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Master thesis

Foraging by elephant, giraffe and impala during
wet and dry season in rich and poor
savanna, Tanzania.

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ABSTRACT.

Plants have evolved traits in response to herbivory and these traits depend on soil nutrient status, plants in nutrient rich soils have evolved tolerance to herbivory by being palatable and those in nutrient poor soils have evolved to avoid and prevent future herbivory by being unpalatable. This condition influences interactions between elephants a mega-herbivore with browsers (giraffe) and mixed-feeders (impala) as their interaction depends on food availability. Serengeti National Park is a nutrient rich habitat while Mikumi National Park is a nutrient poor habitat. My study aimed to observe impacts of elephant foraging on giraffe a browser and impala a mixed-feeder in these two habitats with different soil nutrient status during wet and dry season.

Data collected from April to May for the wet season and August to September, 2014 for dry season, overlap in food resource use was calculated using Schoener's overlap index. Elephants did not overlap with giraffe and impala in food resource use in either Serengeti nutrient rich soils or Mikumi nutrient poor soils in both wet and dry season. Overlap observed was between giraffe and impala in Serengeti on dry season. Absence of overlap between elephants and these ungulates was contributed by reliance of elephants on grazing rather than browsing particularly in the wet season signifying influence of season in selectivity of food by elephants and impala.

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1. INTRODUCTION

1.1 Rich and poor savanna

African savanna has been described and categorized in many ways depending on the context in which it is observed. There are principle factors which determine vegetation and ungulate abundances and diversity. Huntley (1982) points out that moisture (precipitation) is a main factor leading to distinction between semi-arid and sub-humid savanna. He further concludes that in semi-arid savanna the nutrients in the soils are not exhausted by plants as growth is limited by water, allowing for a small production of nutrient rich plant material. These areas are known as nutrient rich savannas. In sub-humid savanna more water is available and more plant matter is produced. Nutrients in the soil are exhausted by plants and, plant growth is limited by availability of nutrients. These areas are known as nutrient poor savanna.

In comparison Bell (1982) argues that nature of underlying geological parent material have profound effects on soil nutrient availability and in turn determines the nutrient concentration of plant biomass found in a particular area. This influence of soil nutrient status, he suggests is partly independent of rainfall. For instance, the soil in the Serengeti short grassland plains is made up of volcanic ash giving high soil nutrient concentration. This results in vegetation with high nutrient levels and generally low plant biomass because of intense herbivory. Contrary, the soils found in *Brachystegia* woodlands of south western Tanzania are made up of ancient granitic shields and have poor soil nutrient status leading to low nutrient level in vegetation and generally to high plant biomass (Bell 1982). Both these areas receive about the same rainfall. Rainfall and soil parent material interact and characterize savannas as nutrient rich, often semi-arid and nutrient poor, generally sub-humid savanna (Bell, 1982; Huntley, 1982; Skarpe et al., 2008). Soil nutrient status influence overall vegetation quality, there are nutrient rich vegetations and nutrient poor vegetations which in turn affects plant defense and growth.

Plant growth is highly influenced by availability of resources which include water, nitrogen, phosphorus and other minerals which in turn also affects defenses capability and mechanism. Growth rate hypothesis which is among plant defenses hypotheses explains that genotypic variation of plant defense is largely determined by growth rate of plant which itself is influenced by resources availability (Coley et al., 1985; Stamp, 2003). This means that plants found in resource rich environment which allow maximal growth rate have different morphological and chemical defenses to plants found in nutrient poor environment.

Coley et al. (1985) further argued that presence of readily available resources have led species evolution in nutrient rich environments to have fast turnover of their plant parts and high growth rate of plants which have led to lower amounts of chemical defenses and the evolution of morphological defenses like spines. Meanwhile species evolved in nutrient poor environments evolved to have slow turnover of plants parts and slow growth rate to relate to scarce resource availability thus leading to higher concentration of chemical defenses to deter herbivores (Coley

et al., 1985). Supporting this concept of plant defense strategy in relation to nutrients availability, Skarpe and Hester (2008) comment that plants evolved in nutrient rich soils are adapted to fast growth and have high palatability to animals while plants in nutrient poor soils evolved to be inherently slow growing and invested heavily in defense.

Dynamics of African savanna are complex as there are several factors involved in changes between woodland and grassland in savanna. One notable hypothesis include destruction of woodland by elephants (*Loxodonta africana* (Blumenbach)) (Caughley, 1976). Another hypothesis includes the combination of elephants and fires in modifying woodland in Serengeti ecosystems (Dublin et al., 1990).

Prins et al. (1993) Suggest that intense browsing of impala (*Aepyceros melampus* (Lichtenstein)) and other medium sized herbivores in nutrient-rich grassland hinders woodland regeneration by browsing seedlings of *Acacia*. This was observed during a dramatic reduction of impala and other medium size herbivores during rinderpest outbreak which allowed seedling recruitment of *Acacia* trees in the Serengeti. To confirm this hypothesis an experiment was done along the Chobe riverfront by Moe et al. (2009) . The experiment aimed to conclude on survival of seeds and found that seedlings survival was much reduced by local impala population in open plots compared to semi-permeable enclosure and complete enclosure plots. In general it has been noted that in situation of low elephant density meso-browsers alone played a role in savanna dynamics by eating seedlings of woody species thus limiting woodland regeneration (O’Kane et al., 2011).

Another important aspect which exists in African savanna is the interaction between large and small herbivores. A model by van de Koppel & Prins (1998) argues that dynamics in the African savanna between woodland states and grasslands states is largely determined by interactions between large herbivores and small herbivores. Nature of interactions can be facilitation in woodland state in which large herbivores by removing dense vegetation of low quality facilitates small herbivore giving them access to high quality forage. On other hand it can be competition at grassland state where small herbivores dominate as a result of higher nutrient concentration in the vegetation, ability to utilize effectively low grasses resource that are inaccessible to large herbivores (Illius et al., 1987; Prins et al., 1998). High nutrient concentration in the soil on savanna is a major determinant factor for abundance of meso-herbivores at a given rainfall quantity in an area, thus favoring meso-herbivores dominance over mega-herbivores (Fritz et al., 2002).

1.2 Elephant, impala and giraffe

Elephant is categorized as a mega-herbivore as adult weight is from 2000-5000kg (Fritz et al., 2002). They have been observed to converse woodland to grassland and open up closed

vegetation through killing and destruction of many trees as they forage on them (van de Koppel et al., 1998). This was evidenced in Chobe National Park in Botswana where ungulate species in particular impala were positively impacted by elephant presence in favorable *Capparis tomentosa* and *Combretum mossambicense* shrublands found in the riverfront habitat, but not woodland in vast Kalahari nutrient poor sands though impala were absent (Skarpe et al., 2004).

Elephant, is a hind-gut fermenting mixed-feeder where most of digestion occurs in the hind gut (Clauss et al., 2003; Van Hoven et al., 1981). This is advantageous to them when compared to ruminants. Clauss et al., (2003) comment that above a body weight 600kg for browsers and 1200kg for grazers, ruminants no longer have an advantage over hindgut fermenters in terms of digestive efficiency. Elephants have a unique social systems, in which adult males are solitary and juvenile males leaves the family group when reached puberty between 10-15 years old. Most females live in a family group which normally consists of an old experienced matriarch, her adult daughters and their progeny. This family unit can be made of 2-12 individuals (Stokke et al., 2000).

Families do divide into small units or can fuse with other families to form a bigger clan (Wittemyer et al., 2005). The size of a family group varies a lot with season and is driven by food availability. During dry season groups split into small units, as one observed with two animals, a mature female and immature calf (Vance et al., 2009).

Giraffe (*Giraffa camelopardalis* (Linnaeus)) are the tallest and largest of all ruminants in African savanna. They are pure browsers and able to browse above the height levels accessible to smaller and mostly ruminant species (du Toit, 1990; Woolnough et al., 2001). Males are larger than females and adult males weigh 1200kg and females 800 kg (Ginnett et al., 1997). Males are also observed to be 20% taller than females (Young et al., 1991). Giraffe's social interaction is flexible as they may range as single individuals, but also gather in clusters of 20-40 animals, with solitary bulls being more common than solitary cows (Bercovitch et al., 2010).

Impala is a medium sized ruminant mixed feeder found in African savanna. A female mean body mass is 40kg. (Fritz et al., 1996). Impala are gregarious animals and occur in two types of groups which are bachelor groups and female groups, which in the breeding season are accompanied by one dominant male (Jarman et al., 1974). Their diet varies with season as in wet season they include more grass than browse and in the dry season they switch to more browsing than grazing to satisfy their metabolic energy demands (Kos et al., 2012; van der Merwe et al., 2014).

1.3 Interaction between elephant, giraffe and impala

Interspecific interactions between ungulates include competition and facilitation and can be influenced by food availability (Makhabu et al., 2006). Van de Koppel & Prins (1998) in their model comment that facilitation or competition between ungulates cannot be concluded following short time observations and it might mainly occur in one vegetation state (either woodland or grassland), and involves large herbivores and small herbivores.

Facilitation occurs where feeding of one herbivore increases accessibility of food to the same or other herbivore species (Guy, 1981; Makhabu et al., 2006; van de Koppel & Prins, 1998). This has been observed in Kruger National Park where browsing of giraffe stimulate shoot production and regrowth of new more palatable foliages which promote repeated foraging of ungulates (Cromsigt et al., 2011; du Toit et al., 1990).

This process might create a feeding loop, when browsing of an animal induces changes in plant shape and/or anatomy which leads to intense herbivory and further changes in the plant (Bergqvist et al., 2003; du Toit et al., 1990; Makhabu et al., 2006). But when the vegetation is in low biomass state (grassland) mega-herbivores in savanna have been observed to suffer from competitive exclusion from smaller herbivores who can eat little biomass (van de Koppel and Prins 1998). In particular small bite size in smaller herbivore is a very important feature as it permits access to areas of plants that a large herbivore, due to its physical dimension, cannot reach (Zavada et al., 1992). This evidence of competition was observed between elephants and wildebeest in which elephants were observed to stop foraging on grasses upon arrival of wildebeest (Dublin, 1995). Other evidence was observed in Sedudu island in Chobe river where elephant grazing was reduced on the patches which had been grazed by buffalo herds (*Syncerus caffer*) (Taolo, 2003).

Interaction between herbivores is further observed according to their body size and diet selection. Fritz et al. (2002) argued that mesomixed feeders and mesobrowsers were negatively affected by the abundance of megaherbivores particularly elephants as megaherbivores are abundant in areas with high rainfall and poor soil nutrient status, but megaherbivores do not affect mesograzers as these are dominant in areas with both high rainfall and good soil nutrient status.

Interaction observed between elephant as a mega-mixed feeder with meso-browsers and meso-mixed feeders is a good illustration of Jarman-Bell principle (Bell, 1971; Jarman, 1974). This explains that increase in body size is relative to gut capacity and slower passage time of food. This factor together with observed lower mass-specific metabolic energy requirement compared to small animals, allowed elephant and larger ungulates to tolerate low quality diet than small ungulates. (Woolnough & du Toit, 2001).

Elephants in particular as a mega herbivore achieve their energy demands by tolerating low quality forage and eat more abundant plant material and with the aid of their large mouthparts and trunk, help to maximize feeding (McNaughton et al., 1986). Elephant also plays a role in physical manipulation of vegetation as feeding of elephant and trampling helps to induce regrowth of new shoots of higher quality in both the herb and shrub layer thus facilitating smaller and more selective species (Fritz et al., 2002).

A study conducted at a nutrient rich area in Chobe National Park in Botswana reveals an important finding of interactions between elephant and meso-browsers and meso-mixed feeders. (Makhabu, 2005) concludes that elephants browsed different plant species relative to those which were browsed by giraffe and other ruminants signifying there was little food overlap between elephants and ungulates in the nutrient rich part of the park. This finding helped to have a better understanding of elephants browsing impacts to ruminants and the role of the hindgut fermenting digestive systems elephant posses relative to ruminants.

Tanzania savanna consists of both nutrient rich and poor soil habitats which are highly influenced by the nature of underlying geology (Bell, 1982), These two types of soils have significant influence on how plants respond to intense browsing by elephants and possible rebrowsing of meso-browsers and meso-mixed feeders (Skarpe & Hester, 2008).

This study was conducted to observe elephant foraging and its impacts on meso-browsers and meso-mixed feeders in areas with different soil properties, the nutrient rich soils and nutrient poor soils during the wet and dry seasons. The impacts to be observed was a possibility of competition of elephant to giraffe and impala in form of food overlap in these habitats with different soil properties and a possibility of facilitation of elephant feeding to giraffe and impala feeding through accumulated elephant impact on browsing species.

- In particular the study observed whether elephants and meso-mixed and meso-browsing ruminants select different tree species in Serengeti and same species in nutrient poor Mikumi.
- It further observed whether accumulated elephant impact facilitate foraging by giraffe and impala in nutrient rich Serengeti but not so in nutrient poor Mikumi.

2. METHODS

2.1 Study site

Serengeti National Park is part of greater Serengeti-Mara ecosystem which covers 25,000km² between 34° and 36°E, 1°15' and 3°30'S.(Sinclair et al., 1984), Serengeti has a semi-arid climate with mean maximum temperature of 27-28°C and minimum temperature vary from 16°C in the wet season in November-April, to 13°C in the dry season from May-September (Sharam et al., 2006). There are two rainfall seasons in which the short rains occurring in November – December, and the long rains in February-April. Annual rainfall ranges from 350mm in the southeast of the park to 1200mm in the northwest part of the park (McNaughton, 1985).

Serengeti is famous for its ungulate populations, and it is home to migrating ungulates which includes more than 1 million wildebeest (*Connochaetes taurinus* (Burcell)), hundred thousand zebras (*Equus quagga* Gray) and thousands Thomson's gazelles “*Gazella thomsoni* Gunther” (Dublin et al., 1990).

Serengeti composes nutrient rich volcanic soils and its vegetation comprises of vast grasslands in the south east of the park (Serengeti plains), rolling grasslands and woodlands to the west (western corridor) and north of the park. In detail vegetations in Serengeti has been described in terms of primary life forms and its density (Reed et al., 2009). In grassland vegetation there is open and dense grasslands according to density of the cover, for the woodland vegetation all of them have grassy undergrowth and it may be shrub grasslands or grasslands with trees. Both of them can be open or dense according to density of cover (Reed et al., 2009). Dominant species in the woodland includes *Acacia tortilies*, *Acacia robusta*, *Acacia mellifera* and *Acacia drepanolobium*.

Mikumi National Park is found on the northern part of the greater Selous Game Reserve, the size of the park is approximately 3230km². The park is transected by a tarmac road between Dar es Salaam and Iringa. The park is found between 7° 12'and 7 ° 20'S, 37° 08'and 37 ° 07'E. Annual rainfall in Mikumi is about 750-850mm, soil in Mikumi is nutrient poor as a result from underlying geology which is ancient granitic continental shields (Bell, 1982). The wet season is from November to May in which the full rainy season is experienced from March to May, the dry season is from June to October (Tanapa, 2007).

Mikumi harbors more than 300 bird species, 60 mammal species and more than 1200 registered plant species (Hawkins and Norton, 1998). Mammalian herbivores species which are mostly found include giraffe, impala, zebra, kudu (*Tragelaphus strepsiceros*), also elephant and buffalo are dominant herbivores and they migrate between Mikumi and Selous game reserve (<http://www.tanzaniaparks.com/mikumi.html>). Vegetations found in Mikumi can be classified into three habitat types when considering the elevation gradient. They are flood plain grassland

with low shrubs dominated by *Harrissonia abyssinica* found in the north part, mixed shrub savannah dominated by *Diospyros usambarensis* and *Combretum hereroense* found in the eastern part extending to the coast and the open Miombo-woodland which is the main dominant vegetation in Mikumi. That is primarily dominated by *Combretum zeyheri* and *Combretum collinum* this community is found in the south part of the park (Ginnett & Demment, 1997).

Generally Serengeti National Park is quite different from Mikumi in terms of Serengeti habitat composed of nutrient rich soils. This in turns has led to low plant biomass (grassland savanna) in the Serengeti and a higher diversity and density of meso-ungulates. Meanwhile Mikumi National Park has nutrient poor soils which have led to high plant biomass (woodland savanna) and Elephant and buffalo are the only dominant ungulate in this park.

2.2 Data collection

The study was done in two seasons: in the wet season early April to end of May 2014 and the dry season from mid August to mid October 2014. To obtain data a vehicle was driven at 20km/hr along a 3 road transects each about 70km, and stopped when a mature elephant, giraffe or impala were observed browsing within about 50m of the road. Observations at a distance were with binoculars. The tree species browsed was identified using field guide books for trees and shrubs (Dharani, 2002; Mbuya, 1994). To get browsing data a stopwatch was used to get time spent during browsing of our targeted mature animal. Parameters i recorded were name of plant species browsed, time spent browsing, which plant parts are browsed, height browsed by animal as observed on animal height sections, number of bites taken and accumulated elephant impact. When the browsing animal stopped browsing on a particular tree and shifted to another tree the routine of recording parameters started again. When the animal browsed for longer time recording was stopped at 15 minutes.

Accumulated elephant browsing impact was recorded for each browsed tree by assessing four classes, in which 0= no old browsing, 1= signs of old browsing and no impact on growth form, 2= signs of old browsing and impact on tree growth form and 3= old signs of browsing and strong impact on growth form of a tree. For those locations where visibility was obscured walking towards the species browsed was done to get accurate details.

2.3 Data analysis

Part of analysis done was performed using the R-software version 3.0.3 (R development core team, 2009).

To obtain proportion of diet composition of elephant, giraffe and impala the proportion of each plant species of the diet of the animal species was obtained and listed.

A possible feeding interaction between elephant, giraffe and impala was observed as overlap of food resources they consume. Overlap is estimated by several indexes but in our case Schoener index of overlap will be used as recommended by Makhabu (2005) as it meets all required criteria in choosing an overlap measure. The overlap of food resource will be in terms of plant species browsed, plant parts eaten and browsing height.

The formula describing the index is shown below,

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

Where O_{jk} is the overlap of objects eaten between animal species j and k . P_{ij} is the proportion of all browsing events of herbivore j of plant species i and P_{ik} is the same proportion but on herbivore k . Schoener's index ranges from zero to one, it is zero when species do not share any resource from 0.6 to one means there is significant sharing of resources between species (Wallace, 1981).

In R-software Schoener's index is found in spaa package. Overlap was estimated for different plant species, plant parts eaten and height of feeding of each herbivore.

For analysis of small scale facilitation or competition from elephant feeding to giraffe and impala in Serengeti nutrient rich habitat and Mikumi poor habitat, comparison of classes of accumulated elephant impact was done for major plant species browsed by each herbivore species. In detail when class 0 and 1 dominated as dominant accumulated elephant impact class of that browsed species it signifies no possible facilitation from previous elephant browsing events. But when class 2 and 3 dominates as dominant accumulated elephant impact classes of that browsed species it signifies a possible facilitation from previous accumulated elephant browsing events.

3. RESULTS

3.1 Proportion of plant species eaten.

Nutrient rich Serengeti had 19 tree species which were eaten by elephant, giraffe and impala which is more than the 15 tree species which were eaten by the same herbivores in nutrient poor Mikumi habitat. In nutrient rich habitat *Acacia* species together with *Cordia ovalis* and *Balanites aegyptiaca* contributed more than half of total browsing events signifying major influence of these plants to elephant, giraffe and impala browsing (Table 1).

Within nutrient rich Serengeti habitat there was a notable difference in browsing events between wet and dry season. Dry season had more browsed species relative to species browsed in wet season (Table 1).

Table 1; Proportion of plant species browsed in Serengeti National park (nutrient rich habitat).

Plant species	Elephant		giraffe		Impala	
	Wet season	Dry season	Wet	dry	Wet	Dry
<i>Acacia mellifera</i>	0.000	0.090	0.019	0.031	0.100	0.054
<i>Acacia robusta</i>	0.500	0.313	0.019	0.062	0.000	0.000
<i>Acacia tortilis</i>	0.100	0.261	0.587	0.395	0.200	0.447
<i>Acacia drepanolobium</i>	0.000	0.000	0.260	0.185	0.000	0.000
<i>Balanites aegyptiaca</i>	0.200	0.022	0.010	0.031	0.00	0.053
<i>Acacia kirkii</i>	0.000	0.008	0.010	0.105	0.000	0.000
<i>Cordia ovalis</i>	0.000	0.224	0.038	0.124	0.300	0.132
<i>Grewia bicolor</i>	0.100	0.000	0.010	0.000	0.000	0.132
<i>Commiphora africana</i>	0.000	0.022	0.000	0.000	0.000	0.000
Forbs	0.100	0.000	0.000	0.000	0.200	0.000
<i>Capparis tomentosa</i>	0.000	0.008	0.000	0.000	0.000	0.000
<i>Grewia fallax</i>	0.000	0.015	0.000	0.000	0.000	0.000
<i>Hibiscus cannabinus</i>	0.000	0.008	0.000	0.012	0.000	0.000
<i>Phoenix reclinata</i>	0.000	0.015	0.000	0.000	0.000	0.000
<i>Sanseveria ehrenbergiana</i>	0.000	0.007	0.000	0.000	0.000	0.000
Unknown Shrub	0.000	0.008	0.000	0.019	0.000	0.053
<i>Dichrostachys cinerea</i>	0.000	0.000	0.010	0.006	0.000	0.000
<i>Harissonia abyssinica</i>	0.000	0.000	0.000	0.000	0.100	0.000
<i>Albizia amara</i>	0.000	0.000	0.000	0.006	0.000	0.026
<i>Ziziphus mucronata</i>	0.000	0.000	0.010	0.062	0.100	0.026

In nutrient poor Mikumi National Park, elephant had fewer total browsing incidences in relation to other browsers and in those browsing incidences *Philenoptera violacea* was the most preferred plant species (Table 2). In general *Acacia xanthophloea* was the only plant species which was browsed by all our studied browsers. Giraffe proportion of browsing events in nutrient poor Mikumi was dominated by *Harissonia absyynica* and *Spirostachys africana* in the wet season and *Balanites aegyptiaca*, *Capparis tomentosa* and *Combretum fragrans* in the dry season (Table 2). For the case of impala in Mikumi browsing proportion was dominated by *Hoslundia opposita* which accounted for half of total browsing incidences in the wet season, in dry season browsing proportion was dominated by *Harissonia abyssinica* and *Balanites aegyptiaca* (Table 2)

Table 2; Mikumi National park (Nutrient poor habitat), plant species browsed proportion.

Plant species	Elephant		Giraffe		Impala	
	Wet season	Dry season	Wet	dry	Wet	Dry
<i>Acacia xanthophloea</i>	0.429	0.167	0.081	0.141	0.000	0.013
<i>Combretum fragrans</i>	0.000	0.000	0.035	0.155	0.063	0.027
<i>Capparis tomentosa</i>	0.000	0.000	0.058	0.197	0.125	0.027
Forbs	0.000	0.000	0.023	0.000	0.063	0.000
<i>Harissonia abssyynica</i>	0.000	0.000	0.407	0.014	0.063	0.280
<i>Hoslundia opposite</i>	0.000	0.000	0.000	0.000	0.500	0.000
<i>Philenoptera violacea</i>	0.429	0.667	0.023	0.000	0.063	0.000
<i>Spirostachys africana</i>	0.000	0.000	0.302	0.000	0.125	0.000
<i>Senna didymobotria</i>	0.000	0.000	0.058	0.042	0.000	0.013
Shrub roots	0.143	0.000	0.000	0.000	0.000	0.000
<i>Syzygium sp.</i>	0.000	0.000	0.012	0.000	0.000	0.000
<i>Hoslundia sp.</i>	0.000	0.167	0.000	0.000	0.000	0.000
<i>Acacia senegal</i>	0.000	0.000	0.000	0.127	0.000	0.013
<i>Balanites aegyptiaca</i>	0.000	0.000	0.000	0.352	0.000	0.160

<i>Securinega virosa</i>	0.000	0.000	0.000	0.000	0.000	0.107
<i>Senna siamea</i>	0.000	0.000	0.000	0.028	0.000	0.000

3.2 Overlap of food resources utilized between elephant, giraffe and impala.

To check if there are possible interspecific interactions between these mammalian herbivores, overlap of resource use was calculated. For plant species which were browsed by elephant, giraffe and impala, the only significant overlap (Schoener's index >0.6) was between giraffe and impala during dry season in Serengeti nutrient rich habitat (Table 3).

For elephants in Serengeti and Mikumi there is no overlap with plant species browsed by giraffe and impala (Table 3). Though in Serengeti during dry season a near interaction of plant species browsed is noted as Schoener's index value is 0.522.

Table 3; Schoener's overlap indices indicating possible plant species overlap between elephant, giraffe and impala.

Plant species	Serengeti		Mikumi	
Herbivore combination	Wet season	Dry season	Wet season	Dry season
Elephant/Giraffe	0.139	0.522	0.108	0.014
Elephant/Impala	0.200	0.475	0.063	0.167
Giraffe/Impala	0.267	0.611	0.123	0.429

Plant parts browsed by elephant, giraffe and impala were also calculated to assess if there is overlap in parts of plant eaten by elephant, giraffe and impala. Elephant showed no overlap at all (Schoener's index <0.6) in plant parts browsed with giraffe and impala (Table 4). Also giraffe showed no overlap in plant parts eaten with impala (Table 4).

Table 4: Overlap in plant parts browsed by elephant, giraffe and impala from Schoener's overlap indices.

Plant species	Serengeti		Mikumi	
Herbivore Combination	Wet season	Dry season	Wet season	Dry season
Elephant/giraffe	0	0.0449	0	0.336
Elephant/impala	0	0.0451	0	0.012
Giraffe/impala	0.233	0.0486	0.304	0.40

In height overlap between these herbivores, elephant showed a near height overlap (Schoener's index 0.5) with impala wet season Serengeti nutrient rich habitat (Table 5). Overall there was no height overlap in either Serengeti or Mikumi (Table 5).

Table 5: Overlap in height used during browsing by elephant, giraffe and impala from Schoener's overlap indices.

	Serengeti		Mikumi	
Herbivore Combination	Wet season	Dry season	Wet season	Dry season
Elephant/giraffe	0.142	0.432	0.312	0.371
Elephant/impala	0.500	0.170	0.286	0.400
Giraffe/impala	0.009	0.045	0.078	0.043

3.3 Comparison of Accumulated elephant impacts between elephant, giraffe and impala in major plant species browsed by all animals.

3.2.1 In Serengeti nutrient rich habitat

3.2.1.1 *Acacia robusta*

Elephant browsing on *Acacia robusta* showed a possibility of small scale facilitation as browsing events had majority of class 2 and 3 accumulated elephant impact (Fig 1). For giraffe there was no facilitation observed on *Acacia robusta* as browsing observations were similarly low in all accumulated elephant impact (Fig 1). Impala did not browse this species at all in Serengeti.

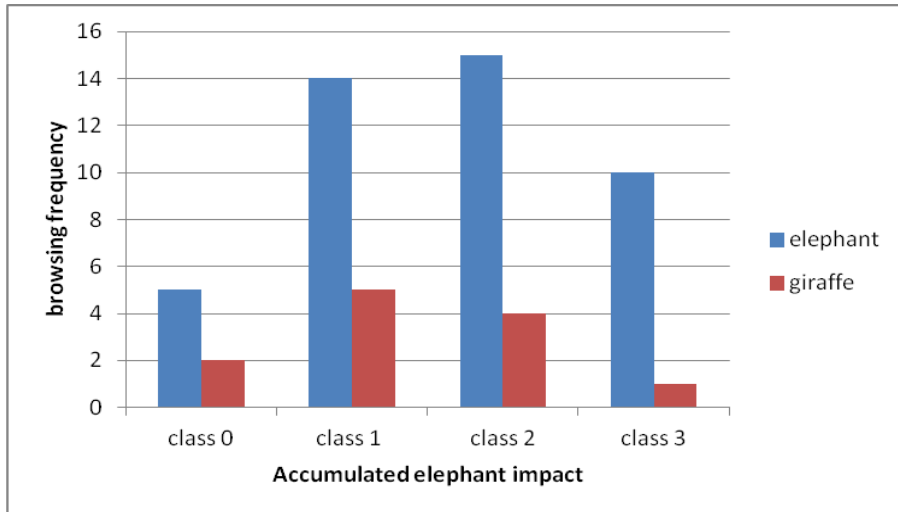


Fig 1: distribution of accumulated elephant impact classes of *Acacia robusta* which was browsed in Serengeti

3.2.1.2 *Acacia tortilis*

This species was browsed by all animals, for giraffe this tree species showed strongest evidence of facilitation as majority of observations are in class 2 and some class 1 and 3 (Fig 2) signifying a possible facilitation from previous elephant browsing events. for elephant and impala browsing observations were similarly low in all accumulated elephant impact to justify facilitation from previous accumulated elephant impact (Fig 2).

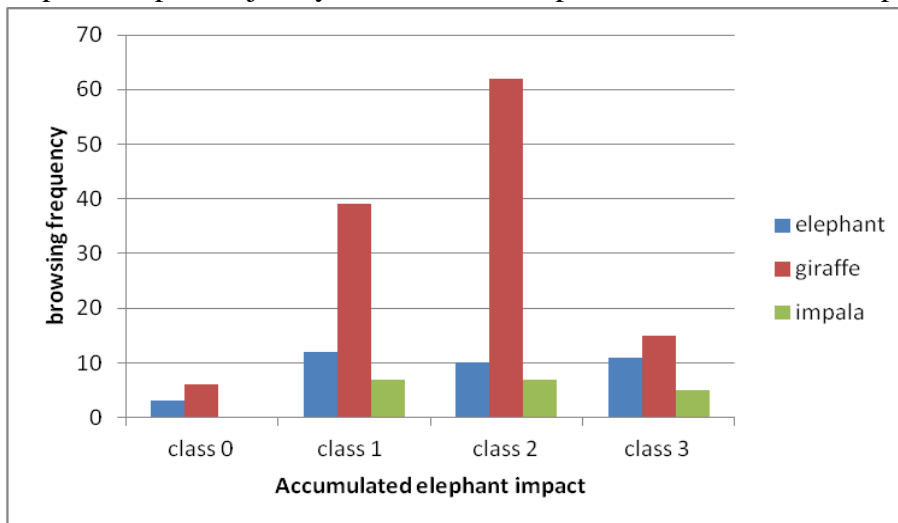


Fig 2: Distribution of accumulated elephant impact classes of *Acacia tortilis* browsed in Serengeti.

3.2.1.3 *Cordia ovalis*

No possible facilitation was observed for any of the three animals (elephant, giraffe and impala) as dominant browsing observations were found in class 0 and 1

accumulated elephant impact class which signify no facilitation but possibly avoidance from previous elephant browsing impacts (Fig 3).

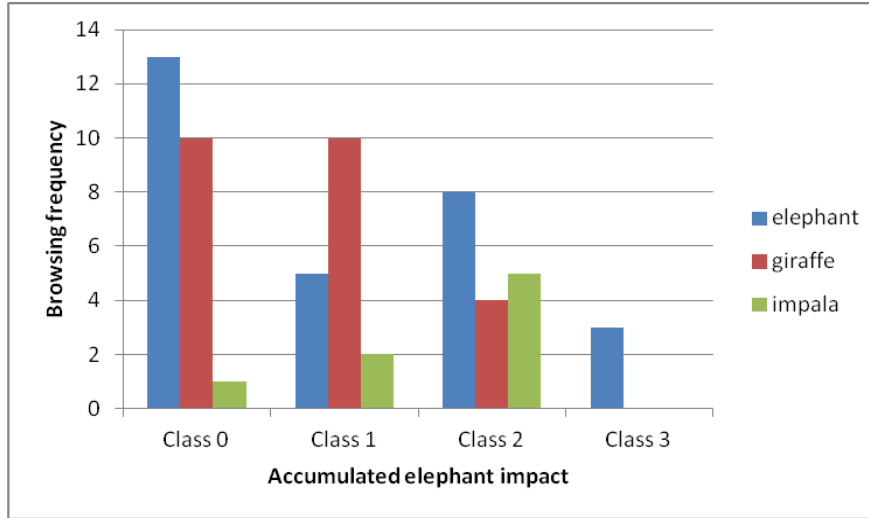


Fig 3: Distribution of accumulated elephant impact classes of *Cordia ovalis* browsed in Serengeti.

3.2.2 Mikumi nutrient poor habitat.

3.2.2.1 *Philenoptera violacea*

Elephant, giraffe and impala showed possible facilitation as distribution of accumulated elephant impact classes on this plant species were all in 2 and 3 signifying a possible facilitation from past elephant browsing events (Fig 4).

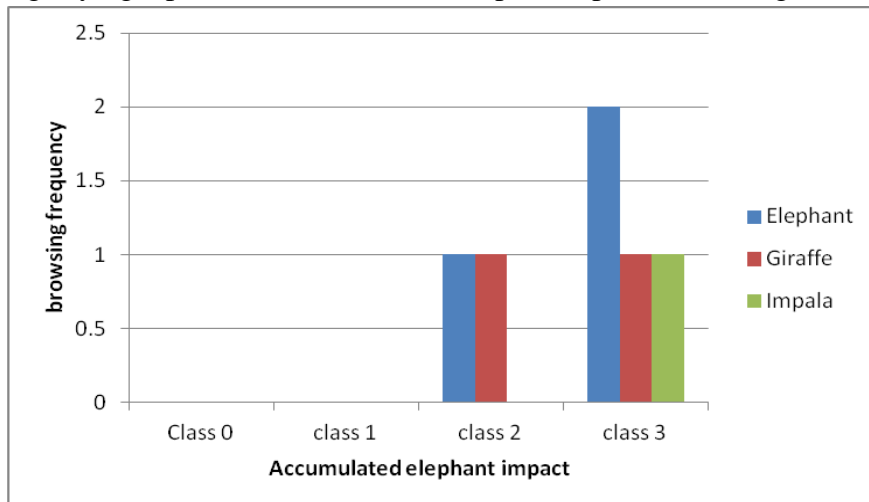


Fig 4: Distribution of accumulated elephant impact classes of *Philenoptera violacea* browsed in Mikumi.

3.2.2.2 *Acacia xanthophloea*

This species was browsed by elephant and giraffe and not by impala. There is no facilitation from previous elephant browsing as observed browsing by both elephant and giraffe primarily targeted class 0 and 1 accumulated elephant impact classes (Fig 5).

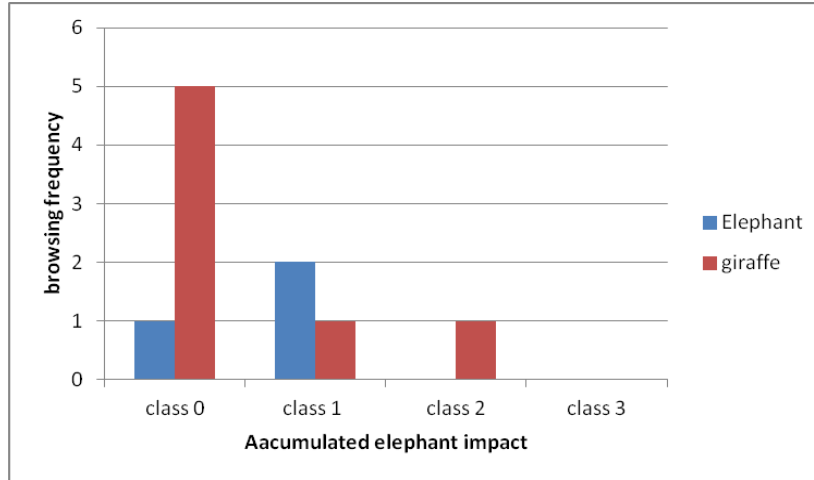


Fig 5: Distribution of accumulated elephant impact classes of *Acacia xanthophloea* browsed in Mikumi.

4. DISCUSSION

Elephant have been observed mainly to browse different plant species compared to giraffe and impala in both Serengeti and Mikumi habitats, with exception of *Acacia tortilis* in Serengeti habitat (Table 1, 2). This result supports my prediction that elephant should browse different plant species to giraffe and impala in Serengeti nutrient rich, but it rejects my prediction that elephant should browse same plant species as giraffe and impala in nutrient poor Mikumi.

In Serengeti elephant have browsed large proportion of *Acacia robusta* compared to *Acacia tortilis* which was the dominant plant species browsed by giraffe and impala. Main reason of why elephant browsed this species can be that *Acacia robusta* has higher level of chemical defense compounds relative to *Acacia tortilis* as evidenced from Chobe National park (Skarpe et al., 2003). Elephants as mega-herbivores are relatively more tolerant to forage of poor quality than are ruminants (giraffe and Impala). Thus elephants browsed *Acacia robusta* which is highly abundant while ruminants in my study preferred high quality *Acacia tortilis* as confirmed with Jarman-Bell principle (Bell, 1971; Jarman, 1974). In addition difference in digestive systems has allowed elephant, a hind gut fermenter, to forage on lower quality food than ruminants (Clauss et al., 2003). These reasons also explain for the difference in diets of elephant relative to giraffe and impala (ruminants).

In Mikumi elephant browsed entirely different plant species relative to giraffe and impala, this finding rejects my prediction that in nutrient poor habitat elephants will browse the same plant species as giraffe and impala (Table 2). This result was further supported by checking possible plant species overlap between elephant a mega-herbivore, giraffe meso-browser and impala as mixed-feeder. In Mikumi there is not any overlap in plant species observed between elephant, giraffe and impala (Table 3). This confirmed rejection of hypothesis which proposed possible food overlap between elephant with giraffe and impala in nutrient poor Mikumi, also prediction by (Fritz et al., 2002) where they proposed that elephants as mega-herbivores should compete with abundances of meso-browsers (in our case giraffe) and meso-mixed feeder (impala).

Absence of overlap in Mikumi can be caused by a congregation and clustering of elephants in a small part of the park relative to scattering of giraffe and impala which was observed personally also (rangers communications). This might be a response to intensive poaching of elephants occurring in peripheral areas around the park. This clustering in a small part of the park led to elephants not browsing a range of available plants in the park and also relying on grazing at most of the time instead of browsing. Also presence of rains during the dry season led to elephants continuing to graze more than browse as grass was still greener and more nutritious than browse. This observation of greenness in grassland vegetation in Mikumi is consistent with other studies which confirms green landscape being nutritionally superior and preferred by elephants (Loarie et al., 2009).

Overlap in plant species (table 3) showed there is no overlap between elephant and these ruminants, though in dry season there is a Schoener's index of 0.52. But in Serengeti during dry season there is an overlap of plant species browsed between giraffe and impala. Overall this result confirmed my main hypothesis which predicted that elephant being mega-herbivore and hind-gut fermenter should browse different plant species from giraffe and impala. For giraffe and impala overlap in plant species browsed may be because impala switch from grazing to browsing in the dry season as confirmed in a study by Kos et al. (2012) where they found decrease in nutrients in grass during dry season forces impala to shift to browse resources. Also this highlights the influence of seasons to impala food selectivity.

Another support to my main prediction of elephant interaction with meso-browser and mixed-feeders in nutrient rich Serengeti is in the wet season where there is no overlap between the species in plant species browsed (Table 3). In wet seasons elephants prefer to eat grass more than browse due to higher nutrient quality, this preference of grass is observed for both sexes as in Ruaha National Park, Tanzania (Barnes, 1982). This reliance of grazing rather than browsing of elephants, signify the influence of season in their overall diet composition. Impala shows the same pattern, with food overlap with giraffe in the dry season but no food overlap in wet season (Table 3). Elephant and impala being mixed feeders have adapted to switching from grazing during wet season to browsing in the dry season influenced by decrease in quality of monocot food over dicot food (Codron et al., 2006; Kos et al., 2012).

Interaction between these mammalian herbivores was further assessed according to plant parts which were browsed and it showed no overlap between elephant, giraffe and impala in either nutrient rich or nutrient poor habitat (Table 4). This result supports my prediction of elephant as mega-herbivore to browse different plant parts relative to giraffe and impala. Elephant browsing was observed to constitute mix of twigs and leaves, while giraffe browsing constitute large proportion of mix of leaves and twigs and a small percent of leaves. For impala it was opposite to these large browsers and its browsing was observed to include more than 90% of leaves and a very small fraction of mix of twigs and leaves. With this observation it was impossible to have an overlap of plant parts eaten. This finding is a good illustration of classical Jarman-Bell principle which explains that large ungulates are tolerant of foraging on low quality diets compared with small ungulate (Woolnough & du Toit, 2001). In this case it was observed that impala as a small ungulate preferred to eat leaves which have high nutrient quality compared to the larger browsers elephant and giraffe which were observed to eat more of twigs and less of leaves.

Height overlap is also a good way to check for possible interspecific interaction between browsers. It has been found to reduce competition between browsers (du Toit, 1990; Makhabu, 2005). The study found no overlap in height browsed between giraffe, elephant and impala, giraffe browsed above average height browsed by elephant and impala. This results of no height overlap between giraffe and other browsers in our study confirms what has been observed in other studies, that giraffe browse at higher levels above the range of most browsers to avoid competition (du Toit, 1990; Makhabu, 2005). For the case of elephant and impala there was no height overlap but a tendency to overlap in Serengeti wet season (Schoener's index=0.5, Table 5). This might depend on the fact that elephants tend to browse at low levels in some plant species (du Toit, 1990).

My hypothesis on possibility of facilitation of elephant feeding to giraffe and impala on nutrient rich and poor soils was accepted in some plant species and rejected in other species. In Serengeti *Acacia tortilis* is the only plant species which showed a possibility of facilitation from previous accumulated elephant impacts to all animals (elephant, giraffe and impala), this finding confirms my hypothesis of possible facilitation in Serengeti nutrient rich habitat. *Acacia tortilis* have less chemical defense compounds compared to *Acacia robusta* (Skarpe et al., 2003), which may attribute it to be preferred by ruminants like giraffe. This species it has been noted to be dominant in Seronera woodland which was part of our transect in Serengeti, it comprises more than 40% of tree species in the area (Pellew, 1983)

Acacia robusta had high accumulated impact and facilitated elephant browsing in Serengeti. This may be as a result of it being more abundant in Serengeti and having higher level of chemical defense relative to *Acacia tortilis* which is the next abundant plant in Serengeti. This factor together with the need to maximize their total energy intake, forced elephant to expand their diets to include lower quality, more abundant plant material (McNaughton & Georgiadis, 1986) like *Acacia robusta*. *Cordia ovalis* is another dominant species which was browsed by our

mammalian herbivores in Serengeti (Table 1), but this species showed no possibility of facilitation from previous elephant impacts which is contrary to my prediction of facilitation from elephants in nutrient rich Serengeti.

In Mikumi all herbivores (elephant, giraffe and impala) showed to be facilitated to browse *Philoneptera violacea* in higher classes of accumulated elephant impact, which is against my prediction of no facilitation from accumulated elephant impact in Mikumi. *Philoneptera violacea* is a prominent tree in nutrient poor savanna and in alluvial soils near rivers, where it has been studied and observed to have ability to fix nitrogen from air though this ability depends on age of plant and on low soil nitrogen conditions (Jacobs et al., 2007). This important feature of the species may explain why it was highly browsed in Mikumi and showed to facilitate our browsers from previous elephant browsing impacts against our prediction of no facilitation.

For *Acacia xanthophloea* it showed no possibility of facilitation from previous accumulated elephant impact to giraffe and impala, this finding supports my prediction of no facilitation from elephant in nutrient poor soils of Mikumi. Plants species in nutrient poor Mikumi like *Acacia xanthophloea* have evolved avoidance traits which discourage future browsing by producing new shoots and leaves which have invested highly in chemical carbon based quantitative defense meanwhile species in nutrient rich Serengeti have evolved to have tolerance to herbivory and use qualitative non-carbon based defense (Coley et al., 1985; Skarpe et al., 2014) This factor is a main reason of no possibility of facilitation from elephant in vegetation with nutrient poor soils.

My study agrees in some part other studies by Guy (1981); Makhabu et al. (2006) they found that elephant browsing do result in more browse to be available to other browsers and meso-herbivore prefers trees with accumulated elephant impact. But in my study it was in nutrient rich Serengeti with exception of *Cordia ovalis* where accumulated elephant impact showed influence on browsing. Also the study points out the influence of season to food selectivity of either grass or browse in elephant and impala influenced by nutrient content. In general this study continues to stress the benefits of coexistence of elephants to ungulates as observed being a keystone species in savanna by opening up vegetation to other mammalian herbivores (Owen-Smith, 1989). This is contrary to past finding of elephant destructive behavior on vegetations (Caughley, 1976) which advocate the need to control elephant populations.

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