

Understanding foraging behaviour of wild animals is an important step for wildlife management and conservation and for learning the animal's role in the ecosystem. I used Maasai giraffe (*Giraffa camelopardalis tippelskirchi* Matschie) as a study animal to see how foraging decisions of giraffe varied in three study sites; Arusha National Park, Mikumi National Park and Serengeti National Park, Tanzania, with focus on Arusha National Park (from here on referred to by names). My focus was on how giraffe make foraging decisions matching the vegetation in a heterogeneous savannah.

I set up the following specific questions;

- (I) does selection criteria differ with hierarchical scales?,
- (II) how do giraffe browse in relation to the trade-off between intake rate and quality selection
- (III) which activities are most important for giraffe, and how and why do activities vary in time?
- (IV) do foraging decisions differ between sexes and environments?

Visual observations were used to collect data on foraging behaviour in both dry and wet seasons in the year 2013 and 2014.

In the first study, our results showed that in Arusha occurrence of *Acacia xanthophloea* was the main determinant of foraging decisions used by giraffes across all scales. In the second study in Arusha giraffe fed mainly from spinescent trees, such as *Acacia xanthophloea*, giving lower intake rate than the spineless trees, but assumed to be nutrient-rich. The third study, also in Arusha, focused on how giraffe allocated time into different activities, and found that time spent on feeding, resting and socializing was influenced by season but did not relate to each other. The fourth study compared sexual segregation in giraffe between Arusha, Serengeti and Mikumi, and focused on whether foraging decisions of giraffes differ between sexes in the nutrient rich and nutrient poor environments. We found that female and male foraging patterns were influenced by variation in tree chemistry and differences in the competing herbivore communities.



FACULTY OF APPLIED ECOLOGY AND AGRICULTURAL SCIENCES

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PHD DISSERTATION

BROWSING BY GIRAFFE IN HETEROGENEOUS SAVANNA

PHD IN APPLIED ECOLOGY

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- No.7 - 2016: **Obeid John Mahenya:** *Browsing by Giraffe in heterogeneous savanna*



Faculty of Applied Ecology and Agricultural Sciences

Obeid John Mahenya

PhD Thesis

Browsing by giraffe in heterogeneous savanna

PhD in Applied Ecology

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Preface

The colour, height and peaceful movement of giraffe caught my interest to study it already as a boy. The idea, however, became real first when I received a scholarship from Norwegian Government through Hedmark University of Applied Sciences in 2012.

I am extremely thankful to my supervisors; Professor Christina Skarpe and Associate Professor Karen Marie Mathisen for their excellent knowledge, supervision, criticisms, comments, views and super reception from the first time I arrived in Evenstad to completion of my studies, hurray! I am thankful to Professor Harry Peter Andreassen, Associate Professors Olivier Devineau and Karen Marie Mathisen for their statistical solutions and statistics skills transferred to me and their time when need arose, thank you very much. Once again, many thanks to Professor Christina Skarpe for being with us in the field during data collection and being able to spend several days in the Park and sleep in a tent without fear of wild animals. Special appreciation is expressed to field research assistant Johannes Ndjamba for his time and energy spent in data collection. I am grateful to Evenstad campus staff; librarians, administrators and everyone in the campus for your excellent services rendered to me whenever deemed necessary.

Thanks to the Norwegian Government and Hedmark University for financial support and to the United Republic of Tanzania and Mweka College for permitting me to pursue further studies in Norway. Thanks to my family for their love and encouragement during my study. Special thanks to my wife Jovina Lamberth Kishato for the love and patience and for taking care of the family during my absence. I would like to thank my children; Lugano, Jonas, Lusajo and Mesija for their patience and support. I appreciate my brothers, sisters and uncles for their support and the love they showed to my family during my absence. I would like to thank the almighty God for giving me power and energy to work and enjoy academic life even at dark times.

Thanks to my Tanzanian friends; Rosemary Mramba, Innocent Joseph, Yuster Mnzeru, Janeth Mbuma, Julius Lasway, Sylvester Mirigo and Suzan Ivan for their company during my stay in Norway. Thanks to Norwegian friends for welcoming me to Norway and spending time together during summer barbecues and *biotopen* music.

I acknowledge my PhD colleagues for their discussions in the office and the social time we enjoyed on Friday (Sifrøl) in the end of every month, master students and everyone in Evenstad for your companionship. *Tusen takk- ahsante sana!*

Summary

Understanding foraging behaviour of wild animals is an important step for wildlife management and conservation and for learning the animal's role in the ecosystem. I used Maasai giraffe (*Giraffa camelopardalis tippelskirchi* Matschie) as a study animal to see how foraging decisions of giraffe varied in three study sites; Arusha National Park, Mikumi National Park and Serengeti National Park, Tanzania, with focus on Arusha National Park (from here on referred to by names). My focus was on how giraffe make foraging decisions matching the vegetation in a heterogeneous savannah. I set up the following specific questions; (i) does selection criteria differ with hierarchical scales?, (ii) how do giraffe browse in relation to the trade-off between intake rate and quality selection (iii) which activities are most important for giraffe, and how and why do activities vary in time? (iv) do foraging decisions differ between sexes and environments? Visual observations were used to collect data on foraging behaviour in both dry and wet seasons in the year 2013 and 2014. In the first study, our results showed that in Arusha occurrence of *Acacia xanthophloea* was the main determinant of foraging decisions used by giraffes across all scales. In the second study in Arusha giraffe fed mainly from spinescent trees, such as *Acacia xanthophloea*, giving lower intake rate than the spineless trees, but assumed to be nutrient-rich. The third study, also in Arusha, focused on how giraffe allocated time into different activities, and found that time spent on feeding, resting and socializing was influenced by season but did not relate to each other. The fourth study compared sexual segregation in giraffe between Arusha, Serengeti and Mikumi, and focused on whether foraging decisions of giraffes differ between sexes in the nutrient rich and nutrient poor environments. We found that female and male foraging patterns were influenced by variation in tree chemistry and differences in the competing herbivore communities.

Sammendrag

For viltforvaltning, bevaringsbiologi og for å lære ulike dyrs rolle i økosystemene er det viktig å forstå deres spiseatferd. Jeg har brukt Maasai giraffer som studieobjekt for å studere giraffers spiseatferd i 3 nasjonalparker i Tanzania: Arusha, Mikumi og Serengeti, med hovedvekt på Arusha nasjonalpark. Jeg har studert hvordan giraffer velger hva de spiser i forhold til den tilgjengelige vegetasjonen i heterogene savanner. Jeg har satt opp følgende problemstillinger: (i) vil valg av spiseatferd avhenge av romlig skala fra regioner, landskaper, vegetasjonspatcher og helt ned til en enkelt plante; (ii) hvordan velger giraffer mat avhengig av spisefrekvens og kvaliteten på maten; (iii) hvilke aktiviteter er viktigst for giraffer, og hvordan og hvorfor varierer aktiviteter i tid; og (iv) er det forskjell i spisemønsteret mellom kjønn og miljø. Data ble samlet gjennom å observere giraffers spiseatferd både i tørke- og regntiden, i 2013 og 2014. I Arusha foretrakk giraffene den tornete *Acacia xanthophloea* på alle romlige skala. Kvistene spist var større, og giraffene hadde dermed også en lavere spisefrekvens enn for mange andre plantearter uten torner. Tid brukt til å spise, hvile og sosialisere, var først og fremst avhengig av årstid – tørke- og regntid. Begge kjønn valgte beiteplanter forskjellig i næringsrik og næringsfattige savanner. Den sterke preferansen for *Acacia xanthophloea*, spesielt hos hunner, i den mellomrike Arusha nasjonalpark skyldes at det der var en lav tetthet av giraffer.

List of publications

The present thesis is the outcome of the four papers listed below;

- I. Mahenya, O., Mathisen, K.M., Andreassen, H.P & Skarpe, C. (2016). Hierarchical foraging by giraffe in heterogeneous savannah, Tanzania. *African Journal of Ecology*, 54, 136–145
- II. Mahenya, O., Ndjamba, J.N., Mathisen, K.M. & Skarpe, C. (2016). Giraffe browsing in response to plant traits. *Acta Oecologica*, 75, 54-62
- III. Mahenya, O., Mathisen, K.M. & Skarpe, C. (2016). How activity budget of giraffes varies with season. (Submitted)
- IV. Mramba, R.P, Mahenya, O., Siyaya, A., Mathisen, K.M, Andreassen, H.P & Skarpe, C. (2016). Sexual segregation in foraging giraffe (Accepted, *Acta Oecologica*)

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Introduction

Herbivore foraging and tree defences

The interaction between herbivores and plants depends on the resource availability in the environment and on the history of herbivory in the region. Plants utilize resources for growth and reproduction and to defend themselves from herbivory (Herms & Mattson 1992; Skarpe *et al.* 2000; Stamp 2003). Herbivores feed selectively on plants or plant parts to maximize intake rate of nutrients and digestible energy while avoiding chemical and mechanical plant defences (Herms & Mattson 1992; Coley & Barone 1996; Skarpe *et al.* 2000). Herbivores here refer to ungulates (including elephant, *Loxodonta africana*). These can be grouped into hindgut fermenters and foregut fermenters, the latter group including ruminants (Illius & Gordon 1992; Clauss *et al.* 2003), or into grazers and browsers depending on the type of food they prefer (Bergström 1992; Shipley 1999). Grazers feed on graminoids such as grasses and sedges (Gordon & Prins 2008). Browsers feed on various parts of woody plants, including leaves, twigs, thorns, bark, wood, bulbs, tubers, roots, flowers and seed pods and on dicotyledonous forbs (Pellew 1984a; Bergström 1992; Shipley 1999). Some ungulates are regarded as mixed or intermediate feeders, usually belonging to the browsing guild in the dry season and to the grazing guild in the wet, such as impala, *Aepyceros melampus*, and elephant (Bergström 1992; Searle & Shipley 2008).

The statement “The world is green” (Hairston, Smith & Slobodkin 1960) does not mean that all plants are food for herbivores or that what is food for one herbivore is food for all herbivores. In fact, there is more poor quality food (low concentration of nitrogen, high concentration of fibre and phenolics) available than high quality food (high concentration of nitrogen and low concentration of fibre and phenolics) (Senft *et al.* 1987; Sinclair 2006). This suggests that large

herbivores encounter a large quantity of plant material but of low quality, hence forage selection for high quality is important for large herbivores. Through co-evolution of plants and herbivores, and plant adaptation to other factors such as fire and drought, plants have acquired sets of mechanisms to deter herbivory or tolerate herbivory in order to maximise fitness in different environments (Strauss & Agrawal 1999; Skarpe *et al.* 2000; Espinosa & Fornoni 2006; Skarpe & Hester 2008). Plants show avoidance traits or tolerance traits to herbivory; long thought to be exclusive, but now also found to be used by the same plant (Dannel 2006; Skarpe & Hester 2008). The avoidance strategy may include; allocating edible biomass above reach of terrestrial animals, growing in inaccessible areas, producing deterring or poisonous chemicals, having low or unbalanced nutrients or spines (Coley, Bryant & Chapin III 1985; Stamp 2003).

A plant may be regarded as browsing tolerant if it develops traits that minimize long term effects of browsing by maximizing resource uptake and growth (Jefferies, Klein & Shaver 1994; Dannel 2006; Skarpe & Hester 2008). Tolerant plants are commonly occurring in resource rich environments where plants compete by growth and cannot spare carbon to produce defences (Herms & Mattson 1992; Skarpe & Hester 2008). Examples of tolerance traits may include; numerous protected meristems being able to produce many fast growing shoots, high and flexible rates of nutrient acquisition, photosynthesis and growth (Skarpe & Hester 2008). Both avoidance and tolerance strategies have a cost to the plant and only pay off if the gain in resources saved by the trait is larger than the cost (Herms & Mattson 1992; Skarpe & Hester 2008).

The regrowth after browsing would intuitively be expected to show induced defences in the form of increased chemical defences or intensified spinescence (Young 1987; Gowda 1997; DeAngelis *et al.* 2015). However, several studies with both simulated and real browsing have demonstrated that browsed trees generally, but not always, are more palatable than unbrowsed conspecifics

(Bergström, Skarpe & Danell 2000; Skarpe *et al.* 2000; Mahenya *et al.* 2016b). As the number of buds is reduced from browsing, these trees grow fewer but larger shoots compared to un-browsed trees (Bergström & Danell 1987; Bergström 1992; Bergström, Skarpe & Danell 2000; Rooke *et al.* 2004; Rooke & Bergström 2007). These shoots might be richer in nitrogen and phosphorous, whereas tannins concentrations might be greatly reduced (Scogings, Hjältén & Skarpe 2011). These shoots give a large bite size and high nutrient concentrations. They grew fast, and are according to the plant vigour hypothesis (Price 1991) much browsed (Makhabu *et al.* 2006). Thus, previously browsed, tolerant trees might encourage future browsing as is often observed (du Toit, Bryant & Frisby 1990; Skarpe *et al.* 2000; Mahenya *et al.* 2016b). On the other hand, herbivores have evolved strategies to deal with plant defensive mechanisms (Herms & Mattson 1992; Skarpe *et al.* 2000) and the effect of tannins and phenolics is reduced by salivary tannin-binding proteins (Fickel *et al.* 1998).

Different food requirement in relation to the size of animals

The Jarman –Bell principle explains the different food requirement in relation to the size of the herbivore (Bell 1971; Jarman 1974; Demment & Van Soest 1985). Large herbivores require much forage but it can be of poor quality (high concentration of fiber and phenolics), whereas small herbivores require little forage but of high quality (low concentration of fiber, high concentration of nutrients). Large bodied animals can feed on poor quality forage, because they have low metabolic requirement/gut capacity ratio compared to small ones (Bell 1971; Jarman 1974). Metabolic requirement scales to the body mass with $3/4$ (metabolic mass), while gut capacity scales isometrically (Demment & Van Soest 1985). Large-bodied herbivores then do not need to extract as much nutrients from their food as small-bodied ones. Large-bodied herbivores are also able to extract more nutrients from low- quality food because they have longer retention

time than small bodied herbivores (du Toit 1990; Ramzinski & Weckerly 2007). The Jarman – Bell principle was presented to compare species, but has also been used to describe sexual differences within species with large size discrepancies between sexes (Stokke & du Toit 2000; Perez-Barberia *et al.* 2008).

Hierarchical foraging

Senft *et al.* (1987) suggested that an animal's foraging decisions are nested in spatial hierarchies, the regional, landscape, patch and plant scale. At regional scale herbivores select between different landscapes, which may be a decision for months or hours. Within a landscape, there are patches with different vegetation varying in forage quality and quantity. Here, a herbivore has to select which patch to browse or graze, representing a decision at patch level, often for many minutes or hours. Within the patch herbivores choose a feeding station representing a decision for a particular plant species, individual plant or plant part (Lamoot 2004), a decision for seconds or minutes. Thus, each foraging decision an animal takes, is constrained by the decisions made at higher levels (Schaefer & Messier 1995; Bailey *et al.* 1996; Skarpe *et al.* 2007). Generally the selection criteria goes from a-biotic factors such as water availability and predation risk at the largest scales to amount of forage available at patch scale and quality of the plants or plant parts at the finest scale (Fortin *et al.* 2003; Skarpe *et al.* 2007). Several studies have been conducted to illustrate the hierarchical foraging theory in different environments (Schaefer & Messier 1995; Skarpe *et al.* 2000; Boyce *et al.* 2003). It has been suggested that for better understanding of hierarchical foraging responses by herbivores several ecological levels have to be studied and these should span a large scale, from the largest to the smallest, in relation to size of the studied animal (Senft *et al.* 1987; Schaefer & Messier 1995; Shipley 2007).

Trees and grasses in African savannas

African savanna has a co-dominance of grasses and woody species (Bergström 1992; Cahoon *et al.* 1992; du Toit & Cumming 1999; Sankaran *et al.* 2005; Sinclair 2006; Bond & Midgley 2012). African savanna is currently the only habitat that supports a high abundance and species richness of ungulates, and their attending predators (Fritz & Duncan 1994; du Toit & Cumming 1999; Skarpe *et al.* 2014). Several factors are responsible for savanna tree - grass dynamics; rainfall, soil nutrients, fire and herbivory (Frost & Medina 1986; du Toit & Cumming 1999; Sankaran, Ratnam & Hanan 2004; Mills *et al.* 2013; Skarpe *et al.* 2014). It should be noted that these factors are not mutually exclusive, they are often interdependent, and they all interact in complex ways (Scholes & Archer 1997; Sankaran, Ratnam & Hanan 2004; Sankaran, Ratnam & Hanan 2008). According to Sankaran *et al.* (2008) the woody cover in an area which receives mean annual precipitation between about 150 to 650 mm increases linearly with water availability but still has grasses as co-dominants. These are the climatic, the arid and semi-arid savannas, existing even without disturbance. With higher rainfall woody growth continues to increase, now excluding grasses. Woody vegetation can, however, be reduced by disturbances such as fire and herbivory, which, at rainfall more than about 650 mm, are required for the coexistence of trees and grass (Sankaran *et al.* 2005; Sankaran, Ratnam & Hanan 2008).

Recently an increase in woody vegetation has been observed in most savannas largely independent of long term fire and herbivory regime (Moncrieff *et al.* 2014; Stevens *et al.* 2016). Many factors might be responsible, but human induced climate change and increasing CO₂ levels, favouring C₃ plants, for example trees, at the expense of C₄ ones, often grasses, might be a reason

(Bond & Midgley 2012), as might the general replacement of browsers with grazers and local extinction of very large browsers such as elephant, *Loxodonta africana*, and black rhinoceros *Diceros bicornis*.

Rich and poor savanna

African savanna has been classified as nutrient-rich and nutrient-poor (Bell 1982; Huntley 1982). Nutrient-poor savannas occur in humid and sub-humid areas where the soils are leached by precipitation and where the soil consists of ancient weathered material, while nutrient-rich savannas are found in arid and semi-arid areas and in areas with recent volcanic soils or human influence (Bell 1982; Scholes, Bond & Eckhardt 2003; Holdo & McDowell 2004). Plants in nutrient rich savannas are water limited and generally of high nutritional quality and those in the nutrient-poor savannas are nutrient limited and of low nutritional quality (Bell 1982; Huntley 1982; Rohner & Ward 1997; Holdo & McDowell 2004). Plants in nutrient-poor savanna are characterized by resistance traits while those in nutrient-rich savanna have tolerance traits (Skarpe & Hester 2008; Skarpe *et al.* 2014). According to the Jarman-Bell principle (Bell 1971; Jarman 1974) and knowledge on fertile and infertile savanna, Bell (1982) predicted that arid nutrient-rich savanna should be dominated by small-bodied herbivores particularly ruminants or other foregut fermenters, and humid nutrient-poor savanna should be dominated by large-bodied herbivores, primarily hind-gut fermenters -the Bell hypothesis (Bell 1982) .

Activity budget in ungulates

Activity budget has been recorded for many ungulates (Jarman & Jarman 1973; Leuthold & Leuthold 1978; Pellew 1984a; du Toit & Yetman 2005; Hamel & Côté 2008). It is commonly described how animals allocate time on some activities, whereas other activities are more fixed

(Hamel & Côté 2008). Examples of activities include feeding, ruminating, walking and resting (Pellew 1984a). According to Hamel & Côté (2008) the activity budget might be influenced by intrinsic factors such as reproductive status, age, and mass and extrinsic factors such as group size, forage availability and quality. Season, group size and sex have been reported to influence activity budget of animals (Shi *et al.* 2003). Body size is a main factor determining how much time a herbivore must spend on foraging and rumination, with small animals spending less time, and large animals spending most of the day (du Toit & Yetman 2005). A study by du Toit *et al.* (2005) found that increase of body size correlated with time allocated to feeding and walking. Owen-Smith (1992) reported that there was a close positive relationship between daylight feeding time and body mass for both grazing and browsing ruminants. Foraging in such cases influences how much time can be spent on other activities.

Sexual segregation

Most ungulate species where the female weighs more than 25 kg have sexual dimorphism, where males are larger than females. These species are likely to have sexual segregation, meaning that males and females use different habitats or forage and live in separate groups outside the mating season (Clutton-Brock, Iason & Guinness 1987; du Toit 1995; Ginnett & Demment 1997; Barboza & Bowyer 2000; Ruckstuhl & Neuhaus 2002). A number of hypotheses have been proposed to explain sexual segregation; sexual dimorphism-body size hypothesis, the scramble competition hypothesis, the activity budget hypothesis, the predation-risk hypothesis and the social factors hypothesis (Ruckstuhl & Neuhaus 2000; Ruckstuhl & Neuhaus 2002; Loe *et al.* 2006; Xu *et al.* 2012).

The sexual dimorphism-body size hypothesis is based on the Jarman Bell principle (Main, Weckerly & Bleich 1996; Ruckstuhl 1998). It therefore predicts that small females and large

males will use habitats with different forage quantity and quality. Males are likely to prefer abundant forage, which in most cases is not the most nutritious, whereas females are likely to prefer high-quality forage to meet high energy demands due to relatively small body size and to gestation and lactation (Main, Weckerly & Bleich 1996; Ruckstuhl 1998).

The scramble competition hypothesis predicts that when small females select the most nutritious forage they deplete that resource so that males have to seek another foraging habitat offering higher intake but often lower quality, or, in browsers, they are forced to browse above the reach of females (Stokke 1999).

The activity budget hypothesis proposes that, females forage for longer periods and are more selective than males (Ruckstuhl 1998), whereas males stay longer at one tree, use more time for bite formation, but have reduced chewing effort compared to females (Ginnett & Demment 1997). The fibrous forage of males is also supposed to need longer ruminating time (Lauper *et al.* 2013). All this might disturb the synchrony between sexes, but, in browsers, not necessarily lead to the use of different foraging habitats.

The predation-risk hypothesis proposes that larger male ungulates are less vulnerable to predation than females and their offspring (Ciuti *et al.* 2004). Females, or at least females with young, select safe areas to reduce predation risk, at the expense of nutrient intake, while males exploit the best feeding areas even if characterized by a higher predation risk (Ciuti *et al.* 2004).

The social factors hypothesis is related to sociality aspects. Males form associations in order to develop fighting skills, establish pre-rut dominance hierarchies and learn locations of potential mates, while females will impart skills to calves including where to find water, food, breeding areas and possibly cover (Conradt 1999; Bowyer 2004; Loe *et al.* 2006). Each sex avoid the

company of the opposite sex outside the rutting season in order to reduce energy loss in power demonstrations for males, and to avoid male harassment for females (Shank 1985).

Basic description of giraffe and its feeding ecology

The giraffe (*Giraffa camelopardalis*) is the world's tallest, heaviest extant ruminant and a strict browser (Leuthold & Leuthold 1972; Pellew 1984b; Baxter & Plowman 2001; Pérez, Lima & Clauss 2009). Giraffids originated in Eurasia and moved into Africa through Ethiopia (Mitchell & Skinner 2003; Dagg 2014). They were a number of bizarre, horned large species, all of which are extinct apart from *Giraffa camelopardalis* and *Okapia johnstoni* and the distant relative the American pronghorn *Antilocapra americana* (Mitchell & Skinner 2003; Dagg 2014). Examples of the earliest giraffids was *Zarafa zelten* from Libya, which was antelope-like with ossicones sticking out on both sides of the head (Dagg 2014), another one was the *Sivatherium maurusium*, which was probably the largest and most massive giraffid over time and went extinct as recently as 8000 years ago (Dagg 2014). Currently, there are nine subspecies of giraffes distinguished by coat colour and patterns (Dagg 2014; Agaba *et al.* 2016). Giraffe height and weight differ between sexes. Males' height is about 5.2 m and females' about 4.3 m and body weights are about 1200 kg in males and about 800 kg in females (Ginnett & Demment 1997; Dagg 2014).. Giraffe's social interactions are loose and flexible, and individuals may join a group and leave it, groups ranging between two and forty animals, males being more solitary than cows (Leuthold 1979; Bercovitch & Berry 2010). Giraffe numbers are decreasing drastically in Africa from 140,000 in the late 1990's to ca. 80,000 in 2008 (Fennessy 2012) due to poaching, habitat fragmentation, rinderpest and climatic change (Dagg 1971; Seeber, Ciofolo & Ganswindt 2012; Dagg 2014). The main predators of giraffes are lions (*Panthera leo*), but on some rare occasions lions themselves might be killed by giraffes (Dagg 1971). Other predators include;

cheetah (*Acinonyx jubatus*) crocodiles (*Crocodylus niloticus*) and hyena (*Crocuta crocuta*) which have been reported to prey on calves. Moreover, giraffes are poached mainly for their meat, hide and tail for use in bracelets and trinkets (Okello *et al.* 2015; Wakili, Sabo & Bala 2015).

Giraffes feed on leaves, fruits, flowers, pods, twigs and shoots from trees and shrubs and also from some dicotyledonous forbs (Dagg 1971; Pellew 1984a; Dagg 2014). Giraffe has advantage to reach forage in high trees where other competing browser cannot (Woolnough & du Toit 2001; Ciofolo & Le Pendu 2002). Moreover, giraffe given its large mouth size occasionally is compelled to pick smaller bites but compensates by picking many bites at a time or stripping.

Aim of the thesis

My overall aim of the study was to contribute information from Arusha on how giraffe make foraging decisions to maintain a high fitness in a heterogeneous savannah. Specific questions were; (i) do selection criteria differ with hierarchical scales (ii) does browsing giraffe try to maximize intake rate or do they select according to quality (iii) how and why do activities by giraffe vary in relation to main activities (foraging) and season, sex and group size (iv) do foraging decisions differ between sexes and with the type of savanna. To answer these questions we use different data collected in Arusha and, for the sexual segregation, in Arusha, Serengeti and Mikumi.

In paper 1 we relate to previous studies showing that foraging decisions of large herbivores vary in time and space (Senft *et al.* 1987; Schaefer & Messier 1995; Skarpe & Hester 2008; Van Beest *et al.* 2010; Van der Merwe & Marshal 2012). Giraffe do not seem to use the habitats homogenously, but are encountered more often in some habitats than in others, and browse certain tree species more than others. A few studies have related giraffe foraging to different hierarchical scales (Ginnett & Demment 1997). In this paper we tried to determine whether

foraging decisions of giraffe differ with scale. We chose three scales: landscape (habitat), patch and tree. We worked in Arusha, where we identified four habitats from field observations; “Acacia shrub” dominated by *Acacia xanthophloea*, “Dodonaea shrub” dominated by *Dodonaea viscosa*, “Grass forb shrub” dominated by grasses and forbs and “Tall shrub” dominated by tall trees, mainly *Euclea divinorum*. The habitat scale was related to the use by giraffe of these four habitats. Patches were defined as 50 m² areas with all the area reachable or almost so for a giraffe standing at its center. Patches were placed around the tree(s) observed browsed, used patch, and a 50 m² patch 100 m away, the available patch. The tree scale was defined as the tree browsed by the giraffe compared to unbrowsed trees in the used patch (Stokke 1999).

We predicted that foraging decisions of giraffe would vary in relation to a-biotic factors, such as water availability, in the habitat scale, forage availability in the patch scale and forage quality as defined by tree species, previous browsing and size in the tree scale.

In paper 2, we studied intake rate, which is a product of bite mass and bite rate (Sebata & Ndlovu 2010). There have been many studies on different aspects of giraffe ecology (Lamprey 1963; Pratt & Anderson 1982; Pellew 1984a; Young & Isbell 1991), but comparatively few have looked into the effect of plant traits on detailed browsing patterns, as we do in paper 2. Theory suggests that intake rate varies with season, time of day and with animal foraging limitations, such as forage availability or predation (Owen-Smith & Goodall 2014), however large giraffes are hardly affected by predation, hence forage availability is more important. For any herbivore intake rate also varies with plant traits (Cooper & Owen-Smith 1986; Spalinger, Robbins & Hanley 1986; Haschick & Kerley 1997; Sebata & Ndlovu 2010). We tested how bite mass and bite rate were affected by plant traits and whether intake rate would mainly follow bite mass or bite rate. We

expected bite mass to be high in non-spinescent trees while bite rate would be high in spinescent trees, as long as the spines were not browsed, and intake rate would follow bite mass.

Having determined intake rate, the next step we ask how much time is allocated to different activities by giraffe and in what way different activities vary. In paper 3, we relate to studies having shown that some activities, such as feeding, ruminating, walking and resting (lying and standing) are necessary for the animal and are comparatively fixed in time whereas animals compromise on how much time to spend on other activities such as socializing and being vigilant (du Toit & Yetman 2005; Hamel & Côté 2008). We observed giraffe over wet and dry season, and did not take spatial and temporal variation of the forage resources into account (Owen-Smith & Goodall 2014). Most previous studies on activity budget of giraffes have related body size with foraging behaviour, diet composition and shade use (Leuthold & Leuthold 1978; Pellew 1984a; Ciofolo & Le Pendu 2002; Adolfsson 2009). In this study, we intended to fill the knowledge gap on the activity budget in relation to season, sex and group size.

Finally we ask if there are sex differences in foraging decisions between environments. In paper 4, we focused on sexual segregation. We studied how sexual segregation in giraffe varied between relatively small females and large males in three sites; the Serengeti as a nutrient-rich savanna, Mikumi as a nutrient-poor savanna and Arusha, as a medium-rich savanna, and changed with plant chemistry and with competing herbivore communities. This study is the first to document on giraffe sexual segregation behaviour in nutrient rich, medium rich and nutrient poor savanna. We expected that females in the nutrient-rich savanna would browse plants with higher nitrogen and lower tannin and fibre content than males, but that selection would be more obscured in the poor savanna. We believed that females in the nutrient rich savanna would browse a higher diversity of plant species compared to males, while in the nutrient-poor savanna

both sexes would browse a high diversity of species, as they might need to ‘dilute’ any particular deterrent in one species (Freeland & Janzen 1974; Freeland & Saladin 1989; Singer, Bernays & Carriere 2002). We expected males to browse above females in all sites, and both sexes to browse higher in the nutrient rich than in the nutrient poor savanna. Males would further spend more time browsing on one tree than do females.

Material and methods

Study areas

The study was done in Arusha apart from the study for the manuscript 4 that was carried out in three sites; Arusha National Park, Serengeti National Park and Mikumi National Park. All three sites belong to the savanna ecosystem, and support different communities of ungulates (Tanapa 2016). I will refer to the areas just by names and present Arusha here, leaving Serengeti and Mikumi to paper 4.

Arusha National Park

Most of our data came from Arusha (paper 1, 2, 3, 4). The park is located on the eastern slope of Mount Meru $36^{\circ} 45' E-3^{\circ} 15' S$, Tanzania. The park size has recently expanded from 137 km² to 552 km² (Tanapa 2016). The park receives rainfall in March-May (long rains) and November – December (short rains) while January–February and June –October are dry months (Amubode & Boshe 1990). Geographically, annual rainfall ranges between 600 to 2400 mm. Mean maximum monthly temperature in January-February (hottest months) is 27⁰C (January) and mean minimum monthly temperatures in June –October is 11⁰C (July; coldest months)(Meteoblue 2016). The soils are mainly originated from volcanic activities of Mount Meru (Razzetti & Msuya 2002;

Tanapa 2003). The Park is dominated by *Juniperus procera*, *Croton macrostachyus*, *Euclea divinorum*, *Dodonaea viscosa* and *Acacia xanthophloea* (Razzetti & Msuya 2002; Tanapa 2003).

Data collection

We used data collected in two seasons; March – May 2013 (wet season) and August –October 2013 (dry season) in Arusha for paper; 1, 2, 3 and 4. However, in Serengeti data were collected in April-May 2014 (wet season) and August-September 2014 (dry season) and in Mikumi May-June 2014 (wet season) and September-October 2014 (dry season). Paper 4 combines data from the three sites.

To determine hierarchical foraging (paper 1), we drove road transects of about 25 km at a speed of 20 km/hr with a four-wheel drive vehicle observing browsing giraffe. For each observation we recorded the following variables: habitat type, tree species browsed and number of trees browsed soon after giraffe moved away. We recorded the proportion of the area covered by the different habitat types, and related the proportions of observations of giraffe to that. We constructed two plots of 50 m² each, the used plot, centered where the browsing giraffe were observed, and the available plot 100 m away to the right of the direction in which the giraffe left.

A total of 266 patches were sampled, of these 133 represented browsed patches and 133 available patches. In both plots, we counted all trees > 0.5 m tall, recorded tree species and measured stem height under the canopy, tree height and gave scores of accumulated browsing, defined as effect of previous browsing on the tree growth form (Skarpe *et al.* 2007; Mathisen *et al.* 2014). In the used plot the trees browsed by the observed giraffe were recorded and their species, height and previous browsing were compared with trees not browsed in the same plot.

For paper 2, we used the 25 km road transect and observed browsing giraffe as described for paper 1. Our sample size was 132 giraffes. We observed a mature male or female giraffe browsing and recorded the following variables; time spent browsing per tree, number of bites taken, bite diameters and previous browsing of the tree and we also collected and oven dried shoots to calculate bite mass. Intake rate was calculated from the product of bite mass and bite rate (bite mass x bite rate = intake rate) (Haschick & Kerley 1997; Sebata & Ndlovu 2010).

In paper 3 we again used the 25 km road transect but collected new giraffe data. We observed a mature male or female giraffe (N = 76) for two hours and recorded time of different activities performed. Observations continued from the vehicle or from foot when the giraffe moved away and observed from a high elevation and vantage where necessary (Fennessy 2004). Main activities recorded were;

- Feeding: Time when giraffe was picking or stripping leaves or biting shoots, chewing and swallowing
- Ruminating: Time when giraffe was chewing its cud while walking, standing or lying
- Resting: Time when giraffe rested, recorded separately, not performing other activities.
- Walking: Time when giraffe was moving from one point to another (not moving between plants), and not doing other activities
- Vigilance: Time when giraffe was observant for predators, vehicles or other giraffes
- Socializing: Time when giraffe was necking or doing other social activities

We used continuous observations of one mature animal during 2 hours to determine the mean time spent by giraffe on different activities and how and which activities varied with sex, season, and group size.

Paper 4, here we used road transects to observe mature female and male giraffe browsing in Arusha, Serengeti and Mikumi. We recorded tree species browsed, number of bites and time the

animal spent feeding on each tree. Browsing height was recorded in relation to the animal body as: below knee, above knee, chest, first half neck, second half neck, head and above head.

Heights were converted into meters by using information from the literature (Estes 1991; Skinner & Chimimba 2005). Chemical data for some tree species were gathered from literature (Ernst *et al.* 1991; Rooke 2003b; Bakshi & Wadhwa 2004a; Rubanza *et al.* 2008a; Melaku, Aregawi & Nigatu 2010; Khanyile, Ndou & Chimonyo 2014; Colgan *et al.* 2015).

Statistical analysis

For all analyses, I used the R program (RCoreTeam 2014) with relevant packages therein.

Models applied were generalized linear mixed modelling (GLMM); binomial and Gaussian, and all statistical assumptions were checked including homogeneity of variances, independence and normal distributions of data and overdispersion (Zuur *et al.* 2009; Zuur, Ieno & Elphick 2010).

More details are found in each paper.

Results and discussion

Do selection criteria differ with hierarchical scales?

Herbivores make foraging decisions hierarchically in response to forage variability and other factors, and decisions in the larger scale constrain those at smaller scale (Schaefer & Messier 1995; Bailey *et al.* 1996; Skarpe *et al.* 2007). In Arusha we found that giraffes selected for preferred *A. xanthophloea* at all scales, preference index 1.8 (paper 1). At habitat level giraffe selected habitats according to high availability of foliage of *A. xanthophloea*, in the habitats *Acacia* shrub and *Dodonaea* shrub, whereas Grass forbs shrubs and Tall shrubs habitats were avoided (Table 1). Within habitats, giraffe selected patches with high quantity of *A. xanthophloea* compared to control patches (Table 1). Within patches, giraffe also selected primarily for *A. xanthophloea* (Figure 1), and the probability of an *A. xanthophloea* to be browsed increased with

height ($\chi^2_{1, 118} = 1.68$; $p < 0.001$) and with increasing accumulated browsing level ($\chi^2_{3, 115} = 18.99$; $p < 0.001$; Figure 1). We expected criteria for selection by giraffes to vary with different scales, as shown by other studies (Senft *et al.* 1987; Boyce *et al.* 2003; Van Beest *et al.* 2010). Giraffe seemed in our study to rely on quantity and quality of the preferred *Acacia xanthophloea* in all scales. The consistent criteria across scales probably was related to absence of predation risk, proximity to water sources and a fairly small scale of the study in relation to the large giraffe. These findings agree with some results from other environments and species (Schaefer & Messier 1995; Skarpe *et al.* 2007; Van der Merwe & Marshal 2012). We found foraging to be governed by the presence of one preferred tree genus, *Acacia*, which is recorded as the forage most eaten by giraffe (Sauer 1983; Pellew 1984a; Bergström 1992; Dagg 2014). *Acacias* are generally known to have high concentration of nitrogen and relatively low of tannin and phenolics (Ernst *et al.* 1991; Rooke 2003b; Rubanza *et al.* 2005a; Khanyile, Ndou & Chimonyo 2014). Arusha is not a nutrient-rich savanna and *Acacia xanthophloea* is the only common *Acacia*. Giraffes are currently few, < 100 (*oral information from park rangers*). If giraffes increase in density the *Acacia* will be insufficient, forcing giraffe to browse on other plant species such as *Croton macrostachyus*, as they did in the 1980's when there were more than 400 giraffes in the park (Pratt & Anderson 1982) (Paper 1). The *Acacia* might decrease in abundance (number of trees or amount of foliage) but as it is one of the few trees with tolerance traits in the area, that will not necessarily happen (du Toit, Bryant & Frisby 1990; Cromsigt & Kuijper 2011). Then also the diversity of plant species browsed might increase as giraffe have to dilute one type of defence compound (Freeland & Janzen 1974; Singer, Bernays & Carriere 2002) or have to combine many species in order to obtain a balanced diet (Westoby 1974).

Table 1: Preference indices, MANOVA results with means and standard errors among habitat types for species diversity, tree density and tree height in Arusha National Park

Habitat type	Distance along roads of habitat (km)	Proportion (%) of habitat available	Number of browsed patches per habitat	Proportion of patches browsed (%) per habitat	Proportion of patches browsed over proportion of habitat available (preference index)	Species diversity (H')	Tree density (per m ²)	Tree height (m)
Acacia Shrub	3.3	19.5	73	54.9	2.8	0.22 ± 0.05	0.05 ± 0.01	1.53 ± 0.16
Dodonaea Shrub	1.9	11.2	33	24.8	2.2	0.48 ± 0.09	0.11 ± 0.01	1.56 ± 0.29
Grass forb shrub	7.5	44.3	12	9.0	0.2	0.66 ± 0.14	0.06 ± 0.02	2.98 ± 0.42
Tall shrub	4.2	24.8	15	11.3	0.5	0.70 ± 0.13	0.07 ± 0.02	3.01 ± 0.39
Total distance	16.9	100	133	100				

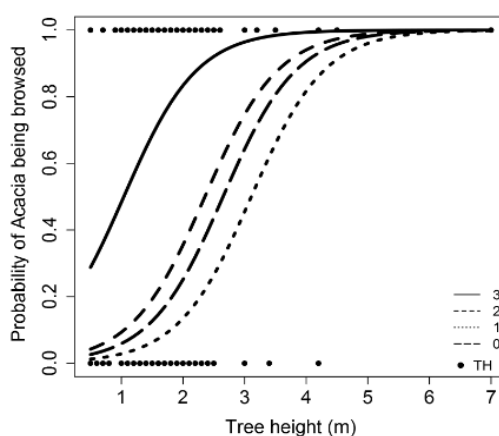


Figure 1: Probability of *Acacia xanthophloea* being browsed as influenced by tree height and accumulated browsing. Levels were defined as: 0 = no sign of previous browsing, 1 = old browsing visible but tree growth form had not changed, 2 = old browsing visible and growth form had changed and 3= old browsing visible and growth form had strongly changed.

Does browsing giraffe try to maximize intake rates or do they select according to quality?

Here we studied if giraffes, who are large browsers, follow the possibilities by the Jarman–Bell principle (Bell 1971; Geist 1974; Jarman 1974), and maximize intake rate while tolerating low forage quality, or if they instead go for high quality, accepting a lower intake rate (paper 2). It should, however, be remembered that the Jarman-Bell principle points at possibilities, it does not say that large-bodied animals should select poor forage, if better forage is on offer in large enough quantities (Bell 1971; Jarman 1974). We examined how intake rate was determined as the product of bite mass and bite rate, and showed that bite mass and bite rate were determined by inherent plant traits and plant traits acquired by previous browsing, and also by season (paper 2). We found that intake rate followed bite mass more than bite rate and was higher in spineless than in spinescent trees, higher in the wet season than in the dry, and tended to increase with tree height (Figure 2 a-c). Generally, giraffe did not prioritize the highest intake rate, but browsed much on spinescent trees, like *Acacias*, giving a high quality diet but a low intake rate. These findings agree with those reported by Mahenya *et al.* (2016a) who found that Acacia trees were the most browsed trees in Arusha National Park. Browsers have been reported to compromise between nutritional quality and bite size, as the bite size determines how much of the shoot is taken (Shipley 2007). Often tree species that give large bite mass have low quality (Shipley *et al.* 1999; Shipley 2007). For instance, in our study area the tree species that offered large bite mass but low quality was *Warburgia ugandensis* (Table 3, paper 2). Moreover, spines, prickles and thorns in trees have been reported to lower bite mass by separating leaves and hampering access to leaf stripping and twig biting, leading to picking individual leaves or leaf clusters and, hence, lowering intake rate from the trees (Shipley 2007). In Arusha, the thorny *A. xanthophloea* was the

most eaten plant species (paper 1) which gave low bite mass compared to spineless species, hence low intake rate.

Although spinescence cannot prevent browsers from feeding it lowers intake rate (Scogings, Dziba & Gordon 2004; Skarpe *et al.* 2012). We found that intake rate was higher in spineless than in spinescent trees (Figure 2a). The probable reason for giraffe achieving high intake rate in spineless trees was that they were able to strip many leaves at a time and/or to take twig bites (Dziba *et al.* 2003a; Shipley 2007). In our area the spineless trees that were eaten were the nutrient poor *Euclea divinorum*, *Dodonaea viscosa* and *Warburgia ugandensis* (Table3, paper 2). Giraffe was able to crop large bite mass on spineless trees probably due to its large mouth size when compared other browsers (Dagg 2014).

Food availability changes with seasons as trees change their phenology (Pellew 1984a; Renecker & Hudson 1986; Dziba *et al.* 2003b). Most trees in the savanna are deciduous, and therefore the food availability is low in the dry season, and the production of new shoots or leaves is negligible, thus reducing the intake rate (Pellew 1984a; Dziba *et al.* 2003a). This corresponds with our results that intake rate was higher in the wet season than in the dry (Figure 2b).

Intake rate is assumed to depend on tree height (Searle & Shipley 2008). Our results showed that intake rate tended to increase with tree height (Figure 2c), as a larger tree also offered a larger canopy volume with more browse available. Forage at low heights might in addition be depleted by small competing browsers (Woolnough & du Toit 2001). Woolnough and du Toit (2001) showed that leaf mass per giraffe browsing unit increased up to 2.5 m, thus giraffe achieved a high intake rate above 2.5 m which was above the reach of other browsers, with exception of elephants which were rarely observed (paper 2).

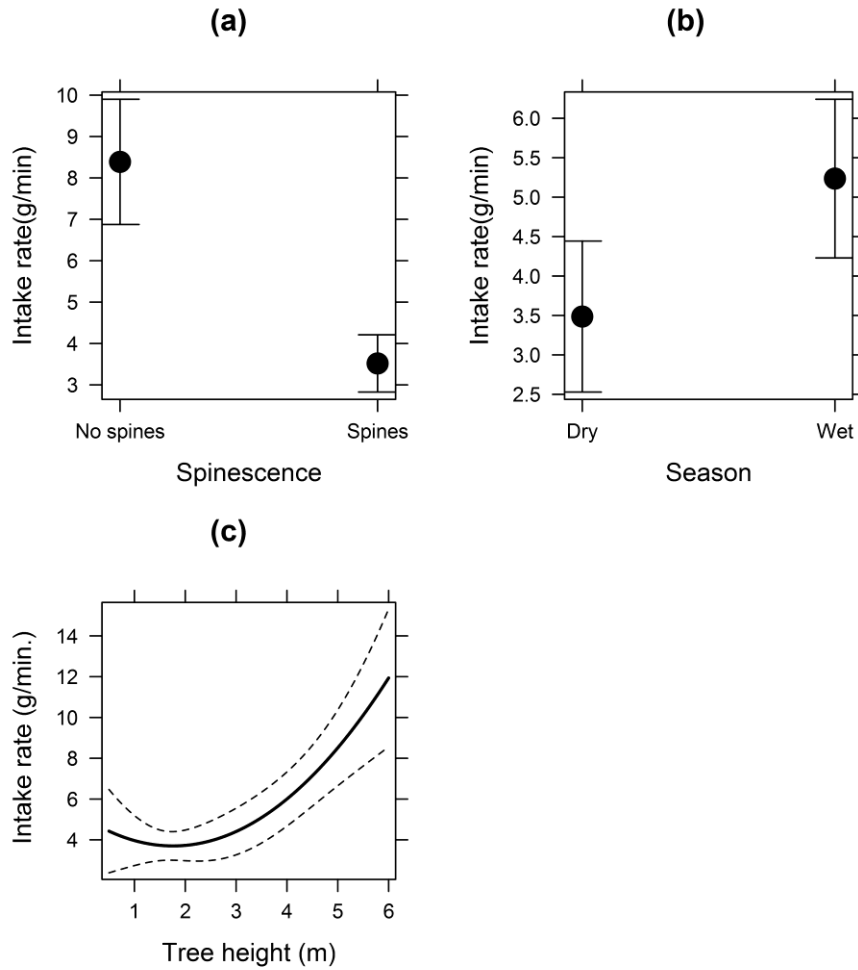


Figure 2: Intake rate of giraffe in relation to spinescence, season and tree height. Mean values are shown as the middle point while error bars above and below the mean show confidence intervals 95% upper and lower, (a) effect of spinescence on the intake rate, (b) effect of season on intake rate, (c) effect of tree height on intake rate. The dashed lines represent upper and lower 95% confidence interval.

Which activities are most important for giraffe, and how and why do other activities vary?

In paper 3, we determined how much time was used for the most important activities for giraffe and how time spent on different other activities were affected by sex, season and group size, and also how less important activities were correlated with main activities. Time spent on activities such as feeding and walking, which include physical movement, increases with body size,

contrary to passive activities such as ruminating and resting, (Belovsky & Slade 1986). Hence, large sized herbivores spend longer time feeding than small ones (Belovsky & Slade 1986; du Toit & Yetman 2005). Giraffe as a large browser, allocated most time to activities such as feeding (38.6%), ruminating (26.6%) resting (19.6%) and walking (8.7%) and less time on activities such as vigilance (4.1%) (Table 1). Our results are consistent with those reported by Fennessy (2004) on diurnal activity of giraffe. Time spent on foraging by giraffe may be affected by many factors including forage availability and quality, for example digestibility and fibrousness (Pellew 1984a; Fennessy 2004; Dagg 2014). In a ruminant low digestible or fibrous forage might reduce forage intake. Giraffe is likely to spend more time walking when food availability is low or patchily distributed, thus more time is required for walking and searching for food (Ciofolo & Le Pendu 2002). Giraffe spend time resting as a strategy for conserving energy (Pellew 1984a). Energy acquisition and conservation was a primary goal for giraffe to survive. Giraffe devoted little time to vigilance (Table 2) . Giraffe size makes mature animals more or less immune to predation. Also height gives an advantage for easy predator detection and avoidance (Young & Isbell 1991; Fennessy 2004), possibly explaining the little time spent being vigilant (paper 3). However, lion, *Panthera leo*, predation on giraffe might vary with availability of other prey species and prey condition (Owen-Smith & Mills 2008; Owen-Smith 2008). Socializing and resting were more common activities in the dry season than in the wet (paper 3, Figure 3 &4). Socializing only involved males and was an energy-costly activity that was mainly done in the dry, cool season (Fennessy 2004). Most necking behaviour, which is used by males to show dominance hierarchy to other males, and most copulation attempts have been reported to occur in the dry season (Fennessy 2004). Giraffe spent more time resting in the dry than in the wet season as energy conserving strategy (paper 3, Figure 4) (Pellew 1984a; Fennessy 2004; Dagg 2014).

It is predicted that as group size becomes larger; time of feeding increases following forage competition and less time devoted to vigilance (Roberts 1996; Dalerum *et al.* 2008). We found that group size of giraffe had no effect on time spent on any activity (paper 3). Individual time spent being vigilant is supposed to decrease with increasing group size (Roberts 1996; Beauchamp & Ruxton 2003), which we did not find. Giraffe is little sensitive for predation, and in addition the social organization is very weak, which may lead to the lack of a relationship between group size and vigilance (Cameron & du Toit 2005).

Table 2: Behavioural activity, percent time spent on different activities

Behavioural activity	% time	Standard error (SE)
Feeding	38.6	± 4.6
Ruminating	26.6	± 4.1
Resting (lying and standing)	19.6	± 2.8
Walking	8.7	± 1.3
Vigilant	4.1	± 0.9
Socializing	2.4	± 1.4

Does foraging decisions differ between sexes and environments?

In paper 4, we compared sexual segregation in giraffe in one nutrient-rich savanna, the Serengeti, one nutrient-poor, Mikumi, and one medium-rich savanna, Arusha. We investigated effects of sexual size dimorphism on intraspecific and interspecific competition and activity budget hypotheses. Energy requirements and foraging behavior are affected by body size (Bell 1971; Jarman 1974; Demment & Van Soest 1985; Main, Weckerly & Bleich 1996; Ruckstuhl 1998). In nutrient rich Serengeti, a large proportion of the forage was *Acacia* spp, and females browsed *Acacia drepanolobium*, and *Acacia tortilis*, while males concentrated on *Acacia tortilis* (Table 2). A likely reason for females to browse more on *A. drepanolobium* is related to its low levels of

ADF, tannins and phenolics and high concentration of nitrogen compared to other species (Pellew 1984a; Furstenburg & van Hoven 1994; Caister, Shields & Gosser 2003). Males browsed more than females on *A. tortilis* which had higher levels of ADF, tannins and phenolics than *A. drepanolobium*. Tannin levels are still low compared to broad leaved plants in the nutrient poor savannas (Table 2), and males may tolerate the somewhat higher concentration of defence compounds due to high efficiency in digestive capability compared to females (Demment & Van Soest 1985). In the medium rich Arusha *Acacia xanthophloea* was mainly eaten by both sexes. *A. xanthophloea* has high nitrogen concentration (Table 2)(Pellew 1984a). Males in addition ate the evergreen *Euclea divinorum* probably to achieve a large bite size particularly in the dry season, albeit *E. divinorum* is said to be poisonous (Mebe, Cordell & Pezzuto 1998; Hattas *et al.* 2011). In the nutrient-poor Mikumi females browsed mainly on *Harrisonia abyssinica* in the wet season and *Balanites aegyptiaca* in the dry (Table 2). *H. abyssinica* has high nitrogen concentration and low ADF level (Table 2). *B. aegyptiaca* is evergreen (Bates 2014; Tesfaye 2015), and thus has enhanced palatability in the dry season. Males browsed on the deciduous *Spirostachys africana* in the wet season and the evergreen *Capparis tomentosa* in the dry, both species believed to be poisonous (Ahmed & Adam 1980; Palgrave 2002). In Mikumi, most trees contain high levels of tannins and phenolics (Table 2)(Coley, Bryant & Chapin III 1985; Stamp 2003) (paper 4), and the giraffes' choice of diet does not seem clearly related to plant chemistry.

Differences in plant diversity consumed between sexes.

Diversity of tree species was higher in the females' diet than in the males' diet (Table 2) in the nutrient rich Serengeti. In the medium rich Arusha, however, males foraged on higher diversity of tree species than did females. Both sexes fed to more than 75 % on *Acacia xanthophloea* and males, added *Euclea divinorum* to the diet thus increasing diversity. Diversity of species browsed

by giraffes in Mikumi was higher than in other sites but similar between sexes (paper 4, Table 2). Most trees in Mikumi were nutrient poor and had high levels of defence compounds (Table 2), driving both sexes to browse many species in order to dilute any species specific defence compounds (Freeland & Janzen 1974; Westoby 1974; Freeland, Calcott & Anderson 1985; Freeland & Saladin 1989; Singer, Bernays & Carriere 2002) or to get a balanced diet from these nutrient poor species. Plant diversity was high in all three sites, giving animals an opportunity to select for high or low diversity.

Differences in browsing height between sexes

It has been suggested that animals with different body sizes would compete with each other, and the smaller more selective species forcing large browsers to feed high in the canopies above reach of the small species (du Toit 1990; Young & Isbell 1991). This scramble competition also applies between differently sized sexes. We found that males browsed higher in the canopies than females in all sites (paper 4). Season had an effect on browsing height independent of sex in Mikumi (paper 4). Forage low in the canopy is likely to be depleted by females and their young thus displacing males to browse high in the canopy (du Toit 1995; Cameron & du Toit 2007). Browsing height for both males and females in wet and dry season was higher in the nutrient-rich Serengeti than in the nutrient-poor Mikumi. Serengeti has a rich fauna of small and medium-sized browsers (Sinclair 1995), which might compete with the female giraffe and force them to browse high pushing the males above them.

Differences between sexes in duration of feeding per tree

It has been predicted that males and females of different body-size differ in time spent foraging on one tree (Owen-Smith 1992; du Toit & Yetman 2005). We found that feeding time per tree

was longer for males than for females, independent of site (paper 4). Browsing time per tree was longer in the wet season than in the dry season in Arusha and Mikumi (paper 4), but was not affected by season in Serengeti. The likely reason for no response to season in Serengeti might be related to high quality of the forage

Serengeti is a nutrient-rich savanna, where most browsing was done on *Acacias*, the favorite forage for giraffe. The *Acacias* are relatively nutrient rich and low in defence compounds and can, hence, be browsed also by smaller browsers such as dikdik, *Madoqua kirkii*, impala, *Aepyceros melampus* and bushbuck, *Tragelaphus scriptus*. These browse also the small seedlings and saplings and can strongly reduce the woody vegetation keeping also sub-humid savannas half open (Augustine, McNaughton & Frank 2003; Moe *et al.* 2009; Skarpe *et al.* 2014). Giraffes have, however, the advantage of browsing higher than any other mammal (Makhabu 2005), and might monopolize the browse resources above about 3 m. Elephants reaching this height might largely browse on other species than the ruminants (Makhabu 2005). Mikumi is, on the other hand, mainly nutrient-poor, having few small browsers. Thus, giraffe are free to browse also lower down in the canopies, which it does, Arusha is seemingly fairly nutrient-poor, but has some *Acacia xanthophloea*, that with the present low wildlife densities seems to be largely enough for female and male giraffe. *Acacia xanthophloea* grows in patches, and might possibly mark old kraal sites or other human influence (Scholes & Walker 1993). The numbers of giraffe are strongly reduced, from about 460 in the 1980's to below 100 in 2016 (Pratt & Anderson 1982)(paper 1).

Table 2. Chemical composition of commonly browsed tree species in the three sites. Nitrogen (N) and acid detergent fiber (ADF) are expressed as % of dry matter (DM); tannins are expressed as mg tannic acid/g DM, and phenolics are expressed as mg tannic acid/g DM.

Tree species	N	ADF	Tannin	Phenolics	Source
Serengeti					
<i>Acacia drepanolobium</i>	2.8	23	8.4	9.9	Rubanza <i>et al.</i> (2005b)
<i>Acacia robusta</i>	2.6	27.9	64.4	87.9	Ernst <i>et al.</i> (1991); Khanyile, Ndou and Chimonyo (2014)
<i>Acacia tortilis</i>	3.3	57.2	15.6	44.5	Rooke (2003a), unpublished
Arusha					
<i>Acacia xanthoploea</i>	3.3	31.2	59.5	20.2	Khanyile, Ndou and Chimonyo (2014); Wrangham and Waterman (1981)
<i>Dodonaea viscosa</i>	1.6	54	3.8	5.8	Bakshi and Wadhwa (2004b)
<i>Euclea divinorum</i>	1.1	275	59	115	Colgan <i>et al.</i> (2015); Yisehak and Janssens (2013)
Mikumi					
<i>Acacia senegalense</i>	3.3	26.9	109.4	241.6	Rooke (2003a), unpublished
<i>Balanites aegyptiaca</i>	2.2	26.1	11.9	11.3	Melaku, Aregawi and Nigatu (2010) (N, ADF); Mtui <i>et al.</i> (2008)
<i>Capparis tomentosa</i>	2.6	28.4	14	53.4	Rooke (2003a), unpublished.
<i>Combretum hereroense</i>	1.7	63.9	172	307.9	Rooke (2003a), unpublished
<i>Harissonia abyssinica</i>	2.4	18.3	139	156	Rubanza <i>et al.</i> (2008b)
<i>Spirostachys africana</i>	2.1	24.6	119.7	229.1	Rooke (2003a), unpublished

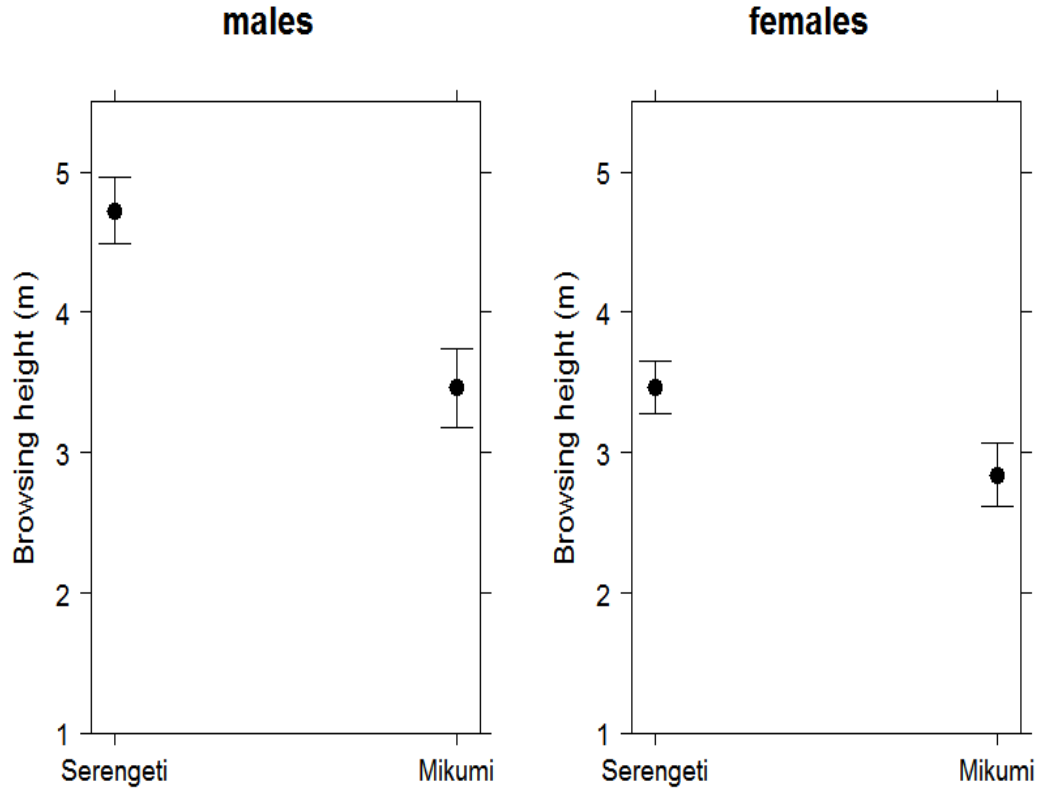


Figure 4: Interaction effect between sex and site on browsing height (means \pm SE).

General discussion

We mainly worked in Arusha which is a National Park that has changed in the last decades. Giraffe has decreased in the park from some 460 in the 1980's to less than 100 in 2014 (*oral information –park rangers*). The browsing pressure must have decreased from the 1980's, when Pratt and Anderson (1982) claimed *Croton macrostachyus* to be the most important giraffe forage, to our study showing *Acacia xanthophloea* to make up 75% of the giraffe diet. *Acacia xanthophloea* was most likely the preferred forage also in the 1980's, but there was too little available of it to last for all the giraffe. Currently giraffe diet in the intermediate rich Arusha must have resembled that of a nutrient rich savanna. This demonstrates that giraffe do prefer

Acacias, and seemingly tolerate the relatively low intake rate they offer (Paper 2). At the giraffe feeding height, they mainly just compete with themselves, and it should, thus, be possible for giraffe to browse both nutrient rich and nutrient poor savanna, in spite of being very big browsers. We show in paper 4 that giraffe can browse also broad leaved comparatively poor browsing species.

The ongoing encroachment of woody plants in savanna, possibly except the arid savannas (Bond & Midgley 2012), might depend on CO₂ stimulated growth rate of seedlings and saplings to above fire sensitive heights, hence, possibly impacted by fires and small browsers. In a longer perspective many of the savanna areas seem to become dominated by woody vegetation and forest (Moncrieff *et al.* 2014). Giraffe is unlikely to have any influence on the process, but might be favoured in a short time perspective, particularly if *Acacias* increase as in Kruger (Bond & Midgley 2012) before woody vegetation takes over, reducing the savanna biome and the animals that belong to it.

Management implications

In this thesis, I have shown that, giraffe as a large and a selective browser in Arusha foraged mainly on *Acacia xanthophloea*. My results support the hypothesis that giraffes prefer *Acacias* as a principal forage (Pellew 1984a; Dagg 2014). In Arusha *Acacias* are not a common genus, but with the current low density of giraffe there seems to be sufficient forage available on *Acacias* for both females and males. Pratt & Anderson (1982) reported that giraffes fed on *Croton macrastachyus* when the number of giraffes was ca. 460 individuals in the 1980s. Since then, the number of giraffes has been decreasing rapidly to less than 100 individuals (paper 1). If the giraffes increase again in number the *Acacias* will not be able to sustain them, and they would

have to select other species in addition, perhaps primarily *Croton macrostachyus*. As the other species contain higher concentrations of defence compounds compared to Acacia (paper 4) they may have to browse on many species to dilute a specific defence compound or to get a balanced diet (Freeland & Janzen 1974; Westoby 1974; Freeland, Calcott & Anderson 1985; Singer, Bernays & Carriere 2002) and the species diversity of the diet might increase.

The current density of giraffe is obviously way below the carrying capacity in the area (Pratt & Anderson 1982) , and a first priority for management must be to increase the number by reducing poaching. The actual cause of the decline is unclear but probably poaching plays an important role (Muller 2008; Strauss *et al.* 2015). Illegal hunting of giraffe in Africa (Muller 2008; Dagg 2014; Bercovitch & Deacon 2015; Strauss *et al.* 2015), is mainly done through use of snares (Kideghesho *et al.* 2005; Strauss *et al.* 2015), bows and arrows, pit fall traps and guns. The motives for poaching are many, but mainly local meat hunting might be important (Kideghesho *et al.* 2005; Muller 2008; Strauss *et al.* 2015). While strict law enforcement must be performed, a number of conservation programmes involving local communities have been carried out by governments and management agencies in Africa (Kaltenborn, Nyahongo & Tingstad 2005; Kideghesho *et al.* 2005; Røskaft *et al.* 2012; Dagg 2014) to stop wildlife poaching. A number of community based conservation programmes and community based natural resource programmes aimed at reducing the unsustainable wildlife exploitation (Kaltenborn, Nyahongo & Tingstad 2005; Kideghesho *et al.* 2005; Røskaft *et al.* 2012) have been established, yet, the problem continues in many parts of Africa. In Tanzania, several policies have been put in place to address human-wildlife conflict including the Environmental Policy 1997 and the Wildlife Policy of 1989 that call for sound wildlife management (Kaltenborn, Nyahongo & Tingstad 2005). For instance, Wildlife Policy requires the establishment of wildlife management areas in order to grant

communities hunting rights, so that communities could manage wildlife and benefit economically from the land (Kaltenborn, Nyahongo & Tingstad 2005; Kideghesho *et al.* 2005).

Arusha is relatively large, 552 km², and not fenced and has few large predators. To introduce lions, *Panthera leo*, might help keeping herdsmen and poachers out only as long as the lions are not poached themselves. Kaltenborn, Nyahongo and Tingstad (2005) pointed out that many villagers interviewed in Serengeti had a view that strict law enforcement was an important strategy to deter poaching. However, many park authorities in Tanzania have inadequate staff and equipment (Kideghesho *et al.* 2008). Therefore, the feasible and likely successful initiatives would be for wildlife managers to strengthen anti-poaching operations through use of latest technology such as of drones (Wich 2015) and advanced GPS technology. Increased number of staff and better educated staff for patrolling might increase the motivation, as would equipment such as vehicles and GPSs.

Future research

To conserve giraffe and promote our understanding on feeding decisions of giraffes it is necessary that protection of the species is operational. It is also important with more research on what species are eaten, particularly in nutrient-poor areas that are much less known than the nutrient rich. Such knowledge would be useful for conservationists, researchers and wildlife managers. We particularly need research that quantify the chemistry of tree species, including nitrogen, tannin, phenolics and fibre and their variation with tree age, season and browsing. We might then get closer to understanding the giraffe food choice. Research should preferably include both field observations of natural browsing and an experimental approach, looking into tree chemical responses to controlled simulated browsing of different intensity and timing.

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