



Hedmark University College

Faculty of Applied Ecology and Agricultural Sciences

Johannes Kambinda Ndjamba

Master thesis

**BROWSING BY GIRAFFE IN RELATION TO PLANT AND ANIMAL TRAITS IN
ARUSHA NATIONAL PARK, TANZANIA**



Master in Applied Ecology

2014

Date

Campus Evenstad
Place

Johannes K Ndjamba
Signature

I agree that this thesis is for loan in the library YES NO

I agree that this thesis is open accessible in Brage YES NO

1. Abstract

This paper investigates the feeding ecology of mature browsing giraffes during the wet season in Arusha National Park in Tanzania. I looked at different factors (predictor variables) affecting giraffe's browsing time on a plant, biting rate, bite size, and intake rate (response variables). Predictor variable ranged from plant traits (habitat, spinescence, tree height) to the giraffe's traits and behaviours (sex, browsing height, bite diameter, biting rate). The study reveals that only sex and spinescence was significantly influencing giraffes browsing patterns. Bulls were found to spend more time on a plant than cows, which switched plants frequently. This suggests that females are interested in forage quality rather than forage quantity, as are male giraffes. Biting rate was higher on armed plants than on unarmed plants. Furthermore, this was related to bite size, which was smaller for armed plants than for unarmed. This suggested that biting rate was higher at small bites than at large bites. Females were found to have larger bite size than male giraffes. The same pattern was observed for intake rate that was higher for females than for males. Intake rate was also high for the unarmed plants. This suggests that the bigger the bite taken the higher the intake rate for the giraffes in Arusha National Park.

Table of Contents

1. ABSTRACT	4
2. INTRODUCTION	7
2.1 RESEARCH QUESTIONS	10
3. MATERIALS AND METHODS.....	11
3.1 STUDY SPECIES AND SYSTEM.....	11
3.2 GIRAFFE OBSERVATION, TIME SPENT ON A TREE AND NUMBER OF BITES	12
3.3 TREE MEASUREMENTS.....	13
3.4 BROWSING HEIGHT.....	13
3.5 BITE DIAMETER.....	14
3.6 BITE SIZE, BITING RATE AND INTAKE RATE.....	15
3.7 DATA ANALYSIS	15
4. RESULTS.....	17
4.1 BROWSING TIME PER PLANT	18
4.2 BITING RATE	21
4.3 BITE SIZE.....	23
4.4 INTAKE RATE.....	26
5. DISCUSSION.....	29
5.1 BROWSING TIME PER PLANT	29
5.2 BITING RATE	30
5.3 BITE SIZE AND INTAKE RATE	31
6. CONCLUSION	34
7. RECOMMENDATION	35
8. ACKNOWLEDGEMENTS	36
9. REFERENCES	37

2. Introduction

Depending on food preferences mammalian herbivores can be categorized as (preferential) browsers or (preferential) grazers (Searle & Shipley 2008). Browsers are herbivores which feed on leaves and twigs from woody plants and on dicotyledonous herbs (forbs), by biting and cropping the plant parts. Just like any herbivore browsers have developed strategies to make sure that they efficiently utilize the plant parts they feed on. Herbivore (browser and grazers) have evolved and adapted to maximize intake rate of forage they feed on, especially digestive system and the mouth parts. Grazers have wide muzzles while browsers have narrow muzzles to be able to handle the type of vegetation they feed on (Shipley 2007).

The decision made by browsers to take a bite is very important because it has impact on the biomass and nutrient quality taken which influences their fitness (Prache, Gordon & Rook 1998). The basic feeding modes used by browsers are twig-biting, leaf picking and leaf stripping (Rhodes 1994). Stripping of leaves is found to be more used by goats than picking in plants without spines (Gowda 1996). The size of the bite depends on the size of the animal, shape of the mouth and traits of the particular plant being browsed on (Wilson & Kerly 2002). Larger animals take larger bites than small ones. However, Shipley *et al.* (1999) argued that the most preferred bite size depends on the challenges of finding and harvesting the bite and the digestibility of such a bite. Animals favor large bites as they obtain more energy from it, however taking such bites requires high energy expenditure and they are difficult to digest (Shipley *et al.* 1999). It's a tradeoff between size of a bite and the ability to digest it. Browsers prefer non-thorny woody plants with long annual shoots with large leaves, as this will allow them to strip many leaves in one bite (Searle & Shipley 2008). This is described by the plant vigor hypothesis, which states that browsers are likely to go for the large fast growing vigorous plant parts (Price 1991; Makhabu *et al.* 2006). These fast growing plant parts have high protein low fiber concentration (Parker 2004). If animals take old larger twig bites they are likely to get materials of poor nutrient quality in it. Older leaves consist of material of high tensile strength making it hard to break and they have less nutritious materials than new leaves. On the daily basis, a browser can crop between 10000 and 40000 bites from different plants (Illius & Gordon 1990; Wilson & Kerly 2002). Plant leaves and shoots grow in many different shapes and shape is assumed to regulate the food intake rate of mammalian herbivores (Hobbs *et al.* 2003). The intake rates also are strongly affected by the plant defense mechanisms (Skarpe & Hester 2008). The possibility to

encounter a bite on the plants depends on the habitat occupied by the animals. The detection rate depends on the characteristic of the animal (memory, size, speed, sight, and smell), characteristics of the plant (olfactory and visual cues, size, crypticity), plants predictability, and the animal's social characteristics (Searle & Shipley 2008). Often animals store information regarding the spatial distribution of the vegetation they browse on, and they have to remember and locate it when they browse the next time. For some vegetation they rely on visual cues to locate resources, even vegetation at a distance. When the browse is now seen, located or known where to find it the encounter rate will depend on the speed of the animal and distance between the animals and the food (Searle & Shipley 2008).

Evolutionary plants have developed both physical and chemical defence mechanisms as a response to herbivory (Skarpe & Hester 2008). These forms of defence mechanisms are assumed to be costly to the plant in terms of nutrient allocation within the plant and the interaction with the surrounding environment. Due to this cost the plant will only evolve resistance traits if such traits will result in increased fitness compared to plants without them. For the defence traits to develop or evolve on a plant, the cost of the plant to invest on it should be lower than its cost for compensating for the potential biomass loss (Gowda 1996). Avoidance and tolerance are the two existing forms of strategies used by plants to resist herbivory. Avoidance strategy includes escaping and defending itself against herbivores. Plants avoid herbivores by growing very tall or very short. Some plants grow in dense thickets of other plants where they cannot be reached by the herbivores. While some plants avoid herbivory physically some defend themselves against it. They do this via chemical and mechanical or physical defences. In chemical defence they produce secondary metabolites to avoid herbivory. Chemical defence can be classified as qualitative or quantitative (Skarpe & Hester 2008). In qualitative defence the effect of the compound is high already at low chemical concentration, while in quantitative defence effect increases with concentration of the compound. Quantitative secondary metabolites are carbon based compounds produced by the plant that are not essential for the growth of the plant but for other functions (Rhodes 1994; Henderson 2005), among them deterrence of herbivores. In Kruger National park giraffe prefer to heavily feed on *Acacia nigrescens*, however they are limited by the secondary metabolite (tannin) produced by the plant (Fleming *et al.* 2006). Physical defense are structures on a plant such as spines, prickles and thorns (Skarpe & Hester 2008). Tolerance refers to the degree at which plants are able to regrow and reproduce in the environment with a lot of resources after being browsed on (Skarpe & Hester 2008).

The necessary time required for the herbivore to crop vegetation is influenced by plant features such as spines and thorns (Searle & Shipley 2008). Therefore herbivores have to handle armed plants slowly and take small bites to avoid pain and injuries from such plant traits. As a result this lowers the animal's intake rate. For example, greater kudu (*Tragelaphus strepsiceros*) lower their biting rate when browsing on straight-thorned plant species (Cooper & Owen-Smith 1986). Bite size affects the food intake rate, biting rate and may also influence the time the animals spend feeding in a day (Shipley 2007). An animal taking large bites will get full faster and spend less time feeding on the day than an equally sized animal taking smaller bites. The bite size depends partly on the architecture of the plant. Herbivores achieve greater bite size and intake rate where there are minimum interruptions with plant structures such as spines and thorns (Searle & Shipley 2008).

An experiment with goats showed that they stayed longer on a plant without spines and hooks than on the same species of plants with spines and hooks (Skarpe *et al.* 2012). Less time was spend on plants with spines. Therefore spines and hooks of different sizes, shapes and density are expected to affect browser's foraging behaviors such as food intake rate, size of the bite and cropping time (Gowda 1996). This was shown in the browsing goats experiment, where goats switched their feeding mode from twig biting to leaf picking with spinescence. Similarly the biting rate by goats decreased as the density of spines on a plant increased (Skarpe *et al.* 2012). This could be the case also with other browsers when browsing on different species with or without such physical structures. Intake rate of kudu on average was about 8g per minute in woody plants without spines and thorns while in the armed plant they took less than half this amount (Cooper & Owen-Smith 1986). This observation was also seen in other animals (impala and goats) where the rate of consumption was low in the plants with thorns and spines and high in plants without. According to the goat experiment (Skarpe *et al.* 2012), the intake rate was highest in plants where hooks and spines were removed. No hooks and spines gave an intake rate of 3.0g per minute, no hooks 2.1g per minute, no spines 2.1g per minute, and with spines and hooks present 2.2g per minute. Kudu had the tendency to increase their biting rate as the bite size decreases (Cooper & Owen-Smith 1986). Biting rate was found to be highest in plants without hooks and lowest in plants with hooks (Skarpe *et al.* 2012).

2.1 Research questions

How do habitat, spinescence, tree height, animal sex, browsing height, and bite diameter, affect;

- bite size,
- time spent browsing on a tree,
- biting rate, and
- intake rate

of browsing by giraffes in Arusha National Park, Tanzania?

3. Materials and methods

3.1 Study species and system

In the present study I assess the importance of my predictor variables (spinescence, tree height, browsing height, animal sex, bite diameter) on my response variables (bite size, time spend browsing, biting rate, and intake rate) in foraging giraffe (*Giraffa camelopardalis*). I expect the listed response variables to differ among plants with and without spines, in different habitats, with tree height, between bulls and cows, browsing height, and bite diameter of the giraffe.

Giraffe are the tallest ungulates and are known to be sexually segregated in foraging behaviors (Ginnett & Demment 1997). Males tend to forage in tall dense thickets of vegetation while females together with juveniles forage in open habitats where they can increase vigilance to avoid predators (Bergström 1992; Parker 2004). On average male giraffes are much taller 4.9-5.2 meters and weigh more, 1200 kg than females, who are about 4.3-4.6 meters tall and weigh about 800 kg (Skinner & Chimimba 2005). Giraffes are found in loose groups or social structures and are not territorial and males are more nomadic than females (Jeugd & Prins 2000; Skinner & Chimimba 2005; Emmett & Patrick 2012). They are distributed in a patchy discontinuous manner mainly in the savanna habitat where they forage on trees and shrubs (Jeugd & Prins 2000; Parker 2004). They are referred to as mega-herbivores because their body mass exceeds or closely approaches 1000 kg (Owen-Smith 1992; Parker 2004). Their foraging rate is assumed to vary at different levels of the vegetation height, and it is highest at the optimum feeding height of 2.5 meters for female and 3.0 meter for male giraffes (Simmons & Scheepers 1996). Also it is assumed that the biting rate and feeding mode varies between the plants that are equipped with spines and thorns and unarmed plants. Spinescence may slow down the intake rate of the animals.

This study was conducted in Arusha National Park (36°45'E, 3°15'S) which is located near Arusha town in the northern part of Tanzania (Martinoli *et al.* 2006), between Mt. Kilimanjaro and Mt. Meru. Arusha National Park is within the eastern side of the Great Rift Valley. The park is dominated by the volcanic soil from Mt. Meru, resulting from the mountain volcanic activities. The park covers an area of 137 km² and it is surrounded by

highly populated human settlements which block the movement of migratory animals to other places (Martinoli *et al.* 2006).

The habitat types ranges from grassland, shrubland, thickets, bushland to forest (Shannon *et al.* 2008). However for this study purpose, the habitats were divided in four categories according to the dominant vegetation types. The first one is *Acacia* shrub habitat, which is dominated by *Acacias xanthophloea* shrubs. The second habitat type is *Dodonaea* shrubs habitat, which is dominated by *Dodonaea viscosa* shrubs. The third habitat type is tall shrubs habitat, which is dominated by tall shrubs and big trees. The final habitat type is grass-forb-shrub habitat, which dominated by a combination of grasses, forbs and climbers.

Some of the common tree species found in the area are the *Acacia xanthophloea*, *Dodonaea viscosa*, *Rhus natalensis*, and *Maytenus senegalensis*, and some forbs such as *Solanum sp.* Animals found in the park include the giraffes (*Giraffa camelopardalis*), african buffalos (*Syncerus caffer*), common waterbucks (*Kobus ellipsiprymnus*), common duikers (*Sylvicapra grimmia*), plains zebras (*Equus guagga*), dik diks (*Madoqua kirkii*), common warthogs (*Phacochoerus aethiopicus*), servals (*Leptailurus serval*) and spotted hyenas (*Crocuta crocuta*).

3.2 Giraffe observation, time spent on a tree and number of bites

Giraffe observation was carried out late February to late May 2013 by driving transects. When a mature browsing giraffe was observed within 50 meters distance from the road the car was stopped to observe the giraffe. During the observation species of the tree browsed, number of bites, feeding mode (twig biting, leave picking, and stripping), time spend feeding, height browsed relative to the body height, and sex of animal were observed and recorded. The observation lasted for 15 minutes. If the giraffe stopped feeding or walked away the watch was stopped and continued recording when the giraffe started browsing again. When the giraffe disappeared before 15 minutes of observation was achieved, the stop watch was stopped and that was the end of observation for that particular giraffe, but data were taken. Browsed trees were observed and memorized for later measurements and, if

necessary identification. The browsed trees were assigned a number (e.g. tree 1, tree 2 etc) and were identified by their scientific names later.

3.3 Tree measurements

After the observation was done and the giraffe had left the site I left the car for further measurements and recordings on the ground. First the center within the site in which the giraffe was browsing was determined. The center was assigned to the middle point between the browsed plants or to the most browsed tree depending on how the browsed plants were scattered in the area. Then a circular plot of 50 m² (for another study) was established around the center, GPS position was taken, all trees within the plot were identified and their height was measured in meters. Only trees within the plot had their height measured. This meant that some browsed trees, positioned outside the plot, remained unmeasured. Bite diameters and stripping length for plants browsed by the giraffes I observed were recorded. Some bite diameters were not easily accessible for some trees, so they were not taken. Where there were several bites and strips taken 10 diameters and strips were recorded per plant (Stokke 1999).

3.4 Browsing height

Browsing height (m) was recorded in relation to the height at which the giraffe was browsing (Sklenar 2011). It was recorded in these categories: below knee, above knee, chest, lower half neck, upper half neck, head and above head (Kandume 2012). Later the recorded heights were converted into meters by use of a figure of a mature giraffe. I came up with a scale of the giraffe height using a giraffe figure from a book and the actual average shoulder height of a mature male and female giraffe (Skinner & Chimimba 2005). I determined the ratio and used it to convert the recorded browsing height into numbers of meters (table 1 & 2).

Table 1: Browsing height scale for the giraffes in the park

	Male	Female
Shoulder height on image (cm)	10.6	10.6
Average shoulder height in reality (cm)	331	280
Scale (cm)	1:31.2	1:26.4

Average height= Height at body part on the map x Scale

Table 2: Average calculated browsing height for browsing giraffes for both sexes

Body parts	Male, average height (m)	Female, average height (m)
Below knee	0.7	0.6
Above knee	1.9	1.7
Chest	3.0	2.5
Lower half neck	4.0	3.3
Upper half neck	4.6	3.9
Head	5.4	4.6
Above head	5.8	4.9

3.5 Bite diameter

I determined the bite diameter based on the information collected. For most browsed plants bite diameter (mm with one decimal) were determined. To estimate the biomass per bite, I sampled 1.0 mm, 2.0 mm, 3.0 mm, 4.0 mm, and 5.0 mm sized twigs, encompassing virtually all observed bite diameters. For each diameter I collected 10 samples per species. I collected samples from different individual plants at different heights in different locations. Samples were dried individually in the oven at 65 ° C to constant weight (for 24 hours). I weighed the samples to obtain dry mass at each given bite diameter. These weights were then used to estimate biomass of bite diameters recorded in the field, using a regression curve function between diameter and biomass (Table 3).

3.6 Bite size, biting rate and intake rate

I converted the recorded time from minutes and seconds to minutes. I converted seconds to minutes and decimals. Then I calculated the biting rate (biting rate=number of bite/minutes). Using results from the dry mass at given diameters, I constructed a regression curve in Excel showing the biomass (g) at a given diameter for each browsed plant species (Table 3). From the graph I obtained the equation for determining bite sizes (g) for each plant species.

Table 3: List of plant species and the equations used in the calculation of biomass taken by the giraffes. Where: y is biomass (g), and x is the bite diameter (mm) of the giraffes during browsing

Plant species	Equations
<i>Acacia xanthophloea</i>	$y = 0.5291x^2 - 1.2837x + 0.8134$
<i>Dodonaea viscosa</i>	$y = 0.4708x^2 + 0.0712x - 0.8382$
<i>Euclea sp</i>	$y = 0.8671x^2 - 2.2527x + 1.784$

After calculating the bite size and knowing the bite rate (see above) I calculated the intake rate of browsing giraffes in Arusha National Park as Intake rate (dry mass/minute) = Bite size (g)* biting rate (bites/minute).

3.7 Data Analysis

There were missing observations for tree height on browsed plants outside the plot, and inaccessible bite diameters on some plants. I removed all observations with missing values in some variable, resulting in a sample size of 109 plants. I created two groups containing the three most browsed species of plants, those with spines and those without spines (Palgrave 1977) (Table 4).

I used the R statistical program to analyse my data (package R 2.8.0). I did backward selection using linear mixed effect models to see which predictor variables were affecting

my response variables (Zuur *et al.* 2009; Crawley 2012). I used observation number in each model I ran as a random intercept to account for dependence among the plants browsed on by the same giraffe. I based my selection of the significant variables on p-values ($p < 0.05$). Variables which were not significant were removed from the models and the final model had only significant variables. I only presented graphs and statistical results below under results for significant variables. I further ran a separate t-test on bite size to assess difference between the sexes on plant with spines and those without spines

4. Results

A total of 14 plant species were observed being browsed on by giraffes in Arusha National Park in Tanzania. I recorded 255 individual plants being browsed in 76 observations over a span of 3 month (late February to late May, 2013) in the wet season. The most browsed plant species were *Acacia xanthophloea*, *Dodonea viscosa*, and *Euclea sp.* (at least browsed 5 times) the rest of the species were not browsed much (Table 4). After cleaning the data only 109 individual trees were used in the analysis because of the missing values. Twig biting was used in the analysis because I did not observe leaf picking and too low frequency of leaf stripping was recorded. Functional types were defined as ‘spinescent’ (*Acacia xanthophloea*) and ‘non-spinescent’ (*Dodonea viscosa* and *Euclea sp.*).

Table 4: Different plant species observed being browsed on by giraffes in Arusha National Park, Tanzania

Plant species	Number of plants	Used in analysis	Spinescence	Description
<i>Acacia drepanolobium</i>	1	0	Yes	Shrub, 6 meters
<i>Acacia xanthophloea</i>	208	98	Yes	Medium sized, 10-15 meters
<i>Carissa edulis</i>	3	0	Yes	Shrub, 5 meters
<i>Cordia ovalis</i>	2	0	No	Shrub, 4-7 meters
<i>Croton macrostachyus</i>	1	0	No	Medium sized, 15 meters
<i>Dodonea viscosa</i>	13	6	No	Shrub,3-5 meter s
<i>Euclea sp.</i>	13	5	No	Tree,2 to >5 meter s
<i>Juniperus procerus</i>	1	0	No	Tree,10-20 meters
<i>Maytenus senegalensis</i>	4	0	Yes	Shrub,3-5 meters
<i>Myrithina sp</i>	2	0	No	Shrub
<i>Olea africana</i>	3	0	Yes	Shrub,3-14 meters
<i>Rhus natalensis</i>	1	0	No	Shrub, 5 meters
<i>Turrea robusta</i>	1	0	No	Shrub
<i>Vangueria madagascariensis</i>	2	0	No	Shrub, 5-15 meters

Variables included in the analysis are listed in table 5. Only variables which were not confounded or correlated were included in the full model. The final models after backward selection only consisted of variables with significant influence on the response variable,

which are displayed in figures. Only sex and spinescence were influencing the giraffes browsing, the other variables had no influence (Table 5). Below I displayed figures with variables and their influences on the response variables.

Table 5: List of all predictor variables considered in each of the linear mixed models for the four response variables. These consist of the full model including all variables at the start and the variable that were significantly affecting the response variables (final model).

Response variables	Full models	Final models
Browsing time (minutes): On a given plant	Sex, Spinescence, Tree height, Browsing height, Bite size, Habitat	Sex,
Biting Rate (bites/min)	Spinescence, Habitat, Sex, Tree height, Browsing height, Bite size	Spinescence,
Bite size (g)	Sex, Biting rate, Time, Spinescence, Tree height, Browsing height, and Habitat	Sex, Spinescence
Intake rate (grams/min)	Sex, Tree height, Browsing height, Habitat, Spinescence, Time	Sex, Spinescence

4.1 Browsing time per plant

Sex of the browsing giraffes was found to be the only variable significantly affecting the time the giraffes spend browsing on a given plant (Table 6, Figure 1). The remaining variables did not have significant influence on the time the giraffes spend browsing per plant.

Table 6: Backward selection table of linear mixed effect model results on the analysis of list of variables assumed to affect the time the giraffes spend browsing on a plant. The table consists of the variables degree of freedom, likelihood ratio which compares models with and without the variable considered, and the p-value show the significant level for the listed factors.

Variables	Degree of freedom	Likelihood ratio	P-value
Tree height	1	0.097	0.765
Bite size	1	0.225	0.635
Habitat	3	2.464	0.482
Spinescence	1	0.187	0.666
Browsing height	1	1.384	0.239
Sex	1	7.641	0.002

Time spent browsing on a given plant was highly affected by the sex of the browsing giraffes (Table & figure 1). Males spend significantly more time browsing on an individual plant than females. The variation in time spent browsing per plant was higher in males than in female giraffes (Figure 1).

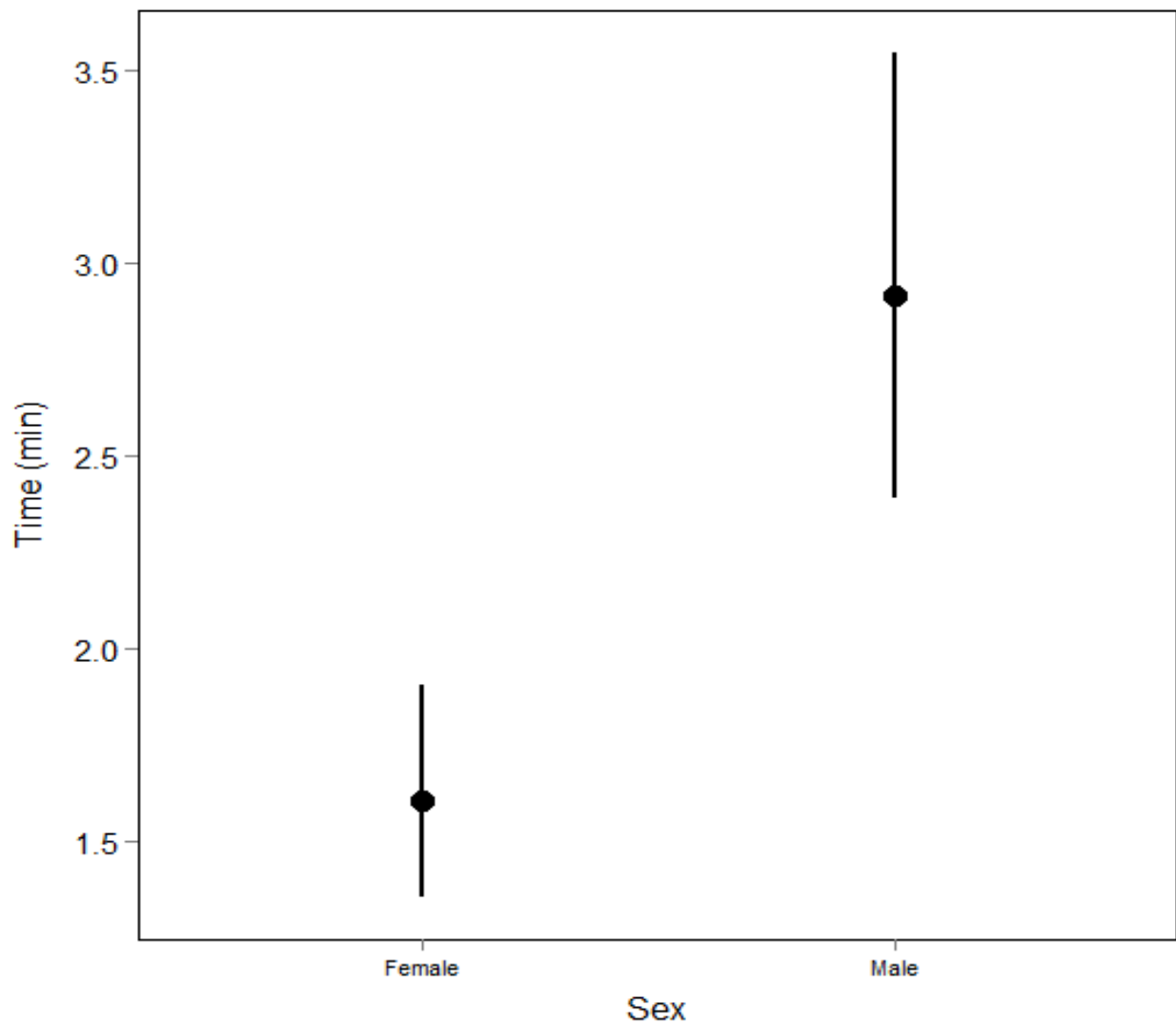


Figure 1: Time spent browsing per plant for each sex of the browsing giraffes. The middle points show the mean time in minutes (min) spent browsing per plant by the giraffes, and the extended lines shows the 95% confidence limits.

4.2 Biting rate

Among all the variables analysed, only spinescence was found to significantly affect the biting rate of the browsing giraffes (Table 7). Browsing height was found to have least influence on the biting rate followed by sex, tree height all the way to the only significant variable, spinescence.

Table 7: Backward selection table of linear mixed effect model results on the analysis of list of variables assed on their effect on biting rate of the browsing giraffes. The table consists of the variables degree of freedom, likelihood ratio which compares models with/without the variable considered, and the p-value show the significant level for the listed factors.

Variables	Degree of freedom	Likelihood ratio	P-value
Browsing height	1	0.450	0.503
Sex	1	0.609	0.435
Tree height	1	1.289	0.256
Bite size	1	1.816	0.178
Habitat	3	5.644	0.130
Spinescence	1	8.017	<0.001

Only spinescence was found to significantly affect biting rate of the giraffe (figure 2). The plants equipped with spines had higher biting rate than those without spines. Plants without spines have higher variation in giraffe biting rate than plants with spines (Figure 2).

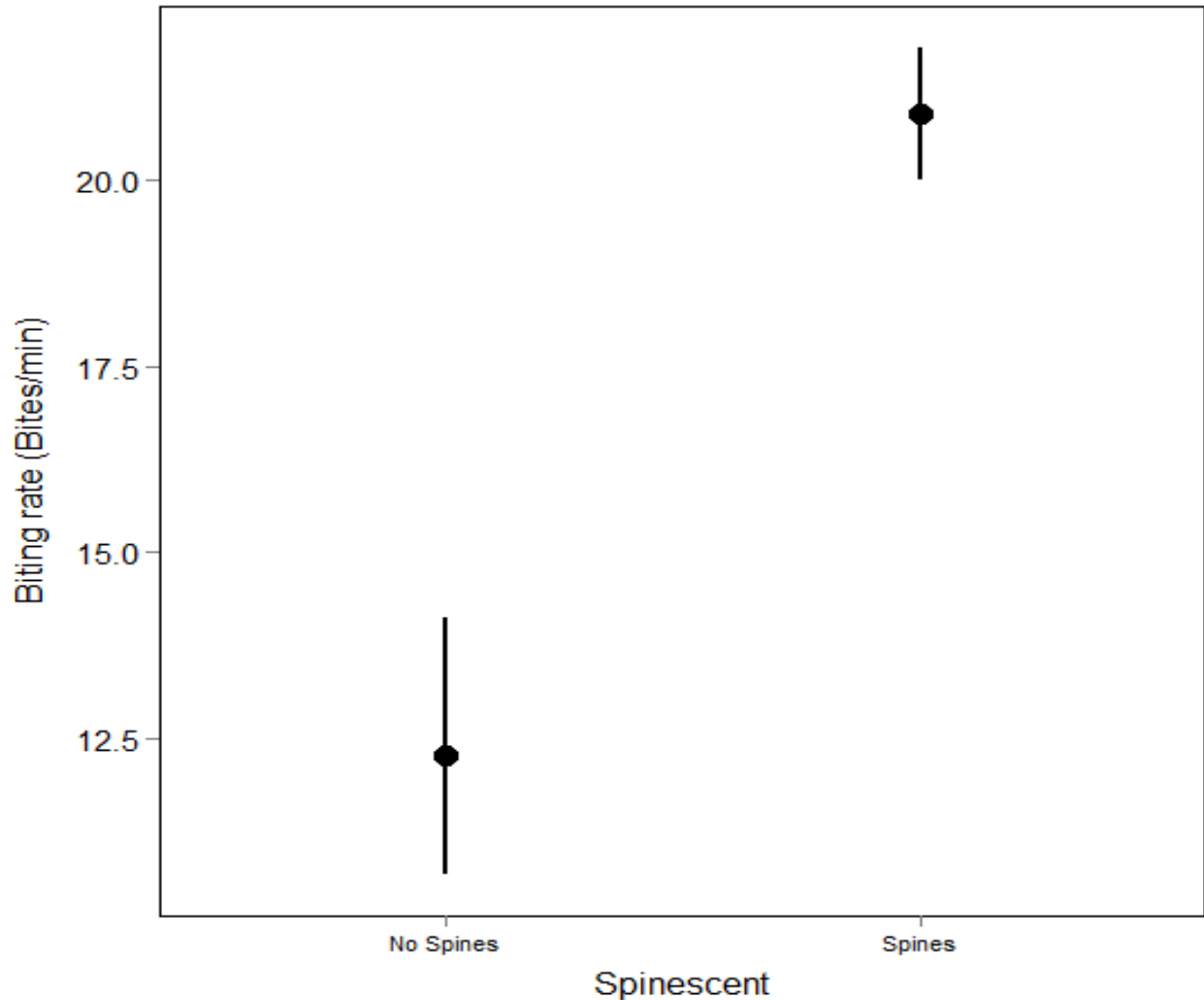


Figure 2: Effect of spinescence on biting rate of a browsing giraffes. The middle points show the mean browsing rate of the giraffes, and the extended lines shows the 95% confidence limits.

4.3 Bite size

Among all variables assed to influence the bite size of the browsing giraffes, only sex and spinescence were found to have an effect. Tree height was the variable with least influence on the followed by habitat all the way to the significant variables. Spinescence is strongly influencing the bite size of the giraffes followed by their sex (Table 8).

Table 8: Backward selection table of linear mixed effect model results from the analysis of list of possible variables influencing the bite size of the giraffes in the park. The table consists of the variables degree of freedom, likelihood ratio which compares models with and without variable considered, and the p-value show the significant level for the listed factors.

Variables	Degree of freedom	Likelihood ratio	P-value
Tree height	1	0.153	0.695
Habitat	3	2.354	0.502
Browsing height	1	0.750	0.386
Time	1	1.496	0.221
Rate	1	1.364	0.243
Sex	1	9.982	0.002
Spinescence	1	36.166	<0.001

Bite size (g) was significantly affected by the browsing giraffe's sex (Table 8 and figure 3). I ran a t- test on spinescent plants and no difference was observed between the sexes ($t=-1.759$, $df=47.97$, $p=0.085$). However, a significant difference between male and female was observed on plants without spines, where female (female = 1.058 ± 0.162 , $t=-3.880$, $df=8.095$, $p=0.005$) took larger bites on average than male giraffes (male = 0.365 ± 0.075).

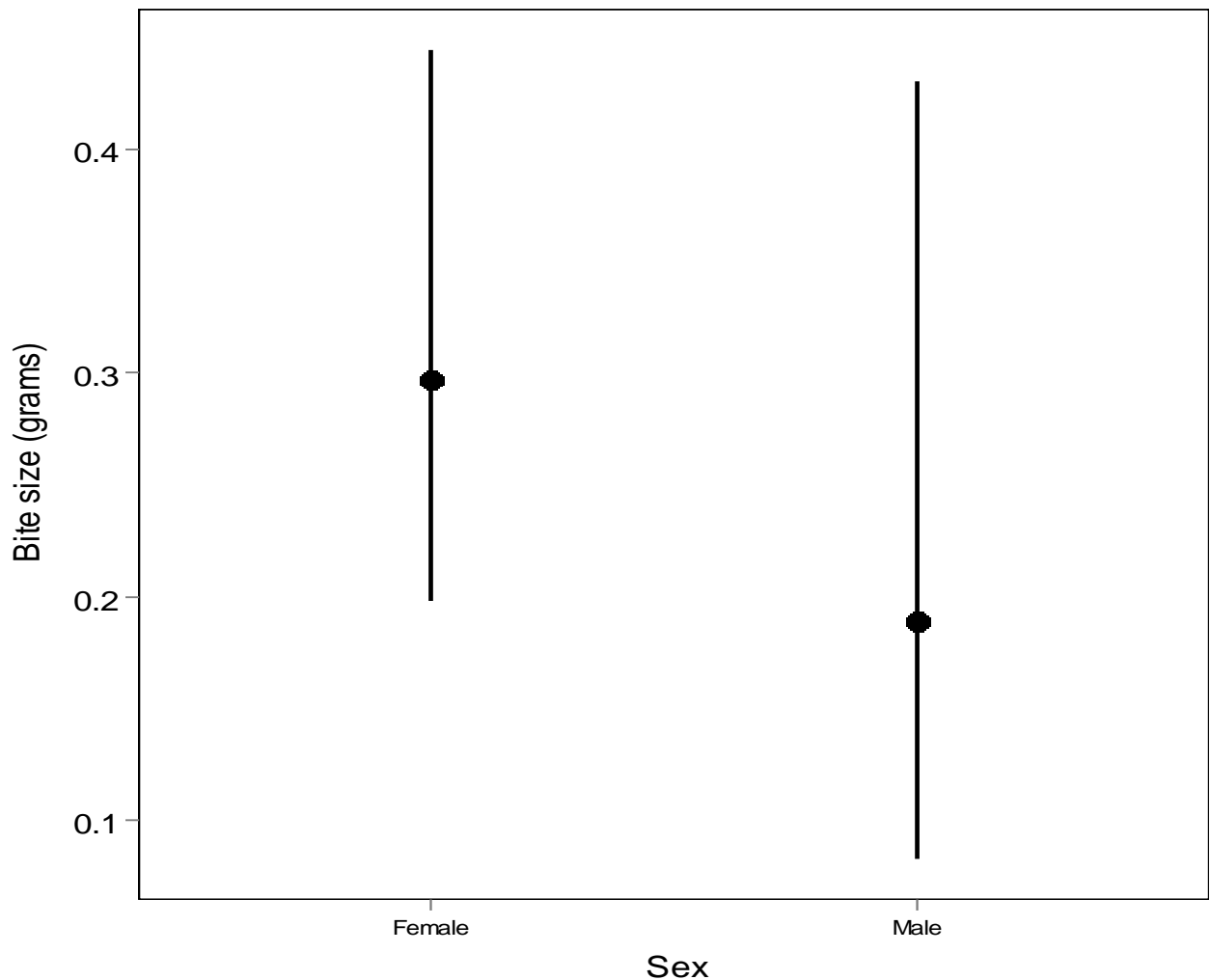


Figure 3: Bite size (g) variation between the male and female browsing giraffes. The middle points show the mean bite size (g) taken by the browsing giraffes per bite, and the extended lines shows the 95% confidence limits.

Bite sizes taken were also affected by spinescence of the plants browsed (Table 8 and figure 4). Plants with spines have significantly smaller bite size than unarmed plants, and there was low variation in bite sizes of armed plant (Figure 4).

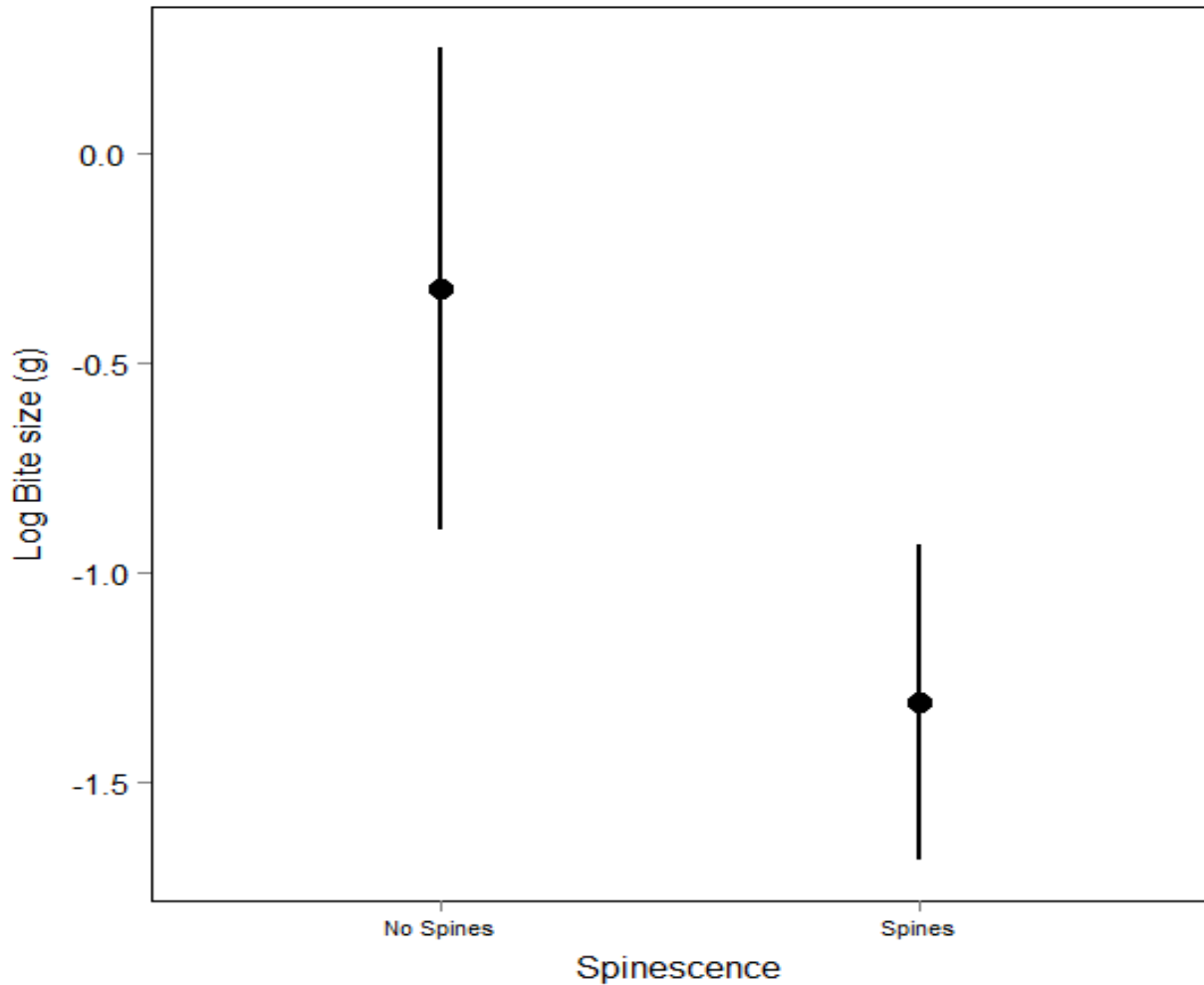


Figure 4: Bite size differences between plants with and without spines. The middle points show the mean bite size (g) taken by the browsing giraffes for armed and unarmed species, and the extended lines shows the 95% confidence limits.

4.4 Intake rate

Spinescence and sex were the only variable found among all variable tested to significantly affect the browsing giraffe's intake rate (Table 9). The remaining variables were not significant. Spinescence has the strongest influence followed by the sex of the browsing giraffes.

Table 9: Backward selection table of linear mixed effect model results from the analysis of list of possible variables influencing the intake rate of the giraffes in the park. The table consists of the variables degree of freedom, likelihood ratio which compare if models with and without the variable considered, and the p-value show the significant level for the listed factors.

Variables	Degree of freedom	Likelihood ratio	P-value
Time	1	0.044	0.833
Browsing height	1	0.261	0.609
Habitat	3	2.075	0.557
Tree height	1	1.383	0.240
Sex	1	9.202	0.011
Spinescence	1	13.579	<0.001

The giraffes intake rate was significantly affected by the spinescence (Table 9). Plants with no spines resulted in high mean intake rate compared to plant without. However they also showed a higher variation than the armed plants (Figure 5).

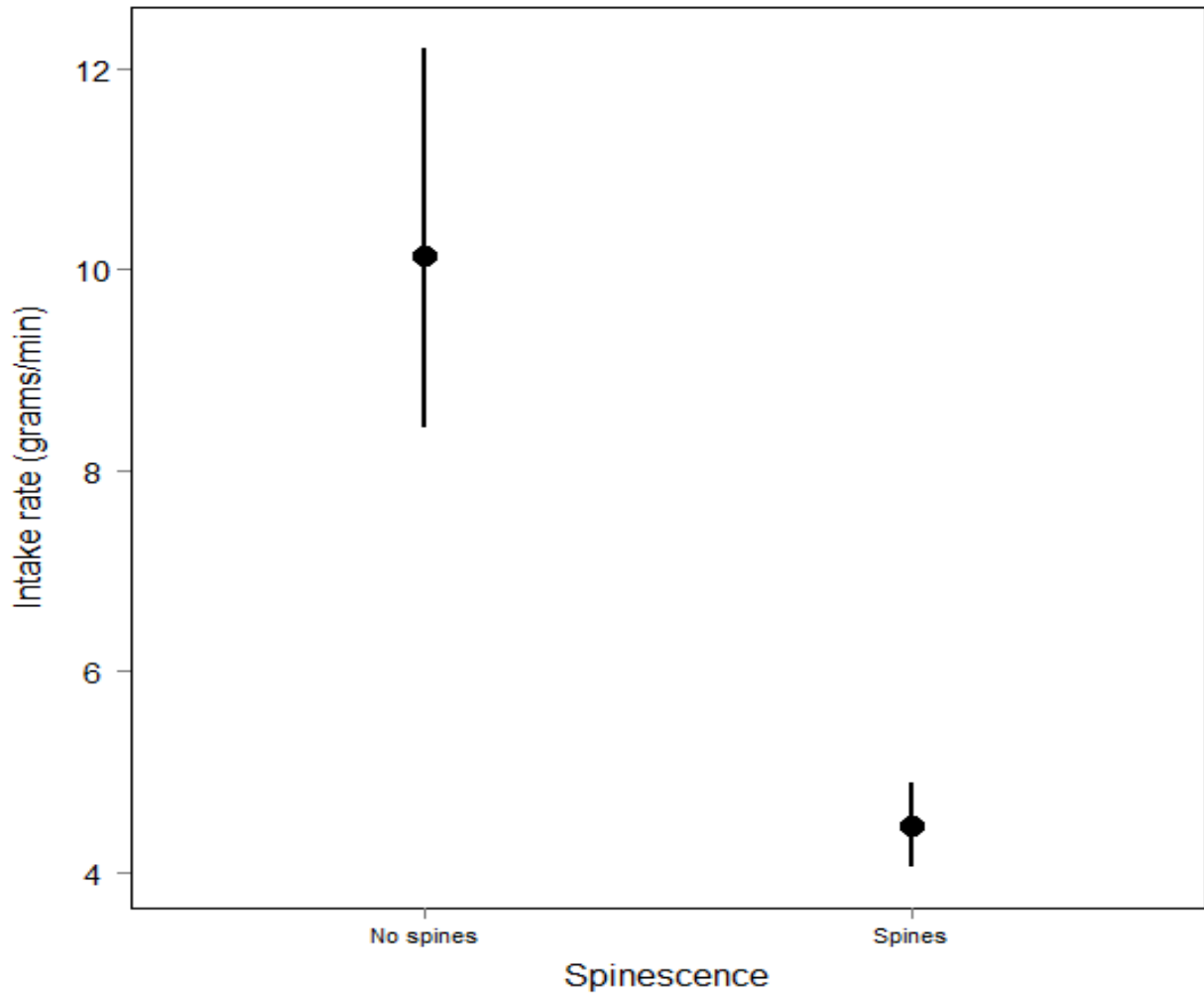


Figure 5: Variation in browsing giraffe's intake rate between plants with and without spines. The middle points show the mean intake rate of plants with and those without spines, and the extended lines shows the 95% confidence limits.

There was difference in intake rate between sexes of the browsing giraffes. Female had high intake rate in comparison to male giraffes (Figure 6).

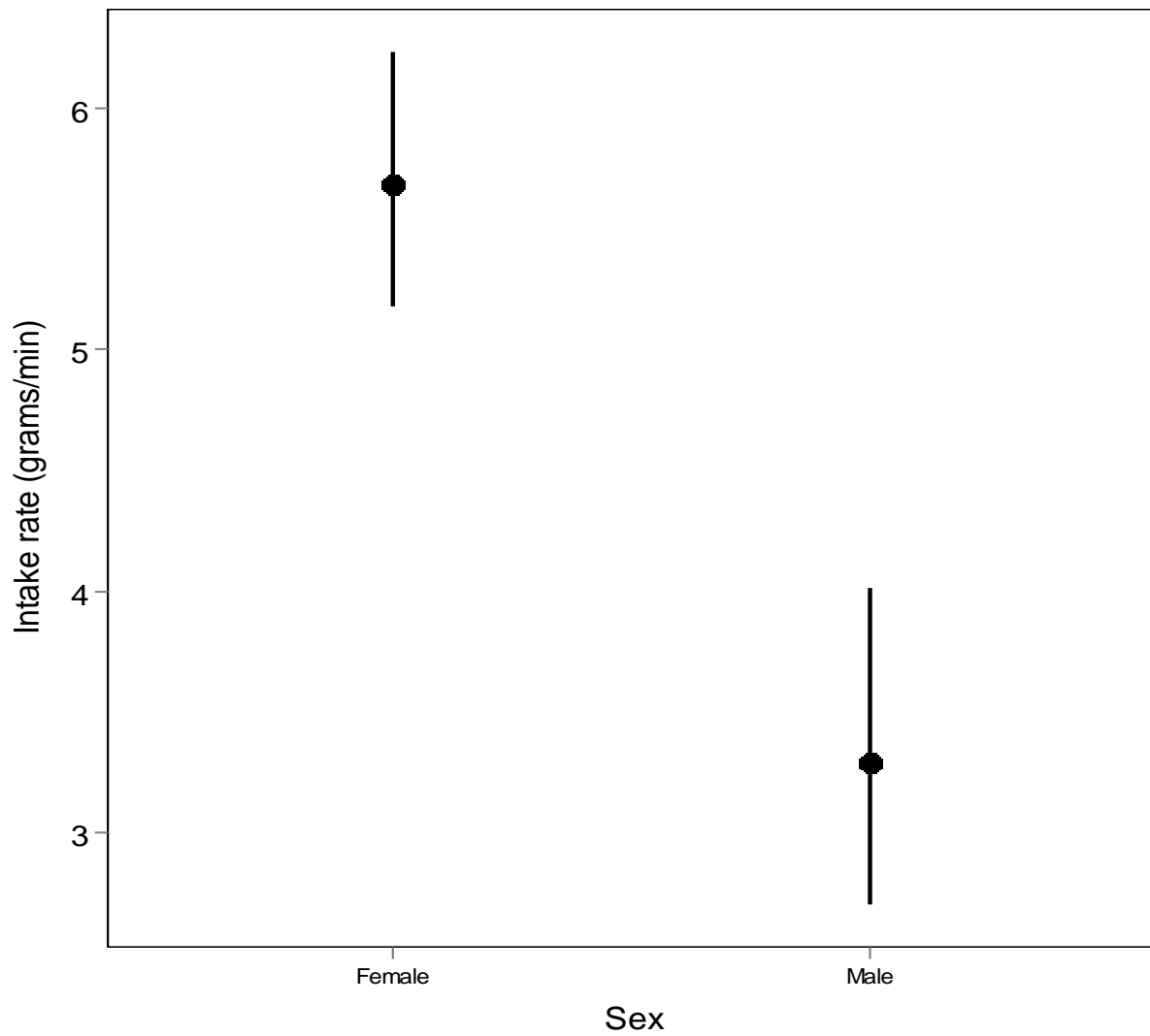


Figure 6: Variation in browsing giraffe's intake rate between the sexes. The middle points show the mean intake rate for browsing giraffes in both sex and spinescence, and the extended lines show the 95% confidence limits.

5. Discussion

There is a high chance that the results are influenced by the unbalanced data set between plant species. There were 98 *Acacia xanthophloea*, 6 *Dodonaea viscosa*, and 5 *Euclea* sp.. This is reflected in the two functional groups, where the group of spine (*Acacia xanthophloea*) have a high number of observations of 98 individual plants, while the no spine (*Dodonaea viscosa*, and *Euclea* sp.) have a very low number of observation of 11 individual plants.

5.1 Browsing time per plant

Time spent browsing on a plant was affected by the sex of the browsing giraffes (table 6). Bulls spend more time on a particular plant than did cows (figure 1). Females browsed less on a plant and then moved on to another while males spend more time exploiting individual plants. Males usually spent less time of their day browsing, and most of it on other social activities such as maintaining dominance status (Ginnett & Demment 1997). However, when they start browsing they spend more time browsing on a given plant than females. Cows on contrary, searched for high quality forage from a larger number of trees. Unlike females, males are large and can tolerate lower quality diet (Owen-Smith 1992), therefore they stay longer exploiting a particular plant than female giraffes (Ginnett & Demment 1997). In an elephant study, bulls were found to feed on a more limited range of plant species than females. Bulls also made use of different plant parts within each plant more than did females and young elephants (Stokke & du Toit 2000). This might be compared with male giraffes browsing and staying much longer on one plant than females. On another study it was indicated that male giraffes invest most of their foraging time on food intake and not on patch to patch movements (Ginnett & Demment 1997). This means that bulls will rather browse on few plants and maximize the food intake, instead of moving from one plant to another looking for nutritious plant parts like female giraffes.

5.2 Biting rate

Biting rate was affected by the plant spinescence (table 7) and it was found to be high on plants with spines and low on unarmed plants (figure 2). This means that giraffes browsed much faster on armed plants than on unarmed plant species in the park. Looking at the bite sizes taken (figure 4), this seem logical as the giraffes took smaller bites on armed plants which then does not require too much time to chew and swallow. Giraffes took larger bites on unarmed plants. In the absence of spines the giraffes find it easy to take larger bites than when there are spines. Large bites require more time to chew and swallow, which slows down the giraffe's biting rate on unarmed plant species. In armed plants during the wet season browsers target new shoots which are not lignified yet, were the thorns and spines cannot affect the biting rate (Cooper & Owen-Smith 1986). Small and soft twigs in armed plants can be chewed fast and thus increase the biting rate. This could be the case in my study because the giraffes were only targeting the new shoots which have just sprouted from the plant. New soft shoots coupled with small diameters resulted in high biting rate due to reduced handling time. In some cases browsers (e.g. kudu) biting rate is more affected by hooked thorns than straight thorns like in the case of *Acacia xanthophloea*, with straight thorns, especially for bigger browsers (Cooper & Owen-Smith 1986). This is supported by Skarpe *et al* (2012) where biting rate was high in plant with no hooks (spine present) with 3.3 bites per minutes and low in plants with hooks with 2.6 bites per minutes. Since *Acacia xanthophloea* have straight thorns and giraffe is a large browsers, it may not have hinder its biting rate. Biting rate was found to increase with decreasing bite size despite spines and thorns (Cooper & Owen-Smith 1986). Therefore, since armed plants have small bite size it is likely the biting rate is high. Also the effect is less for animals used to handling spines and thorns. Giraffes are likely to be able to avoid thorns with its pointed muzzles and long tongue. The finding of my study is that spinescence did not slow the biting rate, which is contrary to the expectations of it to slow down biting rate due to thorn and spines handling, instead speeds it up due to small bite size. According to Bergström (1992) who stated that the presence of spines and thorns lower the biting rate of the browsers, as the browsers have to be careful in handling the plant to avoid injuries. However it is not the case in this study, as the result shows that armed plant have higher biting rate than unarmed plants. In other studies plants with spines resulted in biting rate below the required threshold of 5.0g per minute, except for *Acacia caffra* due to its large leaf size, *Strychnos cocculoides* and *Ziziphus mucronata* which were weekly spinescent (Cooper & Owen-Smith 1986). In my

study the two functional groups were small, with just one species in the thorny group. Therefore, I can not exclude that differences might have been due to species rather than to the functional groups.

5.3 Bite size and Intake rate

The giraffe's bite size and intake rate were significantly affected by the giraffe's sex and spinescence of plants browsed on (tables 8 & 9). Females took larger bites than male giraffes which means female took more biomass in one bite than male giraffes (figure 3). Also t-test result show that for only unarmed plants female giraffes took significantly larger bites than did male giraffes ($t=-3.880$, $df=8.095$, $p=0.005$).

Also browsing giraffes took larger bites on plants without spinescence and smaller bites on armed plants (figure 4). This seems logical as the unarmed plants are not equipped with any physical form of defence to restrict the animals browsing intensity and bite size they took. With armed plants, the giraffes browsing were limited by spines therefore they took smaller bites than on unarmed plants. As taking larger bites in armed plants may mean handling large thorns and spines, which may result in pain, injuries, and more handling effort of the plant parts.

Since bite size strongly influenced intake rate, similarly the same pattern is observed for intake rate, as it was found to be high on unarmed plant due to large bite size (figure 6, and figure 4). This means that when the giraffes browse on plants without spines and thorns, they gain more biomass per minute than on plants equipped with spines and thorns. On plants without spines the giraffes could take large bites without interruption from the spines restricting their bites sizes. In armed plants giraffes only targeted smaller bites twigs of the new shoot of low biomass, resulting in low intake per minutes. Spines protect the plant from being damaged from browsing by mammals (Cooper & Ginnett 1998), therefore the foraging efficiency on this type of plants by browsers is reduced somehow by small bite sizes and low intake rate. In other studies it was observed that large mammals such as kudu's bite size was restricted to smaller bites by spines (Cooper & Owen-Smith 1986). While in plants without spines they could bite a combination of shoots and leaves.

Females took more biomass per time than male giraffes. Although bulls spend more time browsing on a plant, there was a trend that cows took larger bites (figure 3), especially on unarmed plants which then influenced intake rate (figure 6). Bite size influenced the intake rate of the animals, larger bite means more biomass (Shipley 2007). In the study of sex differences in giraffe foraging, it was found that females increased their chewing rate which then elevated their intake rate over male giraffes (Ginnett & Demment 1997). Given equal biting rate between the sexes, the females large bite size and increased chewing rate could have increased their intake rate.

Relative to body mass, large bodied animals have less metabolic constraint than small bodied animals, and they maintain it by feeding on less food (relative to their size) in a day or on less nutritious food materials (Owen-Smith 1992; Reece & Campbell 2011). This might reflect the high intake rate in female giraffes because they require high biomass per unit body mass. According to the study in moose (*Alces alces*) (Spaeth *et al.* 2004), they found that the intake rate was higher for female than for male moose on already browsed plants.

However again this is contrary to the body size theory which says males are larger in most of the ruminants and has a higher total food requirement to maintain their body size compared to female animals (Ginnett & Demment 1997; Stokke & du Toit 2000). Other unforeseen factors could have caused the shift in biomass taken between the sexes. One factor could be the season the collection was conducted. Forage quality changes in different season (Short 1975). In dry season it is likely forage quality is reduced and not so many bites are available to the animals. In wet season animals can choose their preferred bite size when there is more twigs available to them (Sklenar 2011). In dry season is the opposite, not so many twigs are available, therefore it is challenging to see the difference between the sexes. Also Spaeth *et al.* (2004) stated that the size of bites taken by moose could not be understood without the knowledge of the available twig size and the amount of annual growth available for foraging by the animals, not just body size. Therefore, this means that differences between the bite sizes in sexes observed could be due to other causes than differences in body sizes between male and female giraffes. Animal's decision for the bite is influenced by the nutritional quality and bite size available in a given plant (Shipley *et al.* 1999). When the opportunities for good forage quality are reduced, moose will make up by taking large bite sizes (Spaeth *et al.* 2004). This could have been the case in this study; female giraffes could have been taking larger bites of available twigs to compensate for the limited nutrient quality due to their high

metabolic requirement. It could be the time cows needed more food than bulls for calving and lactation

6. Conclusion

My findings reflect that among all my predictor variables (habitat, spinescence, tree height, sex, browsing height, bite diameter), only sex of the browsing giraffes and spinescence of the plants browsed had any significant influence on the giraffe's browsing. Sex has an influence on time spent browsing on a tree, bite size, and intake rate. While spinescence affected biting rate, bite size and intake rate of the giraffes. Therefore in this study it shows that in giraffe's browsing pattern in Arusha National Park, differences exist between the sexes and between plants with and without spines. However this study showed that around the time data was collected males spend more time browsing per plant than females. Although males are known to have large body sizes, require more biomass and tolerate low quality forage, female giraffes took more biomass and have higher intake rate than male giraffes. Therefore females have larger bite size in the park. Giraffe bite size and intake rate is limited by the plant spinescence. Maximum bite size and intake rate is achieved where there is minimum interruption with plants spinescent. There is an observable strong positive correlation link between bite size and intake rate of the giraffes. Foraging time depends on food intake rate. The higher the intake rate the less time spent browsing, and the less intake rate the more time spent browsing. This is observed between the sexes. Males have low intake rate and spend more time browsing on a plant, females have high intake rate and spend less time browsing.

7. Recommendation

For further research, more especially for giraffes in this park, it will be good to see if differences exist on response variable among plant species. Look into daily time allocation for different activities the giraffe has in a day, and this should take both sexes and the juvenile giraffes into consideration. Extend the length of the study period, and also compare different seasons (wet and dry season). It will be good to have a closer look at why female in this park take larger bites than male giraffes. Finally it is necessary to assess the human dimension part also the influence of human settlement around the park on the giraffes browsing behaviors.

8. Acknowledgements

My first big appreciation goes to Christina Skarpe (my supervisor) for all her advices and effort she put in this work. She made it possible for me to be able to reach this final stage of my thesis. I also thank Karen Marie Mathisen for her advice during the data analysis stage. I would like to thank Obeid Mahenya for his contribution to this thesis, the logistics (at Mweka College of African Wildlife Management), and the hard work in the field during data collection stage. Thanks to the National Institute for Medical Research (NIMR) of Tanzania in Arusha town for allowing us to use their laboratory to dry our samples. I would like to extend my appreciation to my classmates and everyone who shared ideas and assisted me when I needed help. I thank god for making everything possible for me to reach the level I am currently at.

9. References

- Bergström, R. (1992) Browse characteristics and impact of browsing on trees and shrubs in African savannas. *Journal of Vegetation Science*, **3**, 315-324.
- Cooper, S.M. & Ginnett, T.F. (1998) Spines protect plants against browsing by small climbing mammals. *Oecologia*, **113**, 219-221.
- Cooper, S.M. & Owen-Smith, N. (1986) Effects of plant spinescence on large mammalian herbivores. *Oecologia*, **68**, 446-455.
- Crawley, M.J. (2012) *The R book*. John Wiley & Sons.
- Emmett, M. & Patrick, S. (2012) *Game ranger in your backpack, all in one interpretative guide to the lawveld*. Briza Publication.
- Fleming, P.A., Hofmeyr, S.D., Nicolson, S.W. & du Toit, J.T. (2006) Are giraffes pollinators or flower predators of *Acacia nigrescens* in Kruger National Park, South Africa? *Journal of Tropical Ecology*, **22**, 247-253.
- Ginnett, T.F. & Demment, M.W. (1997) Sex differences in giraffe foraging behaviours at two spatial scale. *Springer in cooperation with International Association of Ecology*, **110**, 291-300.
- Gowda, J.H. (1996) Spines of *Acacia tortilis*: what do they defend and how? *Oikos*, **77**, 279-284.
- Henderson (2005) *Dictionary of Biology* (ed. E. Lawrence). Pearson Education limited, United Kingdom.
- Hobbs, T.N., Gross, J.E., Shipley, L.A., Spalinger, D.E. & Wunder, B.A. (2003) Herbivore functional response in heterogeneous environments: a contest among models. *Ecology*, **84**, 666-681.
- Illius, A. & Gordon, I. (1990) Constraints on diet selection and foraging behaviour in mammalian herbivores. *Behavioural Mechanisms of Food Selection*, **20**, 369-393.
- Jeugd, H.P. & Prins, H.H.T. (2000) Movements and group structure of giraffe (*Giraffa camelopardalis*) in Lake Manyara National Park, Tanzania. *Journal of Zoology*, **251**, 15-21.
- Kandume, J.N. (2012) Sexual segregation in foraging of greater kudu (*Tragelaphus strepsiceros*) in a heterogeneous savanna, in Chobe National Park, Botswana. *MSc thesis from Hedmark University College*.

- Makhabu, S.W., Skarpe, C., Hytteborn, H. & Mporfu, Z.D. (2006) The plant vigour hypothesis revisited—how is browsing by ungulates and elephant related to woody species growth rate? *Plant Ecology*, **184**, 163-172.
- Martinoli, A., Preatoni, D., Galanti, V., Codipietro, P., Kilewo, M., Fernandes, C.A., Wauters, L.A. & Tosi, G. (2006) Species richness and habitat use of small carnivores in the Arusha National Park (Tanzania). *Biodiversity & Conservation*, **15**, 1729-1744.
- Owen-Smith, R.N. (1992) *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press.
- Palgrave, K.C. (1977) *Trees of southern Africa*. C. Struik.
- Parker, D.M. (2004) The feeding biology and potential impact of introduced giraffe (*Giraffa camelopardalis*) in the Eastern Cape Province, South Africa. *MSc thesis from Rhodes University*.
- Prache, S., Gordon, I.J. & Rook, A.J. (1998) Foraging behaviour and diet selection in domestic herbivores. *Annales de Zootechnie*, **47**, 335-345.
- Price, P.W. (1991) The plant vigor hypothesis and herbivore attack. *Oikos*, **62**, 244-251.
- Reece, J.B. & Campbell, N.A. (2011) *Campbell & Reece biology eight edition*. Pearson.
- Rhodes, M. (1994) Physiological roles for secondary metabolites in plants: some progress, many outstanding problems. *Plant Molecular Biology*, **24**, 1-20.
- Searle, K.R. & Shipley, L.A. (2008) The Comparative Feeding Behaviour of Large Browsing and Grazing Herbivores. *The Ecology of Browsing and Grazing* (eds I.J. Gordon & H.H.T. Prins), pp. 117-148. Springer.
- Shannon, G., Page, B., R., Mackey, L., R., Kevin, J. & Slotow, R. (2008) Activity Budgets and Sexual Segregation in African Elephants (*Loxodonta Africana*). *American Society of Mammalogists Activity*, **89**, 467-476.
- Shipley, L.A. (2007) The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. *Oikos*, **116**, 1964-1974.
- Shipley, L.A., Illius, A.W., Danell, K., Hobbs, N.T. & Spalinger, D.E. (1999) Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. *Oikos*, **84**, 55-68.
- Short, H.L. (1975) Nutrition of southern deer in different seasons. *Journal of Wildlife Management*, **39**, 321-329.
- Simmons, R.E. & Scheepers, L. (1996) Winning by a neck: sexual selection in the evolution of giraffe. *American Naturalist*, **148**, 771-786.

-
- Skarpe, C., Bergstrom., Danell, K., Eriksson. & Kunz, C. (2012) Of goats and spines-a feeding experiment *African Journal of Range & Forage Science*, **29**, 37-41.
- Skarpe, C. & Hester, A. (2008) Plant traits, browsing and grazing herbivore, and vegetation dynamics. *The ecology of browsing and grazing, Ecological Studies* (eds I.J. Gordon & H.H.T. Prins), pp. 222-229.
- Skinner, D.J. & Chimimba, C.T. (2005) *The Mammals of the Southern African Subregion*. Cambridge University Press, Cape Town.
- Sklenar, M. (2011) Sexual differences in feeding behavior of the greater kudu (*Tragelaphus strepsiceros*) in a small nature reserve. *MSc thesis from Uppsala University*.
- Spaeth, D.F., Bowyer, R.T., Stephenson, T.R. & Barboza, P.S. (2004) Sexual segregation in moose *Alces alces*: an experimental manipulation of foraging behaviour. *Wildlife Biology*, **10**, 59-72.
- Stokke, S. (1999) Sex differences in feeding-patch choice in a megaherbivore: elephants in Chobe National Park, Botswana. *Canadian Journal of Zoology*, **77**, 1723-1732.
- Stokke, S. & du Toit, J.T. (2000) Sex and Size related differences in the dry season feeding pattern of elephants in Chobe National Park, Botswana. *Ecography*, **23**, 70-80.
- Wilson, S.L. & Kerly, G.H.I. (2002) Bite diameter selection by thicket browsers: the effect of body size and plant morphology on forage intake and quality. *Forest Ecology and Management*, **181**, 51-65.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R*. Springer.