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Master Thesis

Sexual segregation in the African elephant (*Loxodonta africana*):
a habitat and seasonal perspective



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Abstract

Sexual segregation refers to when male and females of the same species live in separate groups when they are not mating. This behavior is displayed in species that are sexually dimorphic and the African elephant (*Loxodonta africana*) displays extreme sexual dimorphism. I studied elephants in two habitats, Serengeti and Mikumi National Parks, and during the wet and dry seasons as factors that could lead to sexual segregation. The objective of this study was to test sexual segregation based on: the body size hypothesis, scramble competition hypothesis and the activity budget hypothesis. Bull and family groups preferred to graze in the wet season as predicted, and also during the dry season. Browsing may not have been preferred by the sexes owing to abnormal rains that fell in the Serengeti a few weeks prior to fieldwork for this study. This suggests that forage type is selected in proportion to availability, irrespective of habitat type and season, and this could consequently determine whether sexes segregate. Interestingly, female groups browsed more than bull groups in the wet season implying selectivity among the female. Consistent with my predictions, overlap in plant species and plant parts browsed in the dry season between the sexes was not significant. Females incorporated a wide range of plant species in their foraging while males incorporated a wide range of plant parts. This is in support of the body size hypothesis which suggests selective feeding in terms of diet quality, among the smaller females in order to meet their nutritional demands. Males generally preferred to browse on previously impacted *Acacia robusta* due to their ability to tolerate chemical defenses produced by plants, owing to retention time which is directly proportional to body size. The difference in browsing height between the sexes was significant in support of the scramble competition hypothesis. The activity budget hypothesis was not supported by this study as there was no significant difference in biting rate between the sexes. Understanding of sex related feeding preferences could be relevant for management of both plant and animal species that coexist with this megaherbivore.

Key words: Megaherbivore, Sexual dimorphism, body size hypothesis, Serengeti, Mikumi, *Acacia robusta*.

Table of content

Abstract	2
Table of content	3
1. Introduction	4
1.1 Existing hypotheses on sexual segregation.....	6
1.2 Predictions	9
1.2.1 Body size hypothesis.....	9
1.2.2 Scramble competition hypothesis	9
1.2.3 Activity budget hypothesis	9
1.3 Research questions.....	10
2. Methods	11
2.1 Study site.....	11
2.2 Data collection	13
2.3 Data analysis	14
3. Results	15
3.1 Body size hypothesis	15
<i>Foraging type of bull and family groups</i>	15
<i>Plant species browsed</i>	17
<i>Plant parts browsed</i>	18
<i>Accumulated browsing impact</i>	18
3.2 Scramble competition hypothesis	19
<i>Browsing height</i>	19
3.3 Activity budget hypothesis	20
<i>Biting rate</i>	20
4. Discussion	21
4.1 Body size hypothesis	21
<i>Foraging type of bull and family groups</i>	21
<i>Plant species browsed</i>	22
<i>Plant parts browsed</i>	24
<i>Accumulated browsing impact</i>	25
4.2 Scramble competition hypothesis	26
<i>Browsing height</i>	26
4.3 Activity budget hypothesis	26
<i>Biting rate</i>	26
5. Conclusion	28
6. Acknowledgement	29
7. Reference	30

1. Introduction

The African elephant (*Loxodonta africana*) is the largest terrestrial herbivore (Laursen & Bekoff, 1978; Sukumar, 2003; Shrader et al., 2012) and can live up to 70 years (Lee, 2012). Elephants are social animals and the basic family unit is composed of closely related family. These social groups consist of female relatives and their immature offspring (Poole, 1994; Moss, 1983). At sexual maturity the young males depart from their natal families. The female groups are highly mobile and may vary in size and composition (Poole & Moss, 1989). During periods of food scarcity such as the dry season, it may be to the group's advantage to have fewer members and this may necessitate the splitting of the group. Female elephants are in estrus only once every 4-5 years, however this is dependent on availability of food, presence of suckling calf and age of the cow (Poole, 1994). This is because they are pregnant for 21.5 months coupled with extended periods of calf dependence (Poole, 1994). The estrus cycle of elephants is generally 15 to 16 weeks. Thus females do not have a common time of the year when they are sexually receptive and it is not reproductively viable for males to hold a harem. Male elephants live solitary or in small groups with little social acquaintance, apart from association with asynchronously breeding females and their groups (Laursen & Bekoff, 1978; Poole, 1994; Stokke & du Toit, 2002).

Elephants are generalist feeders consuming a large number of plant species and parts however there are wide variations regionally and seasonally in proportion of grasses, sedges, forbs, shrubs and trees (Osborn, 2004; Whoolley et al., 2010; Penderis & Kirkman, 2014). Fruits, bulbs, plant bases and roots will also be consumed (Cerling & Harris, 1999). Virtually, elephants will browse in the dry season (Barnes, 1983) when annuals such as some grasses and some herbaceous plants have died and perennial graminoids and many forbs have dried up. Furthermore, browse is considered to be a high quality food in general (Bergström, 1992) and this is important for lactating females (Owen-Smith, 2002). In the wet season elephants will turn to a more varied diet which includes both graze and browse, or entirely graze when both are abundant. Ultimately whether they browse or graze will depend on the plant type in proportion to their availability. These among other factors make elephants highly adaptable to a wide range of habitats, from semi-deserts i.e. the Namib 'desert elephants', to forests (Laursen & Bekoff, 1978). Penderis and Kirkman (2014) describe browsing herbivores as being highly selective feeders in general,

and especially choosing to forage new shoots and young plant material, since browsing and production rate seem to be correlated Pellew (1983). Pruning for example reduces between-shoot competition for nutrients resulting in increased nutrient concentrations in the remaining shoots (du Toit, Bryant & Frisby, 1990). Rapid growth of plants, as a response to browsing (Bergström, 1992) further demands carbohydrates, which limit the synthesis of carbon-based secondary metabolites (du Toit, Bryant & Frisby, 1990). Browsing and rapid growth therefore allows for plants to channel much of the carbon towards growth and less towards defense, reducing tannin concentration and therefore making shoots palatable. This consequently makes previously browsed plants appealing to herbivores. The impact of previous browsing on a tree is estimated using the ‘accumulated browsing impact’ scale (see methods and materials section). In their way of feeding, elephants influence savannas by preventing bush encroachment, by playing a key role in dispersing tree seeds and by maintaining woodland structure (Prins & Olf, 1998; Simberloff, 1998). This megaherbivore therefore plays a role in influencing the dynamics and functioning of savanna ecosystems (Mapaure & Moe, 2009) and they have been described as a keystone species (Boundja & Midgley, 2009). A keystone species is defined by Paine (1995) as “a species that has a disproportionately large effect on its environment relative to its abundance”. It is therefore important that the use of resources by elephants are understood for better management and conservation of not only this megaherbivore, but other plant and animal species which could benefit or be disadvantaged by elephant instigated impacts e.g. change in species composition of birds (Conybeare, 2005).

Elephants are both sexually dimorphic and polygynous (Main, Weckerly & Bleich, 1996; Poole, 1994; Laursen & Bekoff, 1978). Sexual dimorphism refers to differences in traits such as body size and presence or absence of horns/antlers in male and female of the same species. According to Poole (1994) sexual dimorphism in elephants is extreme. Males continue to grow both in height and weight for most of their lives (Poole, 1994; Laursen & Bekoff, 1987), eventually reaching twice the weight of females. At about 17 years, males reach sexual maturity and are reported to be taller than the largest female (Poole, 1994). Older females may therefore be similar in body size as young adult males (Woolley et al., 2010). Adult females weigh about 2160 – 3230 kg and males 4700 – 6050 kg (Poole, 1994). Polygyny refers to when males mate with several females during any one mating season (Loe et al., 2006). Large body size is the

determining factor for male success in polygynous mating systems and leads to sexual body size dimorphism as this trait is sexually selected for (Weckerly, 1998). This could possibly explain the evolutionary advantage of differently sized sexes in the same species as male elephants have to deal with reproductive competition (Hollister-Smith et al., 2007). Male and female of dimorphic polygynous species live in separate groups when they are not mating (Stokke & du Toit, 2000; Ruckstuhl & Neuhaus, 2002; Stokke & du Toit, 2002; Bowyer, 2004) and subsequently use different habitats and resources (Stokke & du Toit, 2000). This is known as sexual segregation and elephants are no exception to this behavior (Bleich, Bower & Wehausen, 1997). In this study I looked at factors such as rich and poor savannas and the wet and dry seasons to explain sexual segregation in the African elephant. Savanna ecosystems have wet and dry climates, where summer months are characterized by the wet season and the winter months are characterized by the dry season (Anonymous, 1997).

1.1 Existing hypotheses on sexual segregation

Ruckstuhl and Neuhaus (2000) lay emphasis on 4 hypotheses that have been highlighted for causing sexual segregation. These are: predator avoidance, body size, scramble competition and social preference. For this study, the predator avoidance hypothesis is automatically weakened considering elephants do not have natural predators owing to their body size (Stokke & du Toit, 2000). However their young calves fall prey to the lion (*Panthera leo*) once in a while (Loveridge et al., 2006). Their only real predators are humans through poaching (Owen-Smith, 1988), hunting and culling. The predator avoidance hypothesis is also known as the reproductive strategy hypothesis (RSH) which suggests that females with their vulnerable calves will sometimes trade predator safe habitats at the expense of high quality forage (Loe et al., 2006; Mysterud, 2000; Main & Coblentz, 1990), jeopardizing their reproductive success. Males are insensitive to predation, and will utilize habitats that have potential to meet their energy demands for strength and endurance (Main, Weckerly & Bleich, 1996; Mysterud, 2000). These features are important for males since they are correlated with body size, fighting abilities and subsequently, their reproductive success.

The body size or sexual difference in nutritional requirements hypothesis (Bell 1971; Jarman, 1974; Illius and Gordon, 1987; Conradt, 1998; Rucksthul, 1998; Mysterud, 2000; Stokke and du Toit, 2000; Rucksthul & Neuhaus, 2002; Bowyer, 2004; Loe et al., 2006) identifies body size as the major factor in the nutritional requirement of large herbivores. According to the Jarman-Bell principle, large-bodied mammalian herbivores are able to subsist on diets of low quality as a result of lower metabolic requirements (Perez-Barberia, Perez-Fernandez & Alvarez-Enriquez, 2008; Müller et al., 2013). If daily requirements of animals for energy, nitrogen and even minerals scale to metabolic mass ($\text{Bodymass}^{0.75}$), smaller bodied female require more energy per day per unit of body mass than the larger animals (Geist, 1974; Müller et al., 2013). Also, since absolute metabolic needs and retention time increases with body size, it increases the digestibility of cell wall while the specific metabolic needs of the animal decreases, (Demment and van Soest, 1985; Stokke and du Toit, 2000; Müller et al., 2013). Larger animals therefore do not need to be selective as they can tolerate a wide range of varying diet quality and this is the basis of the Jarman-Bell Principle (Bell, 1971; Geist, 1974; Jarman, 1974). The smaller female selectively feed on low-fiber, and high quality forage to satisfy nutritional and reproductive demands (Demment and van Soest, 1985; Main, Weckerly & Bleich, 1996). According to Owen-Smith (2002), during early lactation nutritional demand of mothers reach their peak. Female energy requirements during this time (lactation) may increase almost two-fold, whereas protein requirements may increase more than two-fold (Clutton-Brock, Albon & Guinness, 1989; Owen-Smith, 2002). Males should consent with a lower quality diet and habitat than females. Rucksthul (1998) and Jarman (1974) also point out that there is a negative correlation between forage quality and abundance (quantity) and therefore, high quality forage habitats are predominantly assumed to support female groups and high quantity forage habitats bulls/bull groups.

The scramble or indirect competition hypothesis (Conradt, Clutton-Brock & Thomas, 1999; Mysterud, 2000; Loe et al., 2006) suggests that males will passively be driven away from optimal feeding habitats by females. This hypothesis stems from a study on grazing ungulates which suggests that narrower muzzles and lower absolute food intake requirements of smaller-bodied females and calves enable them to be more efficient than males at grazing on short high quality swards (Clutton-Brock, Iason & Guinness, 1987; Illius & Gordon, 1987; Stokke & du Toit, 2000). Spatial displacement of males therefore results through intersexual scramble

competition which forces males to feed on low quality taller swards (Illius and Gordon, 1987; Stokke and du Toit, 2000). Although intersexual scramble competition is likely in elephants, Stokke and du Toit (2000) point out that this is unlikely to lead to spatial displacement of males as males owing to their taller height can browse at higher levels without having to move away to other feeding areas.

The social preference hypothesis (Bon & Campan, 1996; Main, Weckerly & Bleich, 1996; Ruckstuhl, 1998; Ruckstuhl & Neuhaus, 2000; Stokke & du Toit, 2000) suggests that animals will segregate in same sex or same age social groups to learn important skills such as fighting, where to find food and water, and suitable areas for giving birth or finding potential mates. Male ungulates have been observed to interact and play with other males and the persistence of this behavior into adulthood could apparently result in segregated sexual groups (Bon & Campan, 1996). The learning of fighting skills and establishment of dominance hierarchies is especially important as this may be a determinant of a male's ability to succeed in competition with other males for access to females in estrus. Females have also been noted to segregate from males to avoid the distress and sexual behavior of male (Bon and Campan, 1996) as female groups maybe harassed by aggressive males in musth. Females may also exhibit aggressive behavior toward males (Main, Weckerly & Bleich, 1996) and it would make sense for males to be away from females.

Another promising hypothesis is the activity budget hypothesis (Ruckstuhl, 1998; Mysterud, 2000; Ruckstuhl & Neuhaus, 2002; Loe et al., 2006). Here sexually dimorphic males and females of the same species segregate into different groups as a result of the incompatibilities in their feeding behavior such as biting and movement rates. The selective feeding of females allows them to have shorter feeding bouts (Stokke and du Toit, 2000), while males will spent more time feeding in one area. The result is segregation of the sexes both socially and temporally even when both sexes are using the same general habitat (Ruckstuhl & Neuhaus, 2002).

Extensive research has since focused on this subject in ungulates such as deer (Conradt, Clutton-Brock & Thomas, 1999; Barboza & Bowyer, 2000; Ruckstuhl & Neuhaus, 2002; Loe et al., 2006) and other ruminants (Bowyer, 2004) in temperate regions, however little research has gone into sexual segregation in tropical species such as elephants (Stokke & du Toit, 2000).

Knowledge of sex related feeding preferences and their impacts, in addition to other factors (such as population dynamics) could be of significant importance in the management of this megaherbivore, considering the impacts they are known to instigate (Owen-Smith, 1988). The objective of this study was therefore to test sexual segregation based on the body size hypothesis, the scramble competition hypothesis and the activity budget hypothesis.

1.2 Predictions

To understand what leads to sexual segregation in elephants, I make predictions based on 3 of the above hypotheses: the body size, scramble competition and the activity budget hypotheses. Predictions are made under each hypothesis as follows;

1.2.1 Body size hypothesis

(1) Both bull and family groups will browse more than graze in the dry season, while they will predominantly graze in the wet season. This is because elephants prefer to browse in the dry season when grasses and some herbaceous plants have dried and died.

(2) In the dry season forage quality and quantity is limited. I predict that males and females will forage on different plant species and plant parts to meet energy and nutritional requirements. The wet season will present great overlap in the diets of the sexes.

(3) Males are able to tolerate a high fiber diet than females. I therefore predict that males will tolerate browse from previously impacted trees than females.

1.2.2 Scramble competition hypothesis

(4) Male and female elephants in order to minimize/prevent intersexual competition will browse at different heights in the dry season. The scramble competition hypothesis will not hold in the wet season as forage is abundant during this season.

1.2.3 Activity budget hypothesis

(5) Females being selective in their feeding due to their nutritional needs will spent less time foraging on a patch/tree, while males will spent longer periods foraging on a single patch/tree.

1.3 Research questions

To test each of the above hypotheses I asked the following questions;

- (1) Are there differences in foraging behavior (browsing or grazing) between bull and family groups between seasons and habitats?
- (2) Are there overlaps in plant species and plant parts that the sexes browse during the seasons and in different habitats?
- (3) Is there a difference in preference for browsing previously browsed woody plant species?
- (4) Are there differences in the height at which the sexes browse during the seasons and in the different habitats?
- (5) Are there differences in the browsing rate between the sexes during the seasons and in the different habitats?

2. Methods

2.1 Study site

The study was carried out in the Serengeti and Mikumi-Selous National Parks of Tanzania. The former is located south east of Lake Victoria in northern Tanzania (Sinclair, 1975) and the latter is located in south-eastern Tanzania in the Kilosa District within the Morogoro Region (Figure 1; Venance, 2009). Both National Parks occur in savanna ecosystems and these habitats differ in their soil nutrient availability. The nutrient rich Serengeti is dominated by Acacias such as *Acacia tortilis* and *Acacia robusta* while the nutrient poor Mikumi is dominated by broad-leaved species such as *Philenoptera violacea* and have fewer *Acacia* species (De Boever et al., 2014).



Figure 1: Map of Tanzania with respect to the Serengeti and Mikumi National Parks (Velded et al, 2012).

The Serengeti National Park (hereafter SNP) has been described as a natural laboratory by Sinclair and Arcese (1995). The SNP is also geographically defined by migratory route of wildebeest (*Connochaetes taurinus albojubatus*) and sustains some of the highest concentrations of herbivores on earth (Ruess and Seagle, 1994). Since the SNP is found in the Mara and Simuyi regions, Sinclair (1975) has referred to this ecosystem as the Serengeti-Mara ecosystem and it covers an area of 25 000 km², however the SNP alone makes up about just half of this total area.

The soil in the SNP is characterized by high salinity and alkalinity. In addition, these soils are shallow as a consequence of their recent volcanic origins which have consequently resulted in these soils having higher nutrient content (McNaughton, 1983; Sinclair & Arcese, 1995; Sinclair et al., 2008). A rapidly growing nutrient-rich plant community is supported on soils of the volcanic origin in the south and southeastern plains, where net annual primary production and rainfall are positively correlated (Ruess & Seagle, 1994). As a result high quality forage is produced during the wet months of March – May (long rains) and November – December (short rains), and this system of rainfall is known to follow a bimodal pattern (Sinclair et al., 2008). Annual rainfall in the SNP is between 500 – 1100mm (Mduma, Sinclair & Hilborn, 1999). The dry months are between July – October, a time during which elephants are dependent on *Acacia* spp and *Commiphora* spp and riverine forest trees (Sinclair et al., 2008).

Mikumi National Park (hereafter MNP) on the other hand is located on the northern boundary of the Selous National Park and for this reason, Mikumi and Selous National Parks are considered one ecosystem through which animals move back and forth (Vedeld et al, 2012; Siege & Baldus, 2000). Mikumi covers an area of 3230 km² and is the fourth largest National Park in Tanzania, and consists of 4 diverse ecozones: the miombo woodland in the South, arid bushland in the North, a coastal zone in the east and a mountain zone in the east and west (Vedeld et al, 2012). According to Backéus et al. (2006), vegetation in Mikumi is dominated by miombo woodland. Miombo is a vernacular word (now adopted by ecologists) that describes those woodland ecosystems dominated by trees of the genera *Brachystegia*, *Julbernardia* and *Isoberlinia* (*Leguminosae*, sub-family *Caesalpinioideae*; Abdallah & Monela, 2007; Luoga, Witkowski & Balkwill, 2002). Trees in these woodlands generally have meso- and microphyllus compound leaves which sprout before the rains, with a dominance of tree species with ecto-mycorrhizae (Högberg, 1982). The soils in these woodlands are generally leached, sandy, acidic and poor in nutrients (Cole, 1986; Campbell, 1996; Backéus et al., 2006). The topography in Mikumi was formed due to minor faulting of an older erosion surface from the Gondwana, which has resulted into an old slightly inclined plateau with red soil and alluvial soils surrounding permanent streams (Backéus et al., 2006). The alluvial plain of the river basin Mkata makes up part of the MNP and vegetation species include *Adansonia digitata*, *Acacia* spp and *Tamarindus indica*

among others (Venance, 2009). Annual rainfall in the Mikumi/Selous region is about 750-850mm (Vedeld et al., 2012).

2.2 Data collection

Data were collected from April – May 2014 for the wet period and in August – October 2014 for the dry period in both the Mikumi and Serengeti National Parks. Driving road transects of about 60 kilometers were carried out along one of the road networks per day, in both study areas. Both National Parks contain about 3 main roads and several smaller road networks. The vehicle was stopped whenever a mature elephant or elephant group was sighted at less than or about 50m from road transects. Foraging type (e.g. browsing or grazing) of family and bull groups as well as the number of individuals browsing or grazing were recorded. Observations were done 5 times with 3 minutes interval between each observation and the average grazing or browsing was taken as the final value.

In addition whenever a browsing male or female was spotted binoculars were used to help identify the plant species, the parts of the plants which were browsed and the height at which they browsed. Elephant sex as well as the number of bites and the time spent on browsing was likewise recorded. The time limit for each browsing observation was between 1 - 15 minutes. Browsing height was recorded relative to the animal (e.g. above head, head level, chest level, above knee, below knee) and literature (Laursen and Bekoff, 1978; Poole, 1994, Skinner and Chimimba, 2005) was used to calculate the browsing height in meters. The accumulated browsing impact (hereafter ABI) was estimated and recorded. ABI is an observational estimation scale of the effects of all browsing on tree architecture. This scale ranges as follows;

- 0 – No signs of old browsing**
- 1 – Signs of old browsing with no change tree growth form**
- 2 – Signs of old browsing with obvious change in tree growth form**
- 3 – Signs of old browsing with strong changes in tree growth form**

2.3 Data analysis

Data were analyzed according to the habitat and season in which it was collected. The proportions of the dominant plant species browsed were calculated in excel as percentages. The Schoener's index as described by Makhabu (2005) was used to assess the overlap of resource use between male and female elephants with regard to plant species browsed as well as the height and plant parts browsed using the following formula:

$$O_{jk} = 1 - \frac{1}{2} \sum |P_{ij} - P_{ik}|$$

Where O_{jk} is the overlap between male and female elephants, j and k respectively. P_{ij} is the proportion of the total browsing on plant species i by bull groups, while P_{ik} would be the same but for the family groups. The browsing height overlap was assessed using the above method, however, in the formula "species" was replaced with the height variable.

Overlap in browsed plant parts were also calculated using the Schoener's index by the following formula:

$$O_{jk} = 1 - \frac{1}{2} \sum |P_{hij} - P_{hik}|$$

Where O_{jk} is the overlap between male and female elephants. P_{hij} is the proportion of the total browsing activity on plant part h of the plant species i by male elephants, P_{hik} is the same proportion but for the females. The Schoener's index is zero when the two groups do not share resources and one when they use the same resources according to Wallace (1981). The overlap is significant if the value is equal to or exceeds 0.60.

Statistical significance of differences in height browsed, biting rate, plant parts browsed, plant species browsed and ABI were calculated using Poisson or Linear Models (GLMs) in R-Studio (version 0.98.1078) using Anova or Chi-square tests.

3. Results

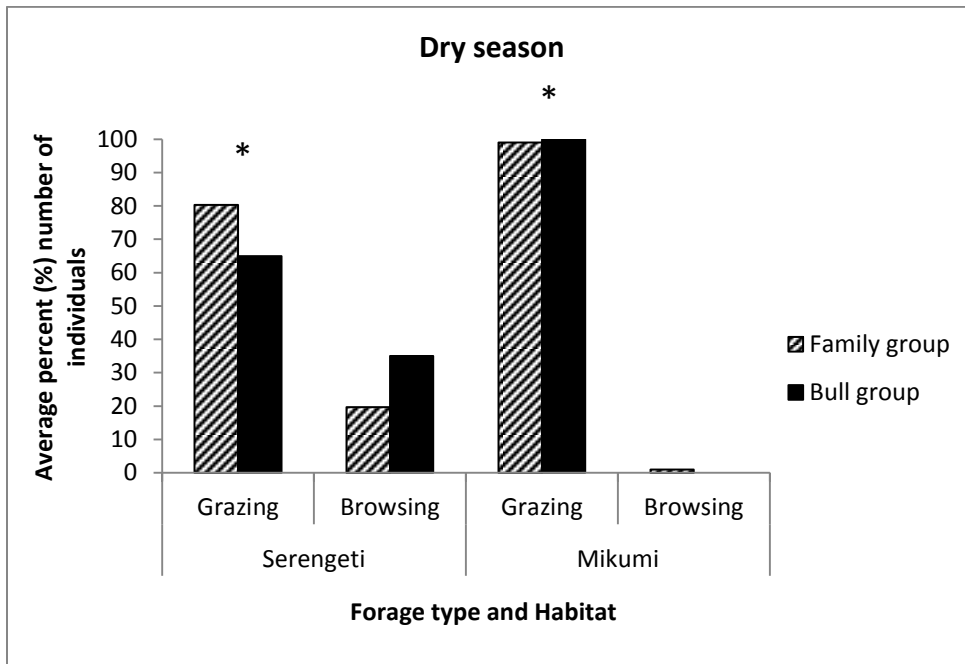
3.1 Body size hypothesis

Foraging type between family and bull groups

Both family and bull groups grazed more than they browsed in both national parks and during both the wet and dry season. During the dry season, bulls in MNP only grazed while 99% of family groups grazed (Figure 2). In the SNP an average of 65% of individuals from bull groups grazed while 35% browsed. In contrast, an average of 80% individuals from family groups grazed whereas 20% browsed (Figure 2). The difference in grazing was significant ($F_{1,111} = 37.87$; $p < 0.001$) in the SNP during the dry season while the difference in browsing was not significant. Similarly in MNP, the difference in grazing between family and bull groups was significant ($X^2_{1,73} = 5.24$; $p = 0.022$). The difference in browsing was not significant during the dry season in MNP.

An average of 90% of family group members grazed in the SNP during the wet season while 10% browsed. Bulls similarly grazed more than browsed in the SNP during the wet season, with an average of 93% grazing and 7% browsing (Figure 2). Similar results were obtained for MNP during the wet season, with an average of 99% family group members grazing and 1% browsing (Figure 2). The differences in grazing or browsing between family and bull groups during the wet season of the SNP were significant (Grazing: $F_{1,60} = 12.89$; $p < 0.001$; Browsing: $F_{1,60} = 5.40$; $p = 0.025$). In MNP during the wet season only grazing was significantly different ($X^2_{1,102} = 26.10$; $p < 0.001$).

(a)



(b)

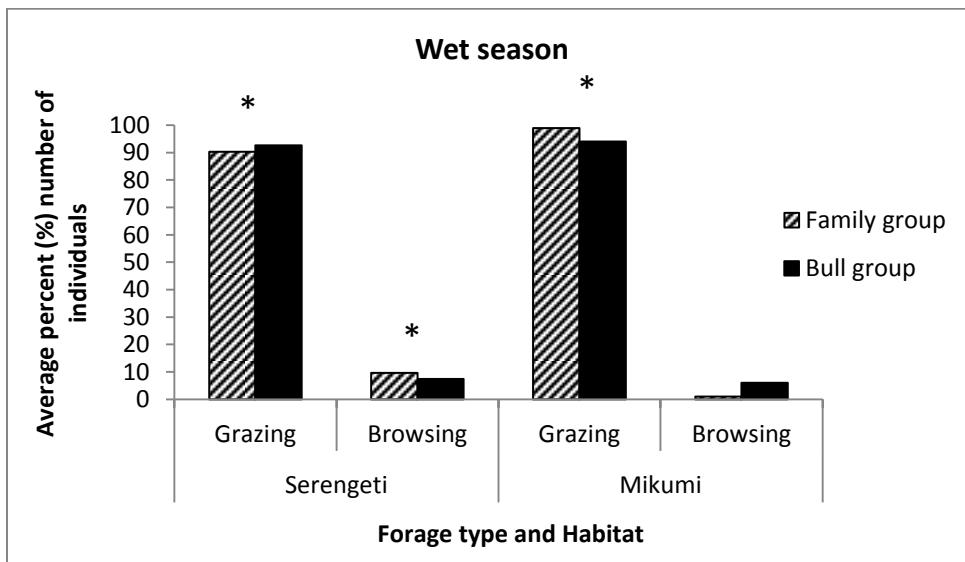


Figure 2: Average percentage of individuals in family and bull groups that were observed grazing or browsing in the Serengeti and Mikumi during the (a) dry and (b) wet season. * Significant difference of forage type between the groups.

Plant species browsed

A total of 21 plant species were browsed by male and female elephants in the two national parks. The 4 most browsed plant species in SNP were *Acacia mellifera*, *Acacia robusta*, *Acacia tortilis* and *Cordia ovalis* (Table 1). In the few recorded observations of other plant species such as *Balanites aegyptiaca* in the SNP and *Philenoptera violacea* in MNP, the species made up all or a large proportion of the species that were browsed. For example one female browsing observation on *Philenoptera violacea* in MNP during the wet season resulted in 100% contribution to the diet composition. The top 4 most browsed plant species therefore made up the greatest contribution to the diet composition of both males and females. SNP and MNP had no common plant species browsed by both male and female elephants.

Table 1: Diet composition of the sexes between the two habitats and seasons. The values are percentage contribution by each plant species to the observed browsing by each sex. This table only shows plant species that contributed at least 4% to the observed browsing of each sex. Plant species that contributed less than 4% are grouped as others.

Plant species	Serengeti				Mikumi			
	Male		Female		Male		Female	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
<i>Acacia mellifera</i>	-	8	-	10	-	-	-	-
<i>Acacia robusta</i>	80	46	40	25	-	-	-	-
<i>Acacia tortilis</i>	-	23	-	25	-	-	-	-
<i>Acacia xanthophloea</i>	-	-	-	-	50	-	-	-
<i>Balanites aegyptiaca</i>	-	-	40	4	-	-	-	-
<i>Cordia ovalis</i>	-	18	-	24	-	-	-	-
<i>Grewia bicolor</i>	-	-	20	-	-	-	-	-
<i>Philenoptera violacea</i>	-	-	-	-	33	-	100	100
<i>Unknown shrub1</i>	-	-	-	-	17	-	-	-
<i>Unknown forb</i>	20	-	-	-	-	-	-	-
<i>Others</i>	0	5	0	12	0	-	0	0

Table 2: Schoener's indices (SI) of resource-use overlap between male and female elephants during the wet and dry seasons for 3 variables; plant species, plant part and browse height.

Overlap	Serengeti		Mikumi	
	Wet	Dry	Wet	Dry
Plant species	0.60*	0.24	0.50	0.50
Plant part	0.20	0.07	0.17	0.12
Height	0.80*	0.06	1.00*	1.00*

*Values equal to or greater than 0.6 are considered significant for single variables (plant species, plant part, browse height).

The overlap (Schoener's Index = SI) in plant species browsed was not significant in the SNP during the dry season (SI = 0.24, Table 2) as well as in MNP during both seasons (SI wet = 0.50; SI dry = 0.50). The overlap in plant species browsed was significant in the SNP during the wet season (SI > 0.6).

Plant parts browsed

The most browsed plant parts by both males and females were leaves and twigs (LT) followed by leaves and twigs and bark (LTB; Table 3). Leaves and twigs were also observed to be browsed in all seasons by both sexes. Both sexes were observed to strip the bark of *Acacia mellifera*, *Acacia robusta* and *Acacia tortilis* (Table 3). These are also the 3 plant species that were most browsed by elephants in the dry season in the Serengeti. Since *Phoenix reclinata* has big leaves, elephants only ate the leaves of this plant. However, they also stripped and ate the leaves of *Acacia robusta* and plucked those of *Sanseveria ehrenbergiana*. The overlap according to Schoener's Index in plant parts browsed was not significant during all seasons and in both sites (Serengeti Dry = 0.07; Serengeti Wet = 0.20; Mikimu Dry = 0.12; Mikumi Wet = 0.17; Table 2).

Table 3: Proportion of plant parts browsed by male and female elephants during the wet and dry season in Serengeti and Mikumi. Where; LT = Leaves & Twigs, LTB = Leaves & Twigs & Bark.

Plant part	Serengeti - Dry		Serengeti - Wet		Mikumi - Dry		Mikumi - Wet	
	Male	Female	Male	Female	Male	Female	Male	Female
Bark	0.02	0.01	-	-	-	-	-	-
Leaves	0.05	0.02	-	-	-	-	-	-
LT	0.74	0.81	0.80	1.00	-	1.00	0.83	1.00
LTB	0.18	0.15	0.20	-	-	-	-	-
Roots	-	-	-	-	-	-	0.17	-

Accumulated browsing impact

ABI was calculated for the top 3 browsed species and all these species were from the SNP. These were *Acacia tortilis*, *Acacia robusta* and *Cordia ovalis*. The highest browsing proportion by males was on *Acacia tortilis* with an ABI value of 1 and 3, both of which were equally browsed by males (browsing proportion = 0.44; Figure 3). Males browsed more on *Acacia robusta* with an ABI value of 2 while they equally browsed *Cordia ovalis* with ABI of 1,2 and 3 (browsing proportion = 0.29; Figure 3). Female browsing proportion of *Cordia ovalis* with an ABI value of 0 was 0.55 (Figure 3) followed by *Acacia robusta* (browsing proportion = 0.50;

ABI = 1) and *Acacia tortilis* with ABI values of 1-3 were equally browsed (browsing proportion = 0.30; ABI = 1, 2, 3; Figure 3).

There was a significant difference in browsing previously impacted *Acacia tortilis* ($X^2_1 = 3.91$; $p = 0.048$) and *Acacia robusta* ($X^2_1 = 4.76$; $p = 0.029$) between the sexes, while the difference was not significant for *Cordia ovalis* ($X^2_1 = 3.17$; $p = 0.140$).

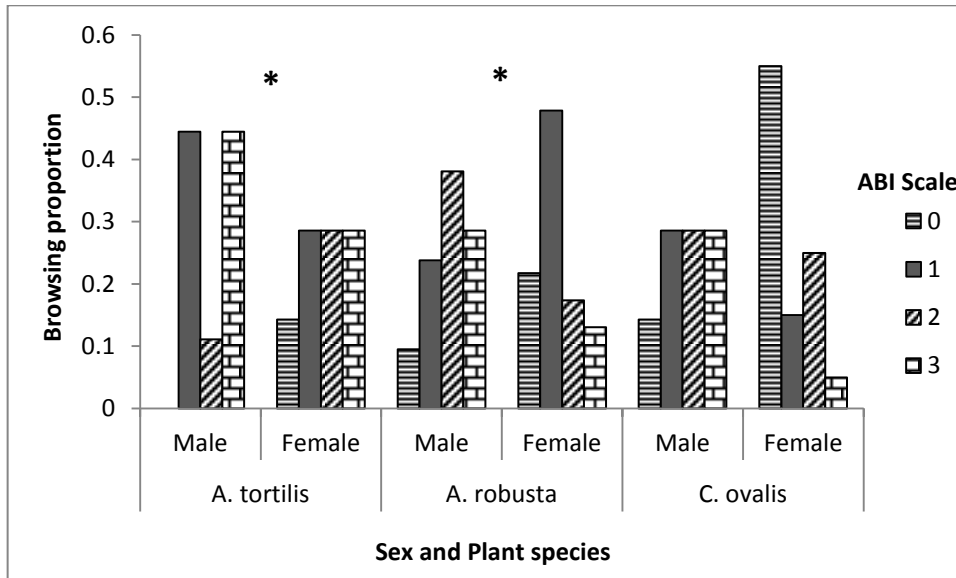


Figure 3: Proportion of accumulated browsing impact of 3 most browsed plant species by male and female elephants. * Significant difference in preference for previously impacted plant species.

3.2 Scramble competition hypothesis

Browsing height

Male elephants browsed at higher heights than female elephants (Figure 4). There was a significant difference in browsing height in the dry season of the SNP ($F_{1,121} = 9.44$, $p = 0.002$).

There was a trend in browsing height between the sexes during the wet season in the SNP ($F_{1,8} = 4.43$, $p = 0.068$). There was no difference in browsing height in MNP during both seasons.

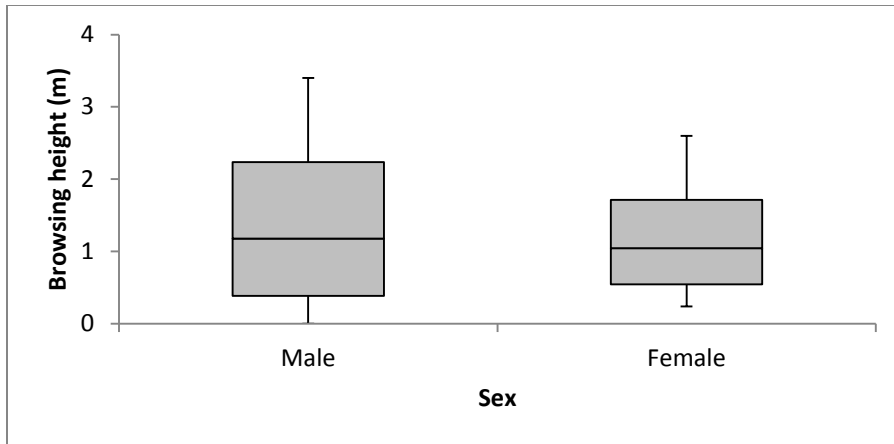


Figure 4: Box plots showing the difference in browsing height male (N = 39) and female (N = 84) elephants in the Serengeti National Park during the dry season. The lines in the boxes are sample medians, the lower and upper box ends are the 25th and 75 quartiles respectively and the lines outside the boxes extend to the minimum and maximum values.

There was no overlap according to the Schoener's index in browsing height in the SNP during the dry season (SI = 0.06). The overlap was significant during the wet season (SI > 0.6; Table 3).

3.3 Activity budget hypothesis

Biting rate

Male and female elephants had similar biting rates, 4.49 and 4.42 bites/min respectively (Table 4) in the SNP during the dry season ($F_{1,121} = 0.008$, $p = 0.929$). Male elephants had a similar biting rate, 8.48 bites/min in the wet season than females, 5.87 bites/min ($F_{1,8} = 0.069$, $p = 0.934$; Table 4). In the wet season of MNP males a similar biting rate of females, 4.67 bites/min and 2.42 bites/min respectively ($F_{1,5} = 0.44$, $p = 0.537$; Table 4). No browsing observations were recorded for males in MNP during the dry season, and statistical significance was consequently not calculated.

Table 4: Average biting rate in (bite/min) for both habitats and during all seasons.

Sex	Serengeti		Mikumi	
	Dry	Wet	Dry	Wet
Male	4.49	8.48	0	4.67
Female	4.42	5.87	8.77	2.42

4. Discussion

4.1 Body size hypothesis

Foraging type of bull and family groups

Family and bull groups grazed more in the wet season than they browsed in both the SNP and MNP, and there was a significant difference in grazing between the sexes. These results are in accordance with the predicted outcome. Interestingly, family groups grazed more than the bull groups in the dry season of the SNP. Preference for grazing by both groups in the wet season suggests that forage type is selected in proportion to availability (Stokke, 1999). The implication is that being generalist feeders, elephants will eat food that is most abundant and palatable in a particular habitat at a particular time. The lower browsing proportions during the dry season could however be attributed to the significant amounts of rain the SNP received 2 weeks prior to fieldwork for this study, consequently resulting in increased forage in the form of graze. Although grazing proportions for both groups in SNP were higher than browsing proportions during both seasons, there was a significant difference in browsing between the two groups during the wet season where family groups browsed more than bull groups. Browse is generally a high quality food (Bergström 1992) and family groups because of their nutritional requirements, for example lactation (Owen-Smith, 2002; Clutton-Brock, Albon & Guinness, 1989), are reported to select high quality forage with less fiber, in support of the body size hypothesis.

Grass abundance is a characteristic of poor nutrient quality habitats, which according to Chapin III, Vitousek and van Cleve (1986), plants from infertile soils generally exhibit. This could explain the preference for grazing in MNP of family and bull groups, where family groups had a higher browsing proportion than male groups. Backéus et al. (2006) pointed out that miombo woodland soils are generally leached, sandy and poor in nutrients, hence the limited browsing opportunities. Miombo woodlands are chemically heavily defended, thus offering a large quantity of low quality food for browsers (Bell, 1982), possibly explaining lower browsing. The implication for minimal browsing during the dry season is that habitat type could play a role in

elephant forage preference and consequently whether the sexes segregate. If forage type or forage quality is constant in a habitat, the need to segregate may not be necessary.

Plant species browsed

As predicted there was a significant overlap in plant species browsed during the wet season while the overlap was not significant during the dry season in both the SNP and MNP, in support of the body size hypothesis. Both sexes mostly browsed *Acacia mellifera*, *Acacia robusta*, *Acacia tortilis* and *Cordia ovalis* during the dry season in SNP and in addition to these top 4 species browsed, females browsed *Acacia kirkii*, *Balanites aegyptiaca* and *Hibiscus calyphyllus* among others. Elephants during the dry season concentrate on a few species that contribute much to the food intake while predominantly grazing in the wet season (Barnes, 1983) which is consistent with what I observed in this study. *Acacia* trees are nutritious (Bergström, 1992) and intensively browsed by herbivores (Fornara and du Toit, 2007) as seen during the dry season in SNP. The lack of overlap in the plant species browsed by the sexes in the dry season consequently suggests that the sexes are not entirely browsing the same species. Females incorporate a wider range of plant species in their diet in order to avoid fiber intake (Stokke, 1999) and to satisfy their nutritional demands as per the body size hypothesis (Bell, 1971; Jarman, 1974; Illius and Gordon, 1987; Mysterud, 2000; Stokke and du Toit, 2000; Loe et al, 2006). This means that the females browse and move from one tree to another, feeding only on the high quality parts leaving the low quality parts behind. This subsequently increases the species diversity of the trees they browse, suggesting that females are selective feeders. The quantity-oriented males do not find plants with a small biomass worth exploiting (Stokke, 1999) and therefore spend more time browsing plants they can get large quantities of food from in a single feeding bout. Field observations indicate that some plant species browsed by both sexes were in proportion to their availability (e.g. patches with an abundance of *Acacia robusta*; Photo 3 & 4) an observation that matches that of Stokke (1999).



Photo 3: *Acacia robusta* patch in the Serengeti National Park during the dry season.



Photo 4: Family group of elephants in SNP browsing on a Patch of *Acacia robusta*.

There was no significant overlap in plant species browsed by males and females during the wet season in MNP. Interestingly however, both sexes browsed *Philenoptera violacea* and *Acacia xanthophloea* as these were the plant species dominant around the park headquarters where browsing was mostly observed. MacGregor and O'Connor (2004) stated that a staple to elephants is often the dominant plant species. This was seen in both national parks where the most dominant tree species in a patch was mostly browsed (e.g. Photo 3 and 4). Browsing observations in MNP were generally few which I suspected is due to a history of poaching (Baldus & Siege, 2003). Elephants were mostly observed to be resting under tree shades (Photo 4) near the park headquarters as this is where they feel safe (Baldus and Siege, 2003; Gobush, Mutayoba & Wasser, 2008). This could have influenced elephant foraging behavior, for example browsing at night further away from the park headquarters. The predator avoidance hypothesis states that females with their young will trade high quality habitats for predator safe habitats (Rucksthul & Neuhaus, 2000), and if indeed elephants browsed during a different time of the day in order to avoid being poached, this could be argued to support the predator avoidance hypothesis. However, the predator avoidance hypothesis was not tested in this study.



Photo 5: Family group in MNP resting in the shade under a tree near the park headquarter.

Plant parts browsed

Both sexes in their foraging debarked, broke branches off of trees and pushed over trees (Personal field observations; Photo 6 and Photo 7). Selectivity in what females browsed can be seen in the plant parts that were browsed. There was no significant overlap in plant parts browsed during both seasons in both SNP and MNP, and this was as predicted for the dry season. Both sexes browsed leaves, bark and twigs. In addition to those plant parts males foraged roots. These results corroborate the body size hypothesis which Stokke (1999). Owen-Smith and Chafota (2012) affirm that selective feeding is mainly expressed in terms of plant parts consumed rather than the diversity of species consumed. Although results from MNP may not be sufficient to draw conclusions, the ones from the SNP suggest that the body size hypothesis could lead to sexual segregation in African elephants.



Photo 6: Two female elephants browsing and debarking *Acacia tortilis*.



Photo 7: Browsed, debarked and stripped *Acacia tortilis*.

Accumulated browsing impact

The differences in browsing previously impacted *Acacia tortilis* and *Acacia robusta* between male and female elephants were significant. There was however no significant difference in browsing previously impacted *Cordia ovalis*. Males generally preferred both previously impacted *Acacia tortilis* and *Acacia robusta* more than females. According to du Toit, Bryant and Frisby (1990) severe browsing causes increased nitrogen concentration and/or reduced tannin concentrations in individual plants. Although carbon-based secondary metabolites function as defenses towards herbivores in woody plants (Skarpe & Hester, 2008), some generalist herbivores tolerate high levels of defensive chemicals in their diets (Provenza et al., 1990). Preference for browsing previously impacted trees by males could imply tolerance to these defenses whereas females may be intolerant. This is confirmed by Owen-Smith and Chafota (2012) who state that larger herbivores are able to use the diluting effect by browsing on many species with different chemical defenses. A study by Skarpe et al. (2003) revealed that *Acacia robusta* had the highest tannin activity measured as mg tannic acid (TA) per g dry mass of leaf, compared to *Acacia tortilis* and *Acacia mellifera* (109.38, 40.56 and 6.24 mgTA/g respectively). *Acacia robusta* in the same study similarly contained the highest percentage concentrations of both nitrogen and carbon. This suggests that although *Acacia robusta* produces chemical defenses, these do not deter elephants from browsing this species. Potentially, this could have something to do with the allocation of plant nutrient resources in the face of severe browsing. Severely browsed trees potentially allocate nutrient resource to growing tissue to maximize photosynthesis and growth, rather than towards defense. Furthermore, tannins and fiber fractions are known to reduce digestibility and these are typical of woody species (Crawley, 1983), and since digestibility of cell wall increases with increasing absolute metabolic needs and retention time, and increasing body size (Demment & van Soest, 1985; Stokke & du Toit, 2000; Müller et al., 2013), this could put males in a position to tolerate tannins. This consequently supports the body size hypothesis.

Du Toit, Bryant and Frisby (1990) studied *Acacia tortilis* and found no significant difference in net shoot extension (total growth minus browsed growth) between heavily and lightly browsed trees. Bergström (1992) reported that this could be due to rapid growth of heavily browsed trees

in order to compensate for almost continuous removal of browse. Additionally, tannin content in *Acacia tortilis* was lower in leaves of heavily browsed trees, while nitrogen and phosphorus content were higher (du Toit, Bryant & Frisby, 1990), females need these nutrients especially lactating cows (Owen-Smith, 2002). This could explain why females browsed equal proportions of *Acacia tortilis* with ABI 1-3. Plant defense mechanisms could therefore influence the plant species male and female elephants choose to browse. Depending on their ability to tolerate these defenses, male and females may segregate from patches or habitats.

4.2 Scramble competition hypothesis

Browsing height

Browsing height between the sexes was significantly different in the SNP during the dry season as predicted. Substantiating this finding is the absence of overlap in browsing height between male and female elephants in the SNP during the dry season. My findings support the scramble competition hypothesis. Stokke and du Toit (2000) report that when females fed shoulder to shoulder with other family members, they fed at a significantly higher level in the canopy than when they were feeding alone. This could consequently suggest that feeding height stratification is only apparent in the presence of intraspecific competition for food resources which could necessitate segregation of the sexes. The overlap in browsing height was 1 for both seasons in MNP. According to Wallace (1981), this indicates that both male and female browsed at the same height, indicative of less competition in browsing.

4.3 Activity Budget Hypothesis

Biting rate

There was no significant difference in biting rate between male and female elephants and the activity budget hypothesis was therefore not supported by this study. Contrary to other studies on ungulate species, females foraged longer than males (Owen-Smith, 1988). Shorter feeding bouts are reported to be representative of a more selective foraging approach, typical of female foraging behavior (e.g. Stokke and du Toit, 2000). Males target larger trees, ingest greater quantities of low quality forage resulting in longer feeding duration and more destructive

behavior (Shannon et al., 2006). Intake rate according to Jung and Allen (1995) is affected by the toughness and digestibility of plant fiber constituted by structural carbohydrates and insoluble phenols. Males being larger have an increased digestive capacity (mean retention) and can therefore tolerate low quality forage i.e. high fiber (van Soest, 1996). Mysterud (1998) stated that increasing body size of African herbivores is associated with an increase in the proportion of daily time spent feeding because of physical differences in forage and increased handling time, e.g. pull out a young tree, prepare it and eat the roots (Personal field observation).

5. Conclusion

In summary my findings support the body size and the scramble competition hypothesis to explain sexual or lead to sexual segregation in African elephants. The activity budget hypothesis is not supported by this study. Although various hypotheses have been tested and suggested Shannon et al. (2006) caution that ecological conditions that an animal is exposed to as well as different spatial and temporal scales in which animals are studied will influence the extent and cause of sexual segregation. Sexual segregation in elephants can therefore be explained by a combination of these hypotheses and which hypothesis becomes relevant in a single case study is mediated by different factors such as habitat type and other local environmental factors. This consequently influences results and outcomes of studies. To alleviate problems emanating from poor data, I suggest replicating the study for 2 or more consecutive seasons to account for abrupt change in weather conditions and other factors. Areas in which poaching is a concern may not be representative of the foraging behavior of elephants and studies such as this one should be carried out in areas where anthropogenic influences are minimal. The management implication from this study is that understanding differences from sex-related feeding impacts of elephants could be important in the conservation of both animal and plant species.

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