Troop (this is defined similar to code 100 for number of neighbours)
WEATHER	10 sun/clear. 20 sun/hazy, 30 cloud/light, 40 cloud/heavy, 50 rain/light 60 rain heavy;

	X0 no wind. **X1** light wind. **X2** heavy wind, e.g. a sun/clear day with light wind = 21
RECORD USING 1-0 AND INSTANTANEOUS: Behaviour is ticked in the interval and/or encircled on the instant if it occurs, unless instructed otherwise. *for these behaviours completed food list table with details of food involved and recorded reference number from food list in interval.	
SEARCH	General search - focal animal actively searches for food: includes moving around with a clear foraging purpose. The subject can do a food scan i.e. looking with eyes for food or a hand search, such as sweeping across grass with their hand. This field requires only a tick (√) because the subject might find any kind of food items.
INVESTIGATE*	Search for specific food - Focal subject searches within a food micro patch for a specific food item. e.g. it picks up a leaf and look inside it to check if it contains an insect larva. This behaviour can easily be confused with "SEARCH" but the difference in terms of our data sheet is that in this field we can record which food item the subject was actually searching for. For example the subject sweeps across leaves under *Brachystegia* tree= the subject is definitely searching for *Brachystegia* seeds or pods. This behaviour can also be wrongly confused with EXAMINE (e.g. smelling amarula fruit to see if it is ripe or not). INVESTIGATE is in a specific food micro patch and is about searching to find something specific- but the package is not yet in the subject's hands and subject does not yet know if it is there or not (has not yet LOCATED it).
LOCATE*	focal subject knows where the package/item/food patch is and is about to ACQUIRE or HARVEST it.
HARVEST*	focal animal tries to ACQUIRE the food but has to make an effort to get it, e.g. digging out root, pulling branch towards mouth. Harvesting represents any behaviour which will result in the animal acquiring a food item.
ABANDON*	focal animal abandons food item or package before acquiring it after unsuccessful effort of harvesting it, e.g. Focal subject attempts to catch a butterfly but the insect gets away and after chasing the baboon gives up.
ACQUIRE*	focal animal now possess a food package. It got hold of it by simply picking it up from the ground or similar easy behaviour that did not require any effort (therefore not HARVEST). The package could need processing or not so the next step will be to PROCESS or INTAKE.
PROCESS 1*	Focal animal has acquire (or harvested) a food package and now process it in order to get hold of the food that the package contains. Many packages do not need any processing, for example small insect is swallowed as whole or grass stem simply bitten off and intaken. Many involve several processing behaviours.
REMOVE*	focal animal get hold of the food item by removing it out of package, e.g. a seed from a pod
PROCESS 2*	Focal subject process the removed food item in order to intake

	displaying, mounting, teeth baring, eye staring, chasing etc.. This can be either *performed* (+) by focal animal or *received* (-).
AFF + and	affiliative behaviour toward other troop members. *e.g. grunting, greeting, touching, hugging, including play (for Subadult maless) etc.* Can be either *performed* (+) by focal animal or *received* (-) or be mutual
SEXUAL + and	Focal subject either performs (+) or receive (-) a sexual type of behaviour, or it is mutual, like copulation (+-). These including female presents her swelling to male, male investigates females' swelling (either by looking or swelling) and other behaviour that can be interpreted as sexual.
GROOM + or -	giving or receiving groom (ID # of other troop member?)
GROOM/SELF SCRATCH	grooming/scratching self
GROOM INTAKE	tick harvested from skin (either of itself or of another troop member) and eaten was not under feeding related behaviour, was under general behaviours
DRINK	ingest of water
OTHER	If the focal animal has performed a behaviour that is not in the list, example of this behaviour are such as regurgitate, alarm barking, urinating etc.
RECORD ON THE INSTANT ONLY:	
POUCH USE	estimate of fullness of pouch, values: **0** 0%, **1** up to 25%, **2** up to 50%, **3** up to 75%, **4** up to 100% . Give a value for each check pouch (left/right)
COVER	From the perspective of a baboon, what cover does the focal animal have in terms of average vegetation. **1** 67-100% visible, **2** 33-66% visible, **3** 0-33% visible
NEIGHBOURS	number of neighbours within 5m, the 5m radius are three-dimensional for both when the focal is on the ground and on the tree. **100**= focal subject is lone and 200+m away from the edge of the group, in this cane no nearest neighbor. **102**= subgroup with two members **103**= subgroup with 3 members..... 1 indicate subgroup and the number after indicate the number of individuals in the sub group, e.g. **125**= subgroup with 25rindividuals. The minimum code is **102**.
CLOSE NEIGHBOUR	ID of individual who is closer to the focal subject within 5m radius
ASSOCIATE	Closest neighbours which are at similar distance from focal subject, for instance when focal subject is groomed by one member and it turn, the focal subject grooming another member. ID numbers of closest neighbours is recorded
MISS DATA	number of 30 second blocks missed within 2 minute intervals. **1**=>30sec, **2**=>60 sec, **3**=>90, **4**=>120 sec (full 2 mins missed)
HEIGHT	**0**=Korongo/below ground, **1**=up to 1 m from ground, **2**=up to 2 m from ground, **3**=beyond 2 m from ground

PATCH	1=Trees Single Species, 2=Trees Multiple Species, 3=Trees Single Species with other discrete, 4=Trees Multiple Species with other discrete, 5=Discrete Single Species, 6=Discrete Multiple Species, 7=Single Species Amorphous, 8=Multiple Species Amorphous, 9=Foraging Single Species, 10=Foraging Multiple Species no trees, 11=Foraging Multiple Species including trees, 12=Not in patch, 13= Highway, 14=Elephant dung, 15=Water If on the instant any patch in which any member of the troop is, is burnt, add 9 at the end of the patch number, e.g. *they are eating on the burnt tamarind tree*= 19 instead of 1. If troop is using two different patches at the same time, then they are both recorded with a comma separating them, e.g. 13, 15= some of troop members are on highway and other are at the water hole (drinking).
BEH. ON INSTANT MISSED	The behaviour of the focal animal on the instant was missed (e.g. not visible).
*RECORD FOR BEHAVIOURS MARKED WITH ON FOOD LIST: *I	
NO.	Reference number (to be added to appropriate interval)
PART	1 Fruits 2 Fruits, flesh, fluid 3 Leaf 4 Flower 5 Inflorescence (flower + all its connections) 6 Bud 7 Stem, connective tissue or structures 8 Grass leaf/stem 9 Grass root, corn, bulb/tubers 10 Grass seeds or seed heads 11 Seeds 12 Seed heads 13 Pods 14 Roots 15 Sedge bulb 16 Bark, skin, casing 17 Exudates 18 Invertebrates 19 Vertebrates 20 Vertebrates/invertebrates/parasite products 21 Insect larvae
PACKAGE	1 Unitary small No parts removed or processed, consumed as a single bite (e.g. small insects, flowers, fruits, sap clumps) 2 Unitary large As above but too large for single bite, it require multiple bite to consume all, e.g. large insects 3 Unitary mixed Have more than one food types but all consumed in a single bite (even large) and no processing is required 4 Unitary clump Single bite package (even large), requires no processing but contains multiple units of the same food i.e. numerous in number (e.g. grass seeds). 5 Single process item-Small Food is processed once to get the edible part which is consumed in a single bite (e.g.

	Seeds from pods) Tylosema pod for example 6 Single process item-Large As above but the food requires multiple bites due to size. e.g. fruit flesh, fluids. larger roots and bulb. Process may include chewing to de-skin, or remove inedible items. or cleaning to remove soil 7 Single Multiple process items-Small Package is processed once to get multiple small items. consumed either individually or in clumps. e.g. single seeds or multiple seeds in one consumption 8 Single Multiple process items-Large As above but require more than one bite to consume each item 9 Multiple process items-Small Package involve process to get the edible part, but the parts requires further process before consumed. it may involves removing and peeling (e.g. dry tamarind seeds, no pulp in fruit) 10 Multiple process items-Large As above but edible part requires multiple bites to consume it all 11 Multiple multipleprocess item-Small Package requires many single bites to get to edible part which in turn requires multiple process before consumed 12 Multiple multipleprocess item-Large Package requires many single bites to get to multiple edible part which in turn each requires multiple process before consumed 13 Mixed process and Multiple process Different food parts consumed from the same package potentially at the same time. Food parts may require further processing or not once processed from package. e.g. sausage fruits 14 Elephant dung Special package that could offer many different food parts and present different processing problems. Food parts found inside it are described without looking at processing details. 15 Unknown package. Package does not fit in any of above
BURNT	If the food part (type) consumed is burnt then put a tick (√). and leave blank if part consumed is not burnt
SPECIES	Write the species name from which the consumed food type was obtained (plant or animal). If the food type is obtained from the highway write the species name of its origin

Appendix 3.1 List of different plant and animal species consumed by yellow baboons (ARO = Anthropogenic originated from the road)

Trees species	**Forbs species**	**Shrubs species**	**Animals species**
Acacia sieberiana	*Aloe spp*	*Cissus rotundifolia*	*Achatina fulica*
Acacia spp	*Amarantha (ARO)*	*Cassia mimosoides*	Bird eggs
Afzelia quanzensis	*Arachis Spp (Peanuts) (ARO*	*Combretum hereroense*	*Coptotermes formosanus*
Balanite aegyptiaca	*Asarum caudatum*	*Combretum molle*	*Lasius niger*
Bauhinia tomentosa	*Balpharia balpharus*	*Combretum mossambicensis*	*Loxodonta africana (dung)*
Berchemia discolor	*Capparis tomentosa*	*Combretum sp*	*Mabuya striata*
Brachystegia bussei	*Carex spp (Sedge)*	*Diospyros usambarensis*	*Mantis religiosa*
Cassia abbreviata	*Clerodendrum ternatum*	*Domestic foods*	*Nymphalidae spp*
Cissus sp	*Commelina erecta*	*Grasses*	*Ommatoiulus spp*
Citrus sinensis (ARO)	*Crotalaria sp*	*Grevia egglingii*	*Periplaneta spp*
Dalbergia melanoxylon	*Cucumis hirsutus*	*Heteropogon contortus*	*Phacochoerus africanus*
Dioscorea sansibarensis	*Cyphostemma gigantophyllum*	*Hyparrhenia spp*	*Phasmatodea spp*
Diospyros kirkii	*Harrisonia abyssinica*	*Lonchocarpus capassa*	*Redunca redunca*
Diospyros mespiliformis	*Hibiscus rosa-sinensis*	*Maerua spp*	Unknown invertebrate
Euphorbia hirta	*Hoslundia oppositifolia*	**Non plant or animal Road food**	Vertebrate and/or their products
Ficus platyphylla	*Hygrophila auriculata*	*Oryza glaberrima (ARO)*	

Haplocoelum inopleum	*Ipomoea spp*	*Pennisetum glaucum*	
Kigelia africana	*Lannea schweinfurthii*	*Phragmites spp*	
Lannea Stuhlmanni	*Lantana camara*	*Rottboellia cochinchinensis*	
Mangifera indica (ARO)	*Lantana rugosa*	*Saccharum officinarum (ARO)*	
Markhamia spp	*Launaea cornuta*	*Securinega virosa*	
Musa spp (banana) (ARO)	*Phaseolus vulgaris (ARO)*	*Sorghum arundinaceum (ARO)*	
Pericopsis angolensis	*Rhynchosia spp*	Spaghetti	
Pseudolachnostylis maprouneifolia	*Sida acuta*	*Sporobolus fimbriatus*	
Psidium spp (Wild guava)	*Solanum lycopersicum (ARO)*	Stiff porridge (Ugali)	
Pteleopsis myrtifolia	*Solanum tuberosum (ARO)*	*Themeda triandra*	
Sclerocarya birrea spp caffra	*Tephrosia spp*	Unknown grass	
Senna siamea	*Tragia pumila*	*Zea mays (Corn) (ARO)*	
Sterculia africana	*Trifolium spp*		
Strychnos madagascariensis	*Tylosema fassoglensis*		
Tamarindus indica	Unknown herb		
Terminalia mollis	Unknown Liana		
Xeroderris stuhlmannii	*Vernonia spp*		
Zanthoxylum chalybeum	*Vigna spp*		

Appendix 3.2 List of frequently consumed plant species

	Number of follows	Percent	Number of intervals	Percent
Unknown grass	690	23	3146	21.14
Tamarindus indica	375	13	2155	14.48
Acacia sieberiana	119	4	1242	8.35
Kigelia africana	162	5	1215	8.17
Rottboellia cochinchinensis	213	7	842	5.66
Ficus platyphylla	89	3	523	3.51
Sclerocarya birrea spp caffra	104	3	482	3.24
Brachystegia bussei	58	2	419	2.82
Xeroderris stuhlmannii	133	4	414	2.78
Hoslundia oppositifolia	93	3	370	2.49
*Carex spp (*Sedge*)*	37	1	328	2.2
Cassia mimosoides	43	1	296	1.99
Diospyros kirkii	41	1	284	1.91
Strychnos madagascariensis	53	2	230	1.55
Oryza glaberrima (African rice)	26	1	220	1.48
Vigna spp	97	3	206	1.38
Pericopsis angolensis	34	1	181	1.22
Asarum caudatum (Wild ginger)	11	0	171	1.15
Tephrosia spp	13	0	165	1.11

Appendix 3.3 List on major foods species, with principal parts consumed

Species	Parts consumed
Trees	
Tamarindus indica	Fruits, bark, stem, seeds
Acacia sabiana	Seeds, exudates, pods, leaves, stem, roots
Kigelia Africana	Fruits flesh, leaves, flowers, seeds, exudates, stem.
Ficus platyphylla	Fruits, exudates
Sclerocarya birrea spp caffra	Fruits flesh, leaves, exudates, bark, fruits
Xeroderris stuhlmannii	Pods, seeds, flowers, gum, exudates, bark
Diospyros kirkii	Fruits, seeds, exudates, bark
Strychnos madagascariensis	Fruits, pods, leaves, seeds, flowers
Pericopsis angolensis	Leaves, flowers, seeds
Shrubs	
Cassia mimosoides	Pods, seeds, leaves, flowers
Diospyros usambarensis	Fruits, seeds, leaves, roots, exudates
Securinega virosa	Seeds, flowers
Hoslundia oppositifolia	Fruits, flowers, leaves
*Carex Spp (*Sedge*)*	Corm/bulb
Brachystegia bussei	Seeds, pods, exudates, barks, leaves
Grasses	
Unknown Grass spp	Seeds, roots, leaves, flowers
Rottboellia cochinchinensis	Roots, seeds, leaves
Dactyledon spp	Seeds
Cynodon spp	Seeds
Forbs	
Vigna spp	Leaves, pods, flowers, stem
Tragia pumila	Pods, leaves
Asarum caudatum (Wild ginger)	Leaves, stem, roots
Tephrosia spp	Pods, leaves, flowers
Unknown herb	Leaves, flowers
Commelina erecta	Flowers