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The Rothschild's giraffe as a potential biological controller of invasive native *Acacia* species in Lake Mburo National Park, Uganda

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Acknowledgments

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Linn Williams

Abstract

Shrub and woody encroachment can have serious ecological impacts and is an increasingly common problem in many ecosystems, from the African savanna to the Arctic. Lake Mburo National Park in Uganda is experiencing severe woody encroachment of the native invasive *Acacia* species. In 2015, 15 Rothschild's giraffes (*Giraffa camelopardalis rothschildi*) were translocated to Lake Mburo as both a conservation effort to expand the range of the endangered giraffe subspecies and as part of a long-term project to control the encroachment of *Acacia* in the park. I investigated if giraffes could potentially act as biological controllers of the invasive *Acacia* species in the park by studying diet preferences and spatial feeding area selection on three scales: landscape, patch, and fine scale. Over 80% of the giraffes total diet consisted of *Acacia*, implying that the small population of giraffes consume more than 200 kg of dry-weight *Acacia* biomass on a daily basis. Giraffes selected for *Acacia* on all scales. On the landscape scale, giraffes foraged in areas with high densities and abundances of *Acacia*. On the patch scale, giraffes fed in homogenous, open areas. On the fine scale, giraffes selected for *Acacia*, utilizing it three times more than its availability. The giraffes also preferred to feed on *Acacia* trees that were 4-5 m tall, selecting taller than average individuals to feed on. This foraging behavior implies the potential for giraffes to act as biological controllers of the native invading *Acacia* species in Lake Mburo.

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Introduction

Shrub and woody encroachment is a global phenomenon that has received increased attention over the past decades (Blaum et al. 2007; Cabral et al. 2003; Eldridge et al. 2011; Ratajczak et al. 2012; Stevens et al. 2017). Invasions by native species can have the same impact on the ecosystem as alien species (Nackley et al. 2017). Changes in woody cover have been shown to affect species richness of a wide range of species at different trophic levels, including small mammalian carnivores (Blaum et al. 2007), birds (Sirami et al. 2009), and herbaceous vegetation (Ratajczak et al. 2012). In line with the habitat heterogeneity hypothesis (MacArthur & MacArthur 1961), a slight increase in woody cover may temporarily increase species richness before decreasing below original values (Blaum et al. 2007; Sirami et al. 2009). Encroachment also affects community composition (Ratajczak et al. 2012), ecosystem structure and function (Eldridge et al. 2011), and services such as carbon sequestration (Coetsee et al. 2013). The livelihoods of pastoralists are threatened by woody encroachment (Dalle et al. 2006; Mugasi et al. 2000). Consequences for farmers include decreased livestock production due to loss of grazing land and secondary invasions by alien plant species (Dalle et al. 2006; Wigley et al. 2009). Woody plant encroachment may also reduce the tourist value of national parks by decreasing the visibility of wildlife and, consequently, tourist satisfaction (Gray & Bond 2013).

In savanna ecosystems, increase in woody cover is often a result of herbivore removal (Kiffner et al. 2017; Lock 1993; Smart et al. 1985), or changes in fire frequency (Dalle et al. 2006; Skowno et al. 1999), rainfall patterns (Gordijn et al. 2012), or land use (Blaum et al. 2007; Roques et al. 2001). The extinction or extirpation of keystone species has the potential to induce trophic cascades, causing long-term changes to population dynamics (Valeix et al. 2011; Waldram et al. 2008). For example, the extirpation of the dingo (*Canis dingo*), an apex predator and keystone species, in the Strzelecki Desert, Australia was linked to shrub encroachment as a result of trophic cascades (Gordon et al. 2017). Megaherbivores are often described as keystone species by their ability to affect vegetation structure and composition (Asner et al. 2009; Hagenah et al. 2009; Ruess & Halter 1990; Strauss & Packer 2015). The extinction of megaherbivores has been linked to changes in ecosystem structure and function as well as community composition, including shrub and woody encroachment (Bakker et al. 2016; Chritz et al. 2016; Doughty et al. 2016). For example, bush encroachment in Lake Manyara National Park in Tanzania was likely caused by herbivore population crashes, most notably of elephant and impala (Prins & van der Jeugd 1993).

These ecological state shifts are often permanent, as seen following the mass extinction of megafauna in the Pleistocene (Owen-Smith 1987; Owen-Smith 1989). However, woody encroachment is influenced by intertwined mechanisms and multiple factors can be at play simultaneously (Riginos & Young 2007; USAID 2017).

Megaherbivores have the potential to act as biological controllers, preventing woody encroachment, by consuming large amounts of plant biomass (O'Connor et al. 2014). Large browsing ungulates, especially elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*), have been documented to suppress woody encroachment in African savannas (Augustine & Mcnaughton 2004; O'Connor et al. 2014; Stevens et al. 2017; Strauss & Packer 2015). Elephants control tree abundance by reducing tree height and densities, and their probability of reproduction, leading to increased tree mortality (Gandiwa et al. 2011; Pringle et al. 2014). It is often the interplay between grazers and browsers that maintain tree-grass ratios (Van de Koppel & Prins 1998). Grazers can prevent trees from outcompeting grasses while browsers regulate the abundance of trees (Van Langevelde et al. 2003). Together, megaherbivores can prevent woody encroachment by maintaining a balance between trees and grasses (Angassa & Oba 2010).

Lake Mburo National Park (henceforth Lake Mburo) in Uganda is experiencing a considerable increase in the density of trees, especially of *Acacia hockii* (Blösch 2008; Infield et al. 2008; Olsen 2016; Uganda Wildlife Authority 2015). *Acacia* species already dominate the open savanna in the park (Moe et al. 2009). Queen Elizabeth National Park and Murchison Falls National Park, both in Uganda, are also experiencing extensive regeneration of *Acacia,* resulting in woody encroachment (Lock 1993; Smart et al. 1985). Due to human activity, frequent fires, and changes in land use, formerly open areas are gradually turning into dense *Acacia* forests (Averbeck et al. 2009; Brown & Fennessy 2014; Uganda Wildlife Authority 2015). Whereas some few species like bushbuck (*Tragelaphus scriptus*) and baboons (*Papio cynocephalus*) may benefit from an increase in woody cover, many common ungulate species, notably grazers and mixed feeders such as zebra (*Equus quagga boehmi*), topi (*Damaliscus lunatus jimela*), buffalo (*Syncerus caffer*), and impala *(Aepyceros melampus*) are likely to be negatively impacted by these changes and reduce in number or possibly disappear altogether from the ecosystem (Kiffner et al. 2017; Smit & Prins 2015; USAID 2017).

In July 2015, 15 Rothschild's giraffes (*Giraffa camelopardalis rothschildi*), 11 females and four males, were relocated from Murchison Falls National Park to Lake Mburo in an effort to increase the giraffe's range as well as diversify the park to increase tourism to the area (African Adventure Travellers 2016; Brown & Fennessy 2014; Marais et al. 2016). The giraffes are also a part of a long-term project to investigate their ability as biologically controllers of the increasing densities of native *Acacia* trees in the national park. This project is based on giraffe's preference for *Acacia* (Gordon et al. 2016; Mahenya et al. 2016b; Parker et al. 2003; Pellew 1980; Strauss & Packer 2015). Overbrowsing by giraffes has been shown to reduce woody encroachment in southern Africa and on a cattle ranch in Kenya (Pellew 1980). Strauss and Packer (2015) observed that in areas where giraffes browsed, plant species preferred by giraffes decreased in abundance while those avoided by giraffes increased. Bond and Loffell (2001) found that giraffes changed the distribution of *Acacia* in a South African savanna, with some species of *Acacia* having disappeared in high-density giraffe areas. Chronic high browsing pressure has also been shown to limit the growth of *Acacia nigrescens* trees in Kruger National Park, South Africa by keeping them in a hedged state (Fornara & du Toit 2007). It was therefore hypothesized that introducing giraffes to Lake Mburo National Park could potentially reduce the woody encroachment of *Acacia,* if the animals are able to establish and increase in population size.

A preliminary assessment of Lake Mburo had encouraging findings as a release site for the Rothschild's giraffes based on floral and faunal communities, but no additional surveys or analyses have been performed since their release (Brown & Fennessy 2014). The diet of extralimital giraffes in South Africa has been studied extensively (Gordon et al. 2016; Parker et al. 2003), but there is limited literature on the diet of giraffes in East Africa. It is therefore necessary to investigate the feeding behavior of the translocated giraffes. The goal of this study was to assess the potential of the translocated Rothschild's giraffe in Lake Mburo as a biological controller of the invasive native *Acacia* species. Because interpretation of selection is dependent on scale (Fryxell et al. 2008; Mayor et al. 2009; WallisDeVries et al. 1999), diet and feeding area preference was analyzed on the landscape scale (comparing feeding and random plots), the patch scale (comparing feeding and adjacent plots), and the fine scale (comparing diet and feeding plots). The research objectives were to investigate to what extent giraffes were feeding on *Acacia* species and if these species were selected for. I predicted that i) giraffes select for *Acacia* in their diet, because of the reported abundance of *Acacia* in Lake Mburo and the wealth of studies reporting *Acacia* selection in giraffe diet (Bond & Loffell 2001; Brenneman et al. 2009; Pellew 1980; Strauss & Packer 2015); ii) giraffes select to forage in areas with a higher concentration of *Acacia*, based on several studies that observed giraffes to feed in *Acacia*-dominated areas (Mahenya et al. 2016b; Pellew 1980; Strauss & Packer 2015); iii) giraffes select to feed in areas with denser woody cover due to increased available forage (Young & Isbell 1991); and iv) giraffes forage on tall trees (3-5 m) to reduce competition from other browsers (Cameron & du Toit 2006; Mahenya et al. 2016a; Young & Isbell 1991).

Materials and Methods

Study Area

Lake Mburo National Park is located in southwestern Uganda between 00°30′ and 00°45′S, and 45°00′ and 31°05′E, at an average altitude of 1210 m (Figure 1; Wronski 2002). It covers 260 km^2 and receives 700-800 mm rainfall annually. It has a bimodal rainfall pattern with a long, wet season between February and June and a short, wet season between October and December. Average temperature is 27.5°C with daily variations between 21.5 and 34.0°C. Lake Mburo is part of the Akagera savanna ecosystem (Averbeck et al. 2009), characterized by heterogeneous savanna grassland interspersed with both dense and open woodland (Blösch 2008; Rannestad et al. 2006). Farmland and the Ankole Ranching Scheme surround Lake Mburo (Averbeck et al. 2009). The park is home to 68 mammal species, including Uganda's only population of impala, and 312 bird species (Averbeck 2002). Excluding giraffes, hippo (*Hippopotamus amphibius*) is the only other megaherbivore species in the park. The largest predators in the park are leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*), and one solitary lion (*Panthera leo*) (Averbeck et al. 2009). The present study was carried out during the dry season from June to August in a study area characterized as open grassland with clumped distribution of trees (Figure A1).

Large parts of Lake Mburo is dense woodland, with reports of *A. hockii* dominating up to 60% of the park (Namara 2017). The increase in dense vegetation in the park is likely to result in decreased biodiversity and wildlife abundance, reducing the tourism value and tourist revenue of the national park, which was estimate at around USD 400,000 in 2013 (Uganda Wildlife Authority 2015). A decrease in tourism will have negative financial consequences for Lake Mburo and the surrounding communities that depend tourism for revenue. There has also been reports of human-wildlife conflict as wildlife migrate to the surrounding ranchlands in search for suitable habitat (Uganda Wildlife Authority 2015). Current efforts to control the encroaching forest cover are costly and include manual clearing by uprooting and burning trees (Brown & Fennessy 2014).

In this study, I use the genus *Acacia*, although the phylogeny of *Acacia* has been proposed reclassified. *Acacia polyacantha* has been suggested to be renamed *Senegalia polyacantha,* while *A. gerrardii, A. hockii,* and *A. sieberiana* have been suggested to be included in the *Vachellia* genus (Kyalangalilwa et al. 2013). However, due to the lack of universal adoption of these proposed changes, these species will retain their original classifications in this paper.

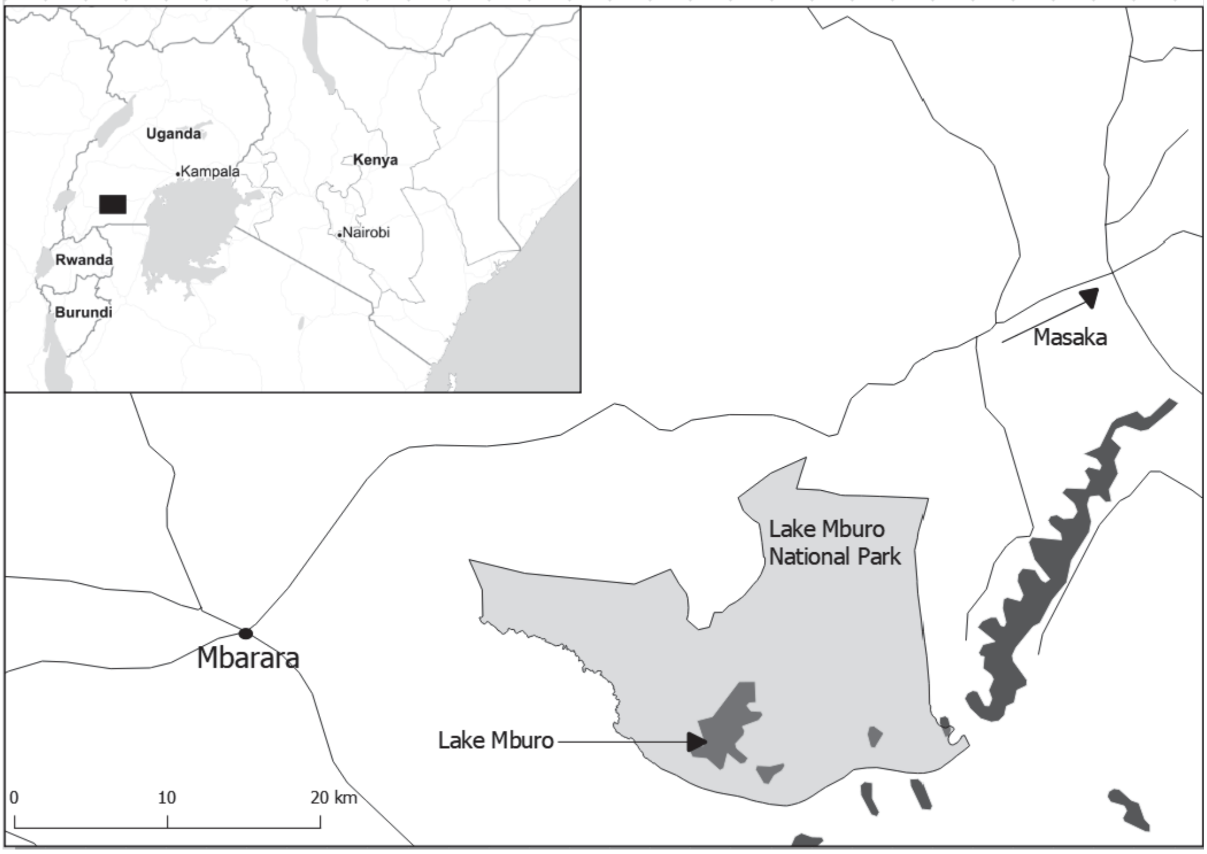

Figure 1. Lake Mburo National Park in Uganda, East Africa.

Study Species

The Rothschild’s giraffe is an endangered subspecies endemic to Kenya and Uganda. It is a subspecies of the northern giraffe *Giraffa camelopardalis* which was recently suggested to be an ecotype of the Nubian giraffe *Giraffa camelopardalis camelopardalis* (Fennessy et al. 2016; Giraffe Conservation Foundation 2017). The current numbers of the Rothschild’s giraffes are estimated at around 1300 individuals. Giraffes are ruminant browsers that forage mostly on tree leaves (Pellew 1984a). Giraffes generally prefer *Acacia* woodland, but habitat preference is also dependent on sex and season (O'Kane et al. 2011; Pellew 1980; Young & Isbell 1991).

Data collection

Giraffes were located using a 4WD car between 0800 and 1700 hours. Using a spotting scope, feeding observations (n=1401) were done at a distance between 100 and 200 m to reduce disturbance to the giraffes. Giraffe height, tree height (highest point of tree within plot, estimated to the nearest 0.5 m), tree species, number of bites, and length of observation was recorded during two minute focal observations (Altmann 1974). Giraffe height was estimate to the nearest 0.5 m and regularly checked in the field by measuring giraffe height in relation trees they fed on. Duration of each browsing observation was recorded using a stopwatch. Giraffes were selected for observation based on their visibility and recently observed individuals were avoided. The same individual was not observed within 2 minutes of the end of its previous observation period. The first giraffe to be observed was the most visible individual. Focal observations commenced from the first bite and ended when the giraffe either moved out of view or moved away from the plant and did not take a new bite within 5 seconds of the last bite. If the giraffe began eating on a new plant individual within 5 seconds of its last bite, it was included in the same observation. If not, a new giraffe was selected for observation. Feeding data was collected until either the giraffes rested, or they disappeared out of sight.

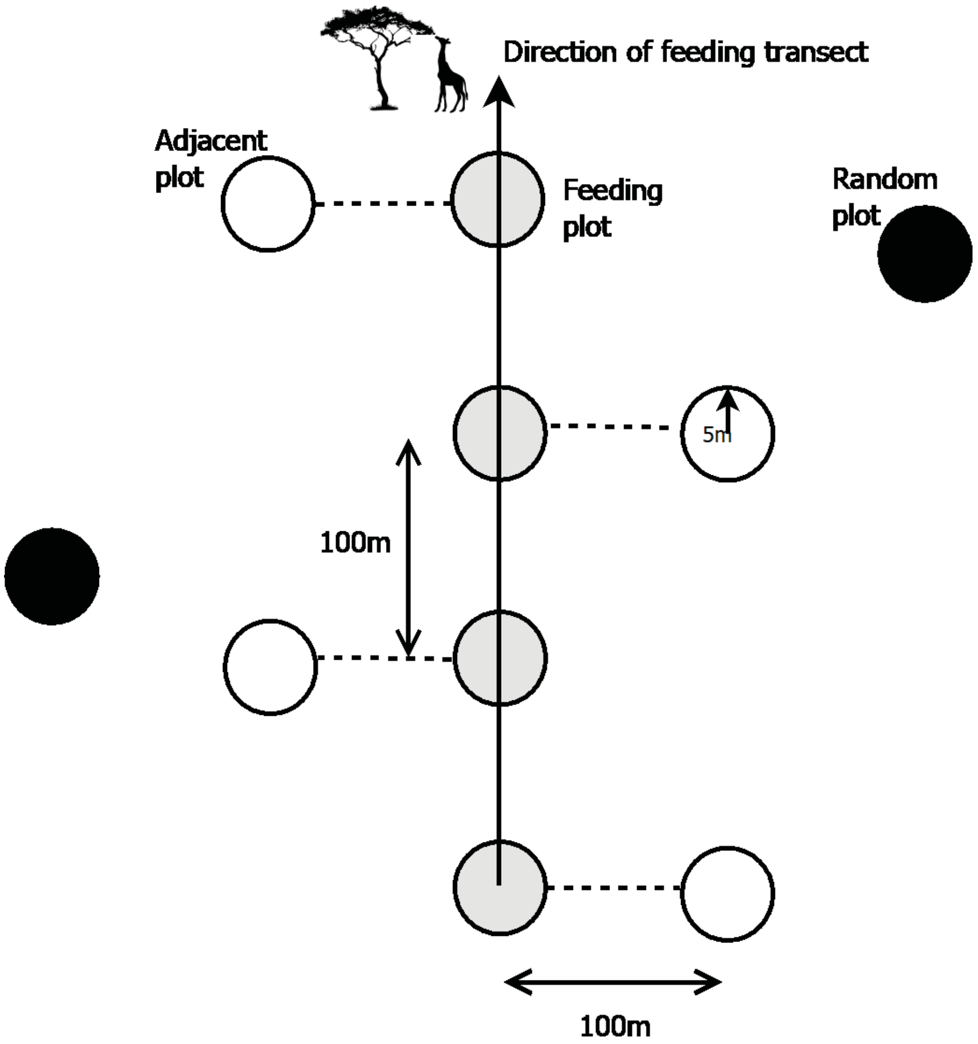

Figure 2. The study design illustrating feeding (gray, n=349), adjacent (white, n=349), and random (black, n=50) plots in relation to browsing path of giraffes. Each plot has a radius of 5 m. The first feeding plot of the feeding transect is in the same position as the first feeding observation. Adjacent plots were 100 m from their corresponding feeding plot at right angles of the transect path, alternatingly left or right. Each feeding plot was situated 100 m from the previous one. Random plots were situated randomly throughout the study area. Distances between plots are center-to-center distances. Figure is not drawn to scale.

Vegetation plots (n=748), defined as a circle with a radius of 5 m, were used to measure available vegetation composition along a feeding transect (Figure 2). A feeding transect was defined as the distance between a GPS point taken at the location of the first feeding observation and the last feeding observation of the transect (i.e. comprising the feeding of an entire group of giraffes). The transect was followed using a GPS and following a straight line from the first to last foraging point. If the direction of the giraffes turned, an additional GPS point was taken to account for the change in general direction. Feeding plots were positioned every 100 m along the feeding transect, with the first plot taken at the beginning of the feeding transect. For each feeding plot along the feeding transect, a corresponding plot (henceforth termed adjacent plot) 100 m away at a perpendicular angle to the transect, was also sampled. The adjacent plot was alternately located to the left or right of the feeding transect, unless some obstacle (e.g. a road) prevented the locations of a plot on that particular side of the feeding transect. The vegetation plots were sampled within 24 hours of the collection of the feeding data in the same transect. In addition to the feeding plots and adjacent plots, 50 random plots were sampled within the study area. The study area was defined as the general area in which giraffes had been observed foraging during the entire study period. In order to select the random plots, 100 points were positioned on a map spaced throughout the study area where giraffe data had been collected, and then 50 plot locations out of 100 candidate sites were randomly selected. Within each feeding, adjacent, and random plot, plant species, number of individuals of each species, and height of the tallest individual of each species within the plot was recorded. Height was either measured with a 4 m long measuring stick or, if above 4 m, estimated to the nearest 0.5 m. All vegetation in the plots, excluding grass and herbs that were not observed to be eaten by giraffes, was included in the analysis.

Statistical analysis

All statistical tests were carried out in R v. 3.4.1 for Windows (R Core Team 2014). To evaluate giraffe preference, I used Ivlev's electivity index formula:

$$E = \frac{u-a}{u+a},$$

where u is the relative abundance of a species in the diet (use), and a is the relative abundance of a species in the environment (availability) (Ivlev 1961). I used Ivlev's index because it does not assume resource depletion and is bounded by -1 and +1, indicating the least and most preferred species, respectively, with a value of 0 indicating a species used at the same proportion as its availability (Lechowicz 1982). Any species which did not occur in the diet, but did occur in the vegetation plots, will have an electivity value of -1.0. Accordingly, species which only occurred in the diet and not in the vegetation plots, will have a value of +1.0. The values of rare species may be more representative of chance or sampling errors rather than actual selection by giraffes

(Lechowicz 1982; Loehle & Rittenhouse 1982). Rare species (species absent from either the diet or vegetation plots) were therefore excluded from the analysis (Lechowicz 1982; Loehle & Rittenhouse 1982; Strauss 1979). Results were tested with chi-square goodness-of-fit and p-values were standardized with Bonferroni correction. GLM with a Poisson error distribution was used to assess the effect of tree height on total number of bites taken. GLM with a Gaussian error distribution was used to investigate the effect of tree height on mean bite rate. Statistical significance of GLMs were based on chi-square tests against null models. Selection for tree height of *Acacia* species was investigated by comparing tree heights of *Acacia* in the diet and in feeding plots. Only the tree heights of the tallest individuals of each species in each vegetation plot were recorded. Therefore, actual median tree height in feeding plots may be considerably lower than recorded.

Differences in the vegetation composition between the three plot types (feeding, adjacent, and random) were tested for using non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances, followed by ANOSIM. Rare species (occurring in fewer than five plots) and plots with few species (< 5 species) were excluded from the analysis in order to reach convergence (Cao et al. 2001). Data was square root transformed and Wisconsin double standardized. To minimize stress, 20 runs with maximum of 1000 iterations and four dimensions were used. The run with the lowest stress was selected. Pairwise equal-weighted and size-weighted Horn indices based on Shannon entropy were calculated using the *SpadeR* package (Chao et al. 2015; Horn 1966). Due to unequal community weights, Shannon measures were chosen (Jost 2007). The Horn index was selected to avoid unproportional weighting of rare or abundant species and due to different plot statistical weights (Jost 2007; Jost et al. 2011). Species diversity was measured as Shannon diversity, weighting species in terms of their proportional abundance (Hill 1973; Hsieh et al. 2016). Species richness estimates were based on the Chao estimator (Chao 1984; Chao 1987). Species diversity between plot types were compared based on sample completeness due to differences in sample sizes between the random plots and the two other plot types (Chao & Jost 2012). Sample completeness was measured as the proportion of total number of individuals of a species in a sample, also known as sample coverage (Hsieh et al. 2016). Homogeneity of the plot types were investigated with beta diversity. Beta diversity was measured as the dissimilarity between plots within a plot type based on the Bray-Curtis index using the *betapart* package (Baselga & Orme 2012). Beta diversity was then compared between plot types using the *vegan* package (Oksanen et al. 2017). Significance testing of beta diversity was done with permutation test of multivariate homogeneity of group dispersions (Anderson 2006). Species richness and species diversity were estimated with the *iNEXT* package (Hsieh et al. 2016).

Data on species proportions, species densities, plot type density, and tree height did not meet assumption of normality (based on Shapiro-Wilk test). Non-parametric Kruskal-Wallis tests and pairwise Wilcoxon rank sum test were therefore used to test for differences between plot types in terms of species proportions, species densities, plot density, and tree height. Mann-Whitney test was used to test for significant differences between tree heights in the diet and feeding plots.

Results

Feeding Preferences

Acacia encompassed over 80% of the total diet of giraffes, with 60% of the diet exclusively *A. gerrardii* (Table A1). Diet composition did fluctuate throughout the study, but *Acacia* was the main diet component throughout (Figure 3). *A. gerrardii* had a steep increase in proportional use in the early dry season before peaking at 80% of the daily diet and then slowly decreasing, while the other species experienced a slight decrease in use in the beginning of the dry season before either gradually increasing or remaining relatively stable throughout the study period (Figure 3).

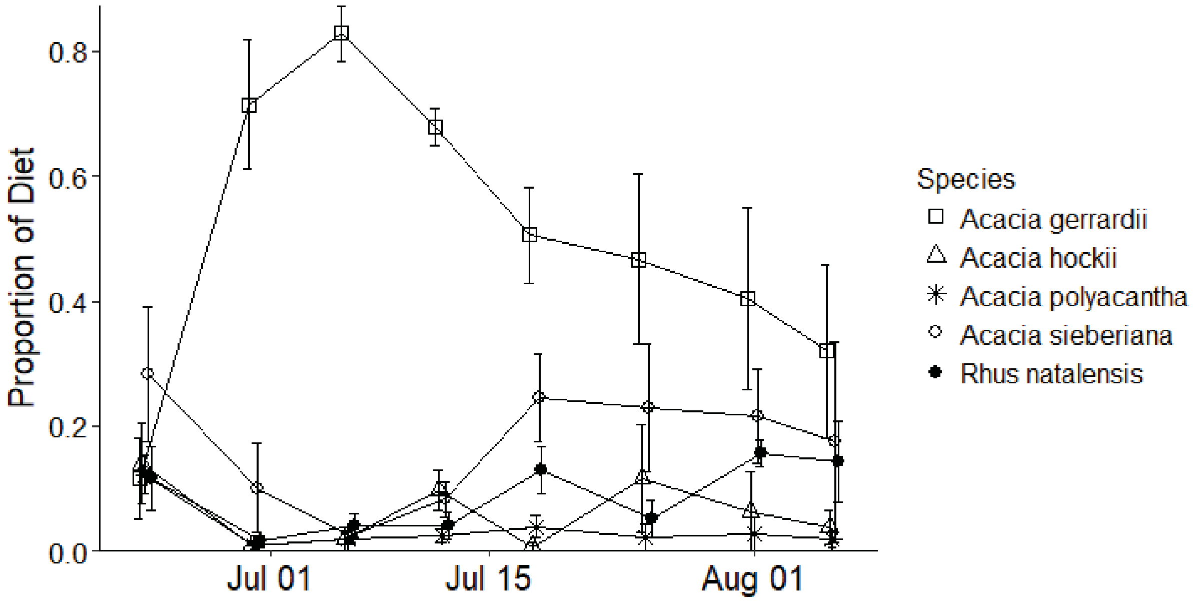

Figure 3. Change in diet composition (proportion of daily diet) over time (weekly means ± SE). Only the five most commonly consumed species are included. Points are positioned to avoid overlap for visual aid.

On the fine scale (comparing diet and feeding plots), *Cissus quadrangularis, Rhipsalis baccifera, A. sieberiana, A. gerrardii, Capparis fascicularis,* and *A. polyacantha* were consumed at a significantly higher proportion than their availability (Figure 4a). The remaining species in the giraffe diet (except *Acacia hockii, Cyphostemma adenocaule, Pappea capensis,* and *Tricalysia niamniamensis*) were consumed at a significantly lower proportion than their availability and thus showed a negative selection (Figure 4a). Despite their low diet ranks, *Cissus quadrangularis* (rank 7) and *Rhipsalis baccifera* (rank 18) had the two highest selection indices, being used at least three times more often than their availability (Figure 4a; Table A1). Comparing diet and adjacent plots, giraffes selected for *A. gerrardii*, *A. polyacantha*, and *A. sieberiana*, while avoiding areas with *A. hockii* (Figure 4b). However, when comparing diet to random plots, *A. gerrardii, A. hockii*, and *A. sieberiana* were all selected for, while *A. polyacantha* was avoided (Figure 4c). Overall, *A. gerrardii*, *A. sieberiana,* and *Cissus quadrangularis* were significantly selected for by giraffes on all scales of diet selection (Figure 4).

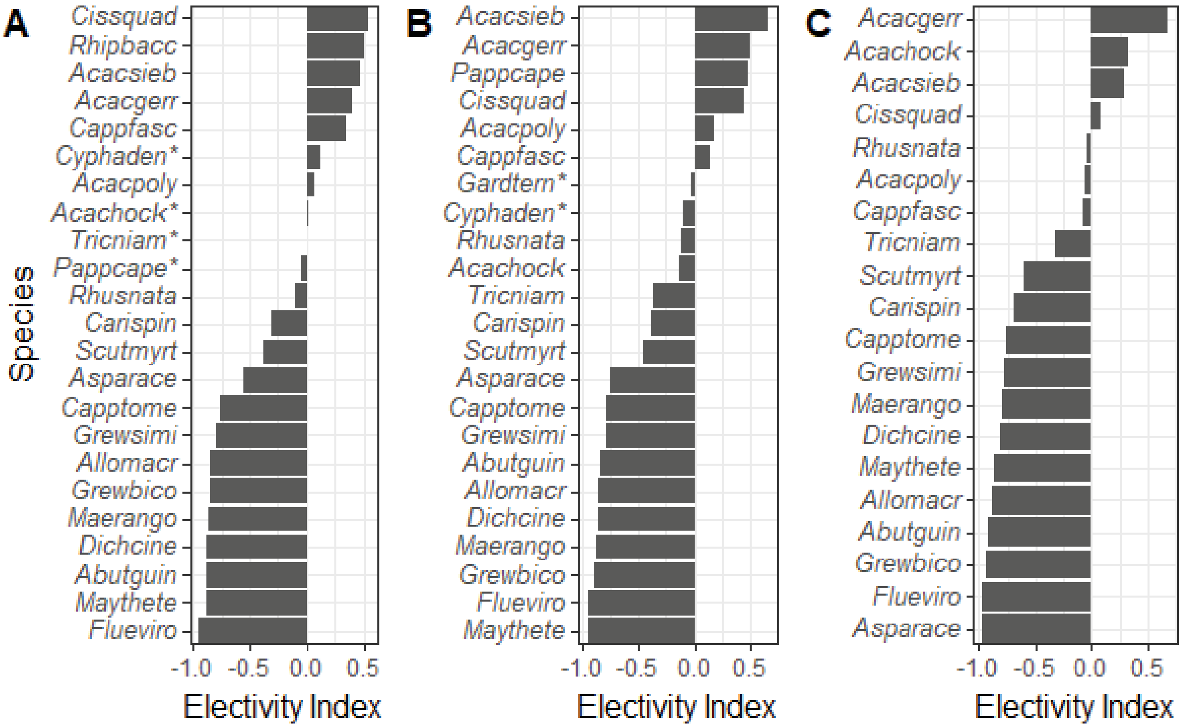

Figure 4. Ranked Ivlev's electivity selection index for plants comparing diet and: A) feeding plots, B) adjacent plots, C) random plots. Rare species (species absent from diet or vegetation plots) were excluded from the analysis (Lechowicz 1982). Differences between proportional abundances of species in diet and plot types were tested for using Pearson's chi-squared test (A: $\chi^2 = 30944$, df = 35, $P < 0.001$; B: $\chi^2 = 52335$, df = 40, $P < 0.001$; C: $\chi^2 = 81417$, df = 28, $P < 0.001$ before Bonferroni correction was applied. Stars (after species names) indicate non-significance ($P > 0.05$) based on Bonferroni corrections of p-values.

Giraffes foraged mostly on *Acacia* trees that were around 5m tall, which was around estimated average giraffe height (Figure 5a). Bite rate decreased with *Acacia* tree height (Figure 5b). Giraffes selected for significantly taller individuals of *A. gerrardii, A. hockii*, and *A. sieberiana* in their diet than there was readily available in the habitat but showed no tree height selection in *A. polyacantha* (Figure 6).

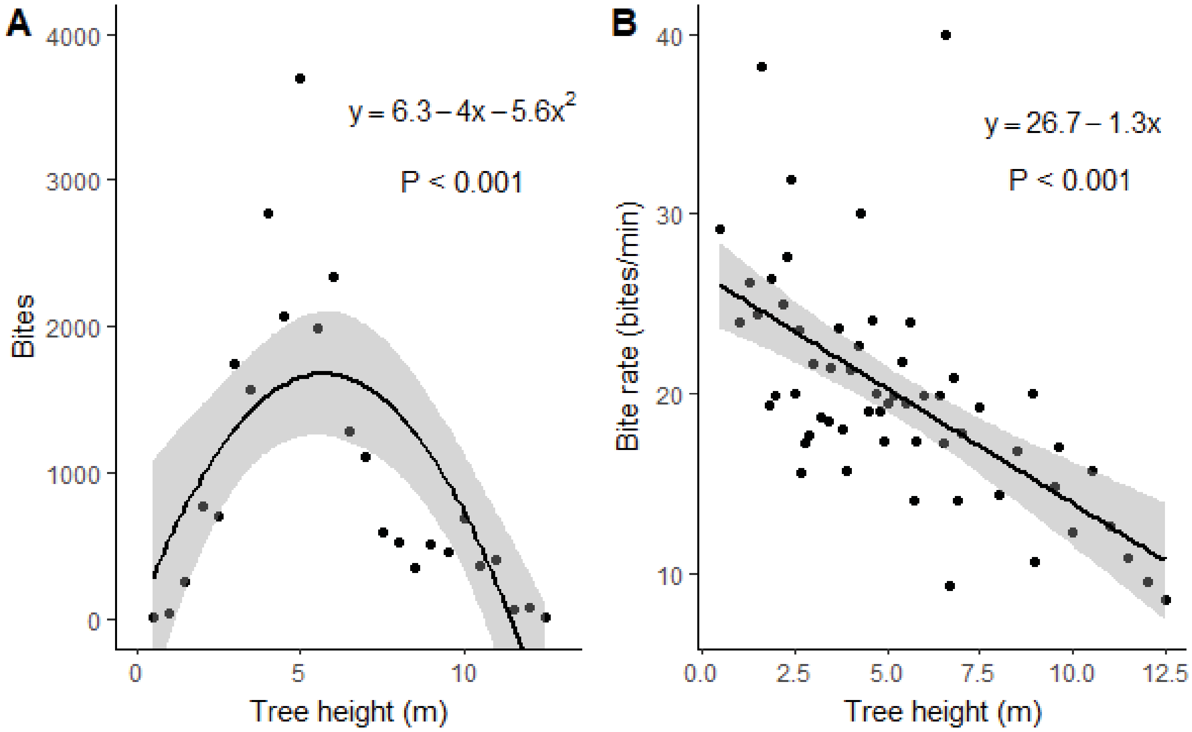

Figure 5. Effect of tree height on A) total number of bites of *Acacia* and B) mean bite rate (bites/m) for *Acacia*. Tree height was rounded to the nearest 0.5 m. Trend lines (± SE) are based on glm. P-values are based on chi-squared test of glm models against null models.

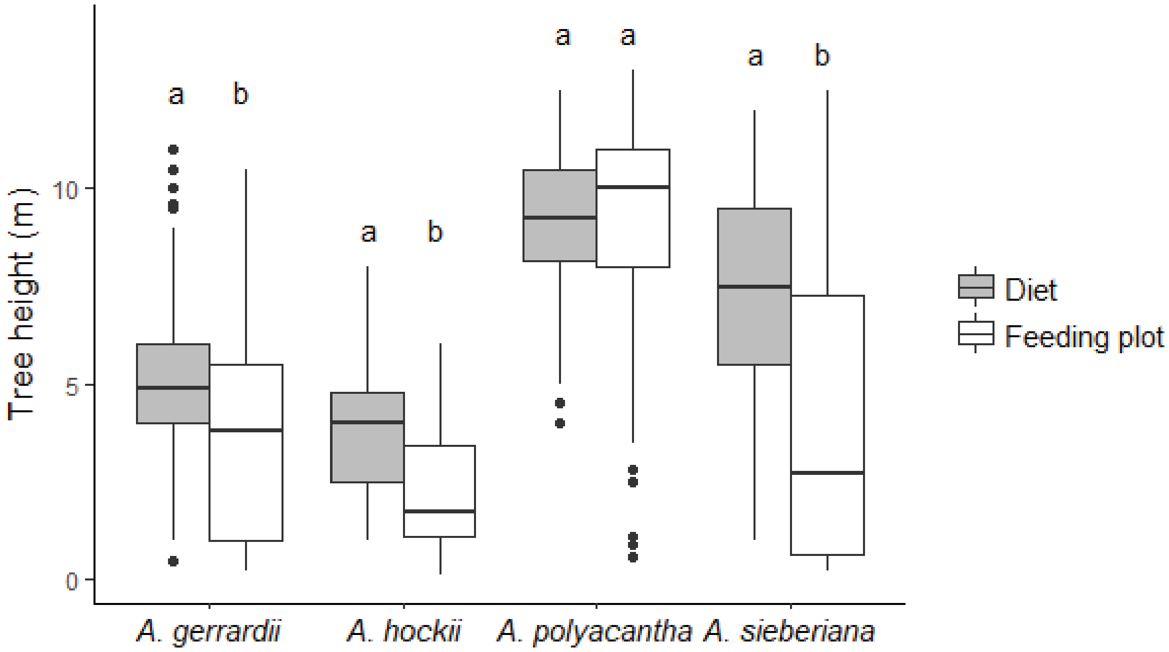

Figure 6. Median tree heights of *Acacia* species in the diet and feeding plots. Different letters indicate significant differences in median tree height within species based on Mann-Whitney tests.

Community Characteristics

Based on a total sample size of 8356 individual plants in 748 vegetation plots, feeding plots (n=349) had 41 species and 4348 individuals, adjacent plots (n=349) had 36 species and 3419 individuals, and random plots (n=50) had 29 species and 589 individuals. Of a total of 46 species sampled, two were succulents, three were herbs, and the remaining 41 were woody species. Feeding and adjacent plots had 33 species in common, feeding and random shared 28 species, and adjacent and random plots had 28 shared species. Feeding, adjacent, and random plots all shared the same 28 species.

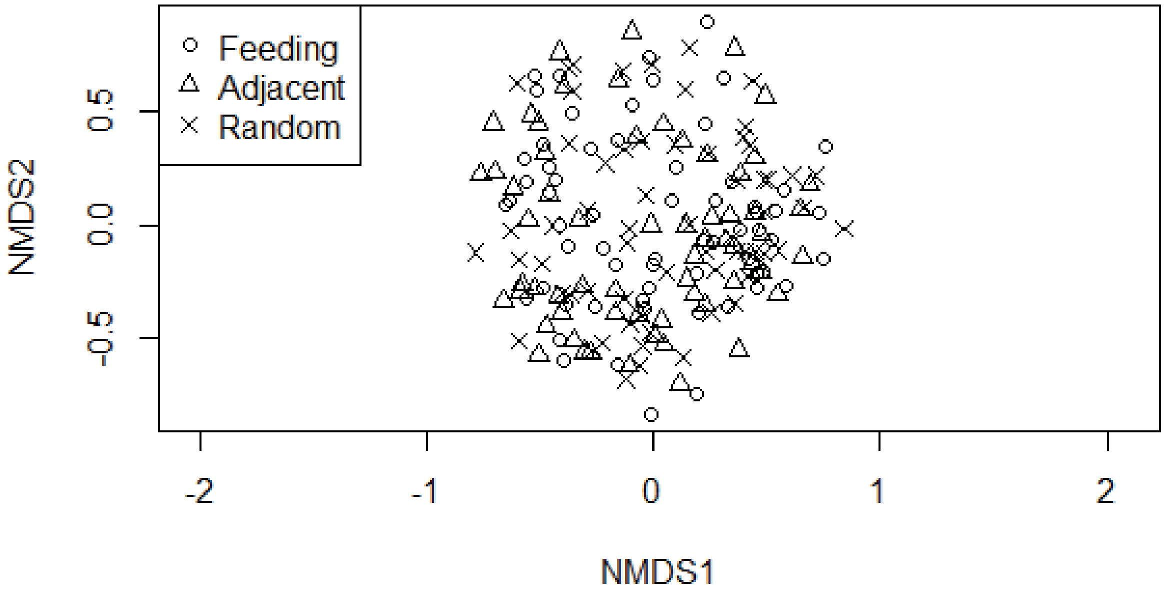

Figure 7. Non-metric multidimensional scaling (NMDS) analysis of species composition in feeding, adjacent, and random plots. Rare species (occurring in fewer than five plots) and plots with fewer than five species were removed before analysis to reach convergence. Stress = 0.176.

There was a small, yet significant difference in vegetation composition between feeding, adjacent, and random plots (Figure 7; ANOSIM: $R = 0.030$, $P < 0.001$). Feeding and adjacent plots were significantly more similar than either plot types were to random plots based on Shannon entropy comparing species relative abundances (Table 1). Controlling for sample size, random plots had significantly less species than adjacent plots (Table 2). There were no significant differences between feeding plots and either random or adjacent plots (Table 2). Although random plots had lower estimated species richness, they had a significantly higher Shannon diversity than both feeding and adjacent plots (Figure 8). Adjacent plots had significantly higher Shannon diversity than feeding plots, though marginally (Figure 8). Feeding plots had a significantly lower beta diversity than random plots (Figure 9). There was no significant difference in beta diversity between adjacent plots and either feeding or random plots (Figure 9).

Table 1. Pairwise similarity indices based on Shannon entropy comparing species relative abundances.

	Equal-weighted Horn			Size-weighted Horn		
	Estimate	SE	95% CI	Estimate	SE	95% CI
Feeding - Adjacent	0.978	0.003	0.971, 0.984	0.978	0.003	0.971, 0.984
Feeding - Random	0.922	0.010	0.902, 0.942	0.928	0.009	0.909, 0.947
Adjacent - Random	0.924	0.010	0.903, 0.944	0.935	0.008	0.918, 0.951

Table 2. Species richness based on Chao estimators (Chao 1984; Chao 1987) with 95% confidence intervals. Observed numbers based on 349 feeding plots, 349 adjacent plots, and 50 random plots.

	Observed	Estimated	Lower CI	Upper CI
Feeding	36	38.99	36.53	52.77
Adjacent	41	44.59	41.65	60.89
Random	29	30.57	29.21	40.61

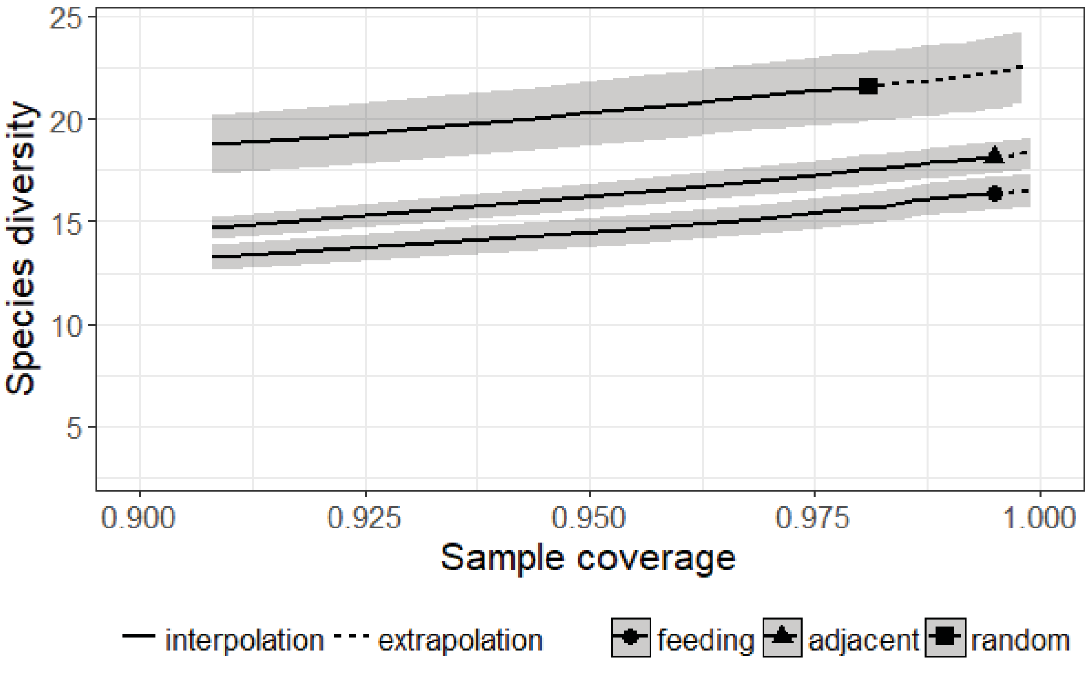

Figure 8. Measure of Shannon diversity (± 95% CI) based on sample coverage. Sample coverage is based on estimated sample completeness (Chao & Jost 2012). Sample coverage was used to control for differences in sample size: 349 feeding plots, 349 adjacent plots, and 50 random plots.

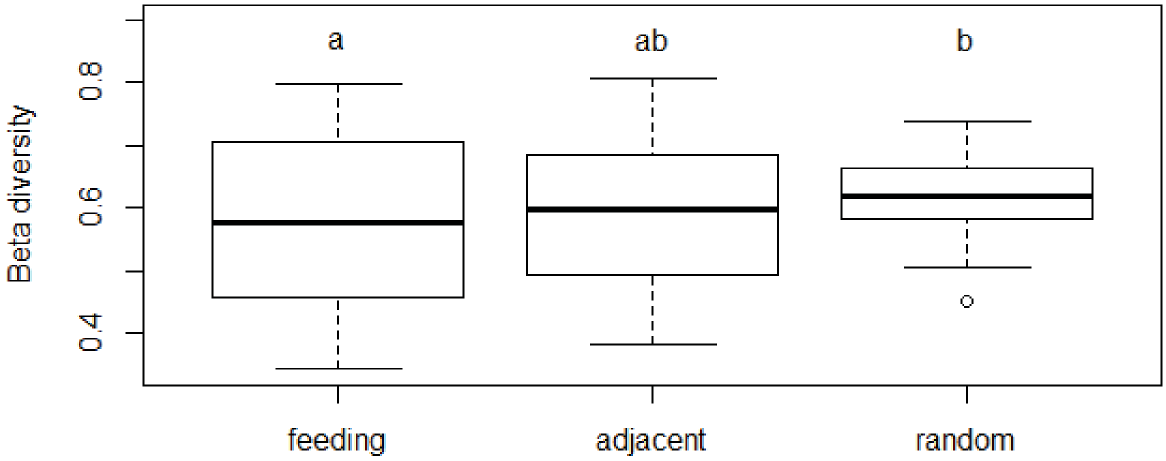

Figure 9. Beta diversity of feeding, adjacent, and random plots measured by Bray-Curtis dissimilarity. Significance testing with permutation test of multivariate homogeneity of group dispersions (F = 3.5334, P = 0.035, 999 permutations). Different letters indicate a significant difference in beta diversity between plot types.

Relative abundances of species varied between plot types (Figure 10). Feeding plots consisted of more than twice as much *A. gerrardii* than random plots did, while *A. sieberiana* was nearly three times more abundant in random plots than in adjacent plots. Regardless of these differences, *A. gerrardii* was the most abundant species in all plot types (Figure 10, Table A1). Significantly higher proportions of *A. gerrardii* occurred in feeding ($P < 0.001$) and adjacent ($P < 0.05$,) plots compared to random plots (Figure 11). Feeding ($P < 0.01$) and adjacent ($P < 0.05$) plots also had significantly higher densities of *A. gerrardii* than random plots (Figure 12). Random plots had significantly higher proportions and densities of *G. bicolor* compared to feeding plots ($P < 0.05$ and $P < 0.05$, respectively; Figure 11, Figure 12). *M. heterophylla* had significantly lower proportions and densities in feeding than adjacent plots ($P < 0.05$ and $P < 0.05$, respectively; Figure 11, Figure 12), while *Carissa spinarum* had significantly higher densities ($P < 0.05$) in random plots compared to feeding plots (Figure 12). There were no other significant differences in the densities or proportions of species between plot types. Feeding plots were significantly more open than adjacent plots ($P < 0.01$; Figure 13) but there were no significant differences in densities between random and the other plot types ($P > 0.05$; Figure 13). There was also no significant difference in maximum tree heights between the plot types (Figure 14).

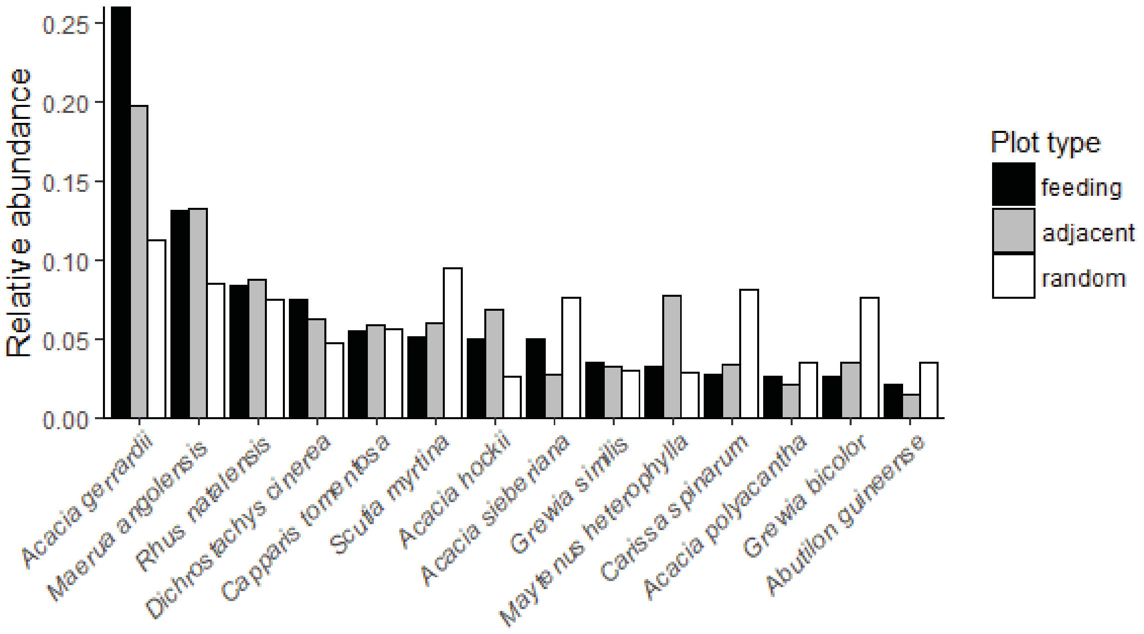

Figure 10. Total relative abundance of each species in each plot type. Only species with relative abundance was >1% in all plot types were included.

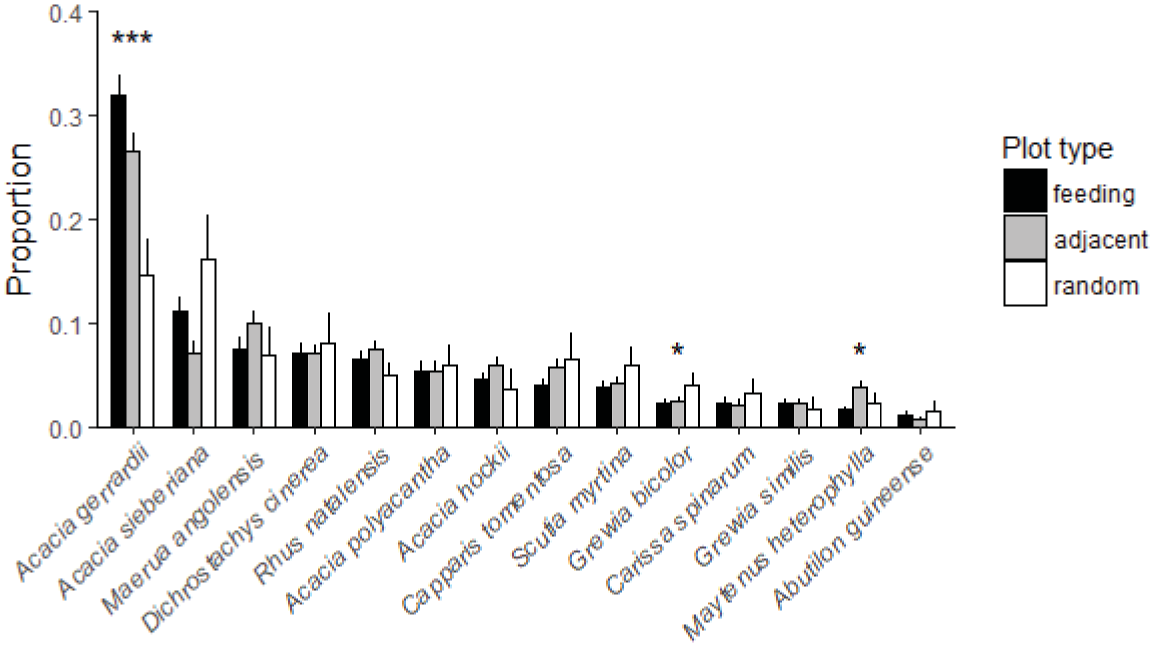

Figure 11. Average proportion (+SE) of species abundance in each plot for each plot type. Only species with relative abundance >1% were included in the analysis. Significance testing with Kruskal-Wallis and Wilcoxon tests. Stars indicate a significant difference in proportional abundance within a species (*** $P < 0.001$, * $P < 0.05$).

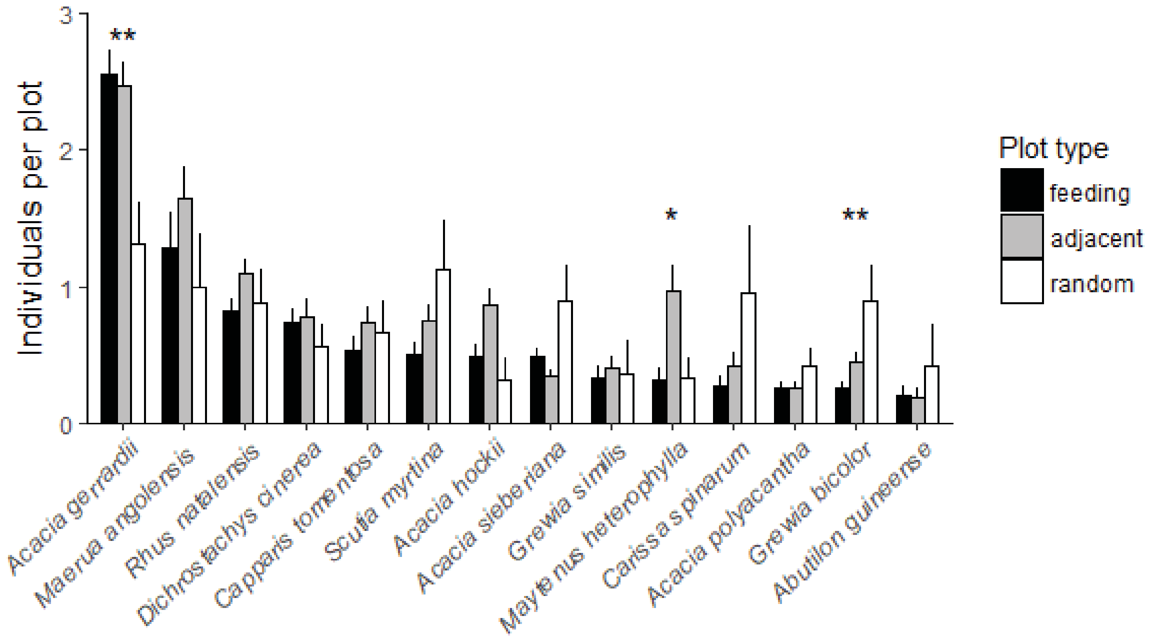

Figure 12. Mean density (+SE) of species in each plot type. Only species with relative abundance >1% in all plot types were included. Significance testing with Kruskal-Wallis and Wilcoxon tests. Stars indicate a significant difference in density between plot types within a species (** $P < 0.01$, * $P < 0.05$).

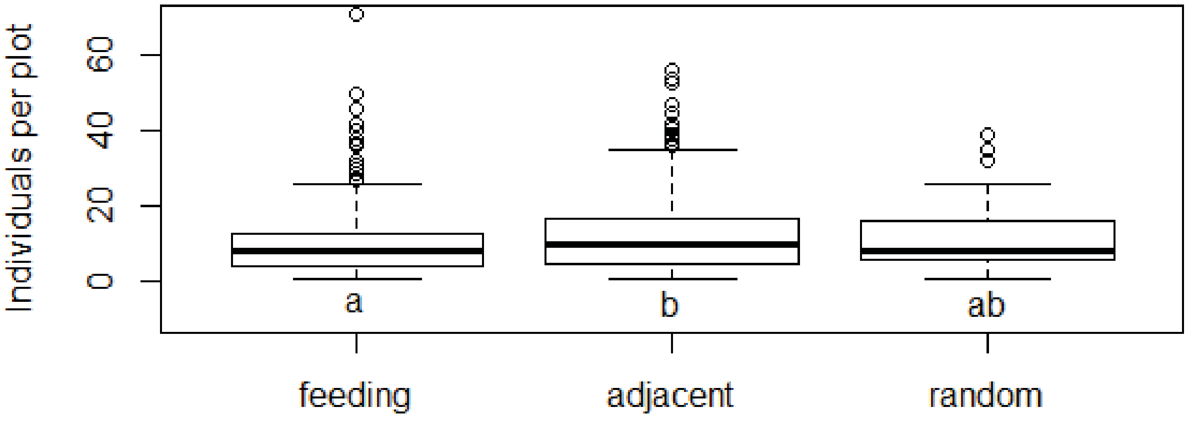

Figure 13. Density of individuals in each plot type based on a total of 3419 individuals in feeding plots (n=349), 4348 individuals in adjacent plots (n=349), and 589 individuals in random plots (n=50). Significance testing with Kruskal-Wallis ($\chi^2 = 11.423$, df = 2, $P < 0.01$) and Wilcoxon tests. Different letters indicate a significant difference in density between plot types.

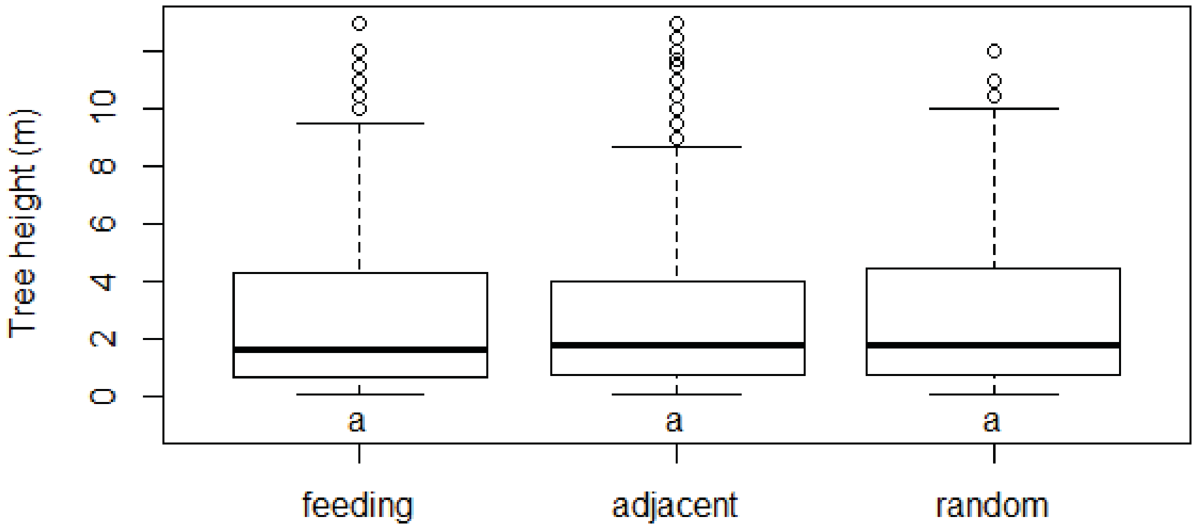

Figure 14. Boxplot of tree heights in feeding, adjacent, and random plots. Significance testing with Kruskal-Wallis ($\chi 2 = 1.5627$, df = 2, $P < 0.05$) and Wilcoxon tests. Different letters indicate a significant difference in tree heights between plot types.

Discussion

The major findings of this study demonstrate that giraffes select for *Acacia* both in terms of die and feeding area. On the fine scale (comparing diet and feeding plots), giraffes selected to feed on *Acacia*, and *Acacia* species comprised more than 80% of their daily diet. On the landscape scale (comparing feeding and random plots), giraffes fed in homogenous areas dominated by *Acacia* trees. On the patch scale (comparing feeding and adjacent plots), giraffes fed in open areas.

As predicted, *Acacia* was a significant portion of the giraffe diet, encompassing up to 80% of the daily diet. While other studies report *Acacia* constituting from 5-45% of giraffe diet, no study has reported such a large utilization of *Acacia* (Berry & Bercovitch 2017; Leuthold & Leuthold 1972; Parker & Bernard 2005). Assuming that female giraffes eat on average 16.6 kg and males eat 19.0 kg of dry-matter every day (Pellew 1984b), the giraffes in Lake Mburo are potentially consuming more than 200 kg of dry-weight *Acacia* daily. There was significant diet selection of all *Acacia* species, except for *A. hockii* which was eaten at the same proportion as its availability. Several studies found similar results with giraffes preferring *Acacia* (du Toit et al. 1990; Hall-Martin 1974; Pellew 1984a). It is largely accepted that diet selection is based on forage quality, as *Acacia* has high nutritional value with high protein and moisture content (Fennessy

2004; Pellew 1984a; Sauer 1983a; Sauer 1983b). This is especially important in the dry season as the nutritional quality and availability of foliage declines (Pellew 1984a). Berry and Bercovitch (2017) suggest that opportunity, in addition to selection, plays a role in feeding ecology. This may hold true for the *Acacia* species which were both abundant and selected for in the diet. The use of *A. gerrardii* may also be related to its evergreen characteristic, providing a continuous supply of new leaves while other trees lost their leaves (personal observation; Kondoh et al. 2006).

Although a total of 26 plant species were consumed, almost 90% of the total diet consisted of only five species (*A. gerrardii, A. sieberiana, Rhus natalensis, A. hockii*, and *A. polyacantha*). Interestingly, although *Rhus natalensis* was one of the top five most foraged on species, it was still used at a proportion less than its availability. This suggests giraffes are selective feeders, eating almost exclusively *Acacia*. The claim that giraffes are selective feeders are supported by some studies (Brand 2007; Fennessy 2004; Pellew 1984a), while Berry and Bercovitch (2017) argue that giraffes are generalized feeders. The contrasting findings are likely due to differences in habitat, vegetation, and season between these studies. Nevertheless, they all report that giraffes have a core diet of a few species and supplement the diet with a range of other species, consistent with the results of this study.

On the landscape scale, giraffes foraged in homogenous areas dominated by *Acacia*, as predicted. This is supported by the significantly higher density and relative abundance of *A. gerrardii* and the reduced beta and Shannon diversity in feeding plots compared to random plots. The selection by giraffes to forage in *Acacia*-dominated habitats has been observed in multiple studies and is likely driven by availability of quality forage (Berry & Bercovitch 2017; Caister et al. 2003; Mahenya et al. 2016a; Pellew 1984a). This selection for habitats with high availability of quality forage has also been found in other herbivores, such as moose (*Alces alces*) (Van Beest et al. 2010), mule deer (*Odocoileus hemionus*) (Pierce et al. 2004), and impala (van Bommel et al. 2006). Other hypotheses concerning drivers of giraffe habitat selection include predation risk and water availability (Smit et al. 2007; Thaker et al. 2011; Valeix et al. 2009). While predation risk is low for giraffes in Lake Mburo due to the limited number of predators (only one single lion) capable of killing them, moist forage is often of higher quality and of limited supply in the dry season (Fennessy 2004; Redfern et al. 2005; Smit et al. 2007; Valeix et al. 2008).

On the patch scale, giraffes selected to feed in more open plots, in contrast to my prediction. Due to the high similarity between the feeding and adjacent plots, there was no significant differences in species abundances on the patch scale, but selection for species was observed on the landscape scale. This selection of giraffes for less woody microhabitats has been found in other studies, though often observed as anti-predator behavior in females with young (Riginos & Grace 2008; Valeix et al. 2009; Valeix et al. 2011; Young & Isbell 1991). Although there was a marginal difference in mean density between feeding and adjacent plots, the difference in relation to the limited size of the plots (78.54 m^2) may have significant effects on visibility on that scale (Riginos & Grace 2008). The selection for open areas may be especially prominent in the dry season when herbivores are at increased risk of predation (Owen-Smith 2008). The high availability of quality forage on the patch scale may also have allowed for a low opportunity cost between vigilance and feeding. Overall, these results indicate that giraffes first select areas with high forage availability and then select for openness.

As predicted, giraffes showed a selection to feed on tall trees, in agreement with previous studies (Mahenya et al. 2016a; Mahenya et al. 2016b). Giraffes fed mostly on 4-5 m tall *Acacia* trees, in the same range as estimated giraffe heights. Comparing use and availability of each *Acacia* species, giraffes selected to feed on trees taller than the median maximum tree height available (except for *A. polyacantha*). The selection to forage on adult trees rather than recruitment-sized trees may indicate a limited negative effect of giraffes on tree establishment. Ruess and Halter (1990) only reported a reduction in mature trees when giraffes foraged on trees under 3 m tall. Higher tree height also corresponded to lower bite rate, indicating less tree damage with higher quality food ingested (Mahenya et al. 2016b).

Although *Acacia* comprised more than 80% of the total dry season diet of giraffes, diet composition did fluctuate daily. Variation in giraffe diet due to seasonal productivity and forage quality is widely documented (Brand 2007; Hall-Martin 1974; Leuthold & Leuthold 1972; Parker & Bernard 2005; Pellew 1984a; Sauer et al. 1977). As the dry season progresses, some species of *Acacia* lose their leaves, produce fewer shoots, and experience a decrease in protein content (Gordon et al. 2016; Leuthold & Leuthold 1972; Pellew 1984a; Sauer 1983b). It is in the dry season when plant productivity is at its lowest and giraffes concentrate their foraging on nutritious plant parts that giraffes may have the highest impact on *Acacia* (Brand 2007; Fennessy 2004). For example, Fleming et al. (2006) found that giraffes reduced *Acacia* fecundity by targeting to consume flowers in the dry season. Although this study only observed giraffe diet in the dry season, many studies report a continuous selection for *Acacia* year-round (Fennessy 2004; Mahenya et al. 2016a; Pellew 1980; Pellew 1984b).

This study has shown that the giraffes in Lake Mburo actively select to forage on *Acacia*. However, *Acacia* trees have evolved multiple herbivore defense mechanisms, including tannin, growth spurts, and spines (Furstenburg & Van Hoven 1994; Pellew 1984b; Zinn et al. 2007). Therefore, the effect giraffes may have on controlling further *Acacia* encroachment in the park depends on the species foraged on (Bond & Loffell 2001). Herbivory by giraffes has been associated with a variety of plant responses. For example, browsing pressure has been linked to shoot regrowth (du Toit 1990), increased tannin levels (Furstenburg & Van Hoven 1994), increased germination levels (Or & Ward 2003), and longer spines (Zinn et al. 2007) in *Acacia*. These are all defense mechanisms to decrease palatability and herbivore damage. However, intense browsing pressure by giraffes has also been associated with a reduction in shoots and flowers (Fleming et al. 2006; Milewski & Madden 2006), tree height (Ruess & Halter 1990) and tree canopy (Dharani et al. 2009). A decrease in average tree height can increase tree vulnerability to fire and other herbivores (Ruess & Halter 1990). Via these negative effects, giraffes can alter the distribution and composition of *Acacia* (Bond & Loffell 2001). The effect herbivores have on trees is therefore dependent upon browsing pressure. The current limited number of giraffes in Lake Mburo are unlikely to have any significant impact on *Acacia* encroachment throughout the whole national park, but perhaps in areas where browsing pressure is concentrated (Roques et al. 2001). Areas of high giraffe browsing intensity have previously been linked to higher rates of tree mortality (Bond & Loffell 2001).

Current climate change models predict an increase in temperature and occurrences of extreme weather events, including drought and increased precipitation, in Uganda (USAID 2017). Warmer and wetter conditions will favor woody encroachment while droughts can increase tree mortality (Bowman et al. 2008; USAID 2017). Giraffe browsing can increase tree vulnerability to drought (Birkett 2002; Birkett & Stevens-Wood 2005). These two factors can act synergistically to reduce and reverse rates of woody encroachment. This was the case in Lake Nakuru National Park in Kenya. The park experienced a decrease of *Acacia xanthaphloea*, a staple in the giraffe diet, due to intense browsing of the species and prolonged drought which reduced the regeneration ability of *A. xanthaphloea* (Brenneman et al. 2009). Kondoh et al. (2006) observed a trade-off between drought resistance and growth rate in some African tree species. The combined effects of drought and herbivory may therefore not have a significant effect on the mortality of drought-resistant species such as *A. gerrardii*. But its slow growth rate may make it more vulnerable to fires which can be an effective way, especially in addition to high browsing pressure and drought, to control woody encroachment (Archibald & Bond 2003; Bowman et al. 2008; Gordijn et al. 2012; Staver et al. 2009; Van Langevelde et al. 2003). With current climate change models, it is necessary to find an efficient and effective way to control woody encroachment before its causes irreversible changes to Africa's unique ecosystems. However, a long-term study is necessary to determine the effects, if any, the giraffes have on *Acacia*. It may be viable to translocate more giraffes to effectively control woody encroachment in Lake Mburo.

Conclusion

The encroachment of invasive native *Acacia* species in Lake Mburo National Park is shifting open savannas into dense woodland, potentially displacing native wildlife and altering ecosystem dynamics. As part of an ongoing long-term project, giraffes were translocated to the park in an attempt to control the abundance of *Acacia*. More than 80% of the giraffes total diet consisted of *Acacia*, implying that over 200 kg of dry-weight *Acacia* biomass is consumed daily by the small population of giraffes in the park. The giraffes selected for *Acacia* on all scales. The giraffes selected to feed in *Acacia*-dominated areas before selecting to feed in more open and homogenous areas. There was also a strong preference for *Acacia* in the diet, with giraffes consuming *Acacia* at proportion three times greater than its abundance in feeding plots. This foraging behavior strongly indicates that the giraffes in Lake Mburo have the potential to act as biological controllers of the native invading *Acacia* species.

References

African Adventure Travellers. (2016). *Giraffes join herd at Lake Mburo National Park*, 2018, April 28: Africa Geographic.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49 (3): 227-266.

Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62 (1): 245-253.

Angassa, A. & Oba, G. (2010). Effects of grazing pressure, age of enclosures and seasonality on bush cover dynamics and vegetation composition in southern Ethiopia. *Journal of Arid Environments*, 74 (1): 111-120.

Archibald, S. & Bond, W. J. (2003). Growing tall vs growing wide: tree architecture and allometry of Acacia karroo in forest, savanna, and arid environments. *Oikos*, 102 (1): 3-14.

Asner, G. P., Levick, S. R., Kennedy-Bowdoin, T., Knapp, D. E., Emerson, R., Jacobson, J., Colgan, M. S. & Martin, R. E. (2009). Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceedings of the National Academy of Sciences*, 106 (12): 4947-4952.

Augustine, D. J. & Mcnaughton, S. J. (2004). Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*, 41 (1): 45-58.

Averbeck, C. (2002). Population Ecology of Impala (Aepyceros melampus) and community-based wildlife conservation in Uganda. *Fakultät für Ernährung, Landnutzung und Umwelt, Technische Universität München*.

Averbeck, C., Apio, A., Plath, M. & Wronski, T. (2009). Environmental parameters and anthropogenic effects predicting the spatial distribution of wild ungulates in the Akagera savannah ecosystem. *African Journal of Ecology*, 47 (4): 756-766.

Bakker, E. S., Gill, J. L., Johnson, C. N., Vera, F. W., Sandom, C. J., Asner, G. P. & Svenning, J.-C. (2016). Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proceedings of the National Academy of Sciences*, 113 (4): 847-855.

Baselga, A. & Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3 (5): 808-812.

Berry, P. S. & Bercovitch, F. B. (2017). Seasonal and geographical influences on the feeding ecology of giraffes in the Luangwa Valley, Zambia: 1973–2014. *African Journal of Ecology*, 55 (1): 80-90.

Birkett, A. (2002). The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. *African Journal of Ecology*, 40 (3): 276-282.

Birkett, A. & Stevens-Wood, B. (2005). Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. *African Journal of Ecology*, 43 (2): 123-130.

Blaum, N., Rossmanith, E., Popp, A. & Jeltsch, F. (2007). Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. *Acta Oecologica*, 31 (1): 86-92.

Blösch, U. (2008). Thicket clumps: a characteristic feature of the Kagera savanna landscape, East Africa. *Journal of Vegetation Science*, 19 (1): 31-44.

Bond, W. J. & Loffell, D. (2001). Introduction of giraffe changes acacia distribution in a South African savanna. *African Journal of Ecology*, 39 (3): 286-294.

Bowman, D., Riley, J., Boggs, G., Lehmann, C. & Prior, L. (2008). Do feral buffalo (Bubalus bubalis) explain the increase of woody cover in savannas of Kakadu National Park, Australia? *Journal of Biogeography*, 35 (11): 1976-1988.

Brand, R. (2007). *Evolutionary ecology of giraffes (Giraffa camelopardalis) in Etosha National Park, Namibia*. PhD: Newcastle University.

Brenneman, R. A., Bagine, R. K., Brown, D. M., Ndetei, R. & Louis, E. E. (2009). Implications of closed ecosystem conservation management: the decline of Rothschild's giraffe (Giraffa camelopardalis rothschildi) in Lake Nakuru National Park, Kenya. *African Journal of Ecology*, 47 (4): 711-719.

Brown, M. B. & Fennessy, J. (2014). *A preliminary assessment of Rothschild's giraffe in Uganda*. Giraffe Conservation Foundation. Windhoek, Namibia.

Cabral, A., De Miguel, J., Rescia, A., Schmitz, M., Pineda, F. & Díaz, S. (2003). Shrub encroachment in Argentinean savannas. *Journal of Vegetation Science*, 14 (2): 145-152.

Caister, L. E., Shields, W. M. & Gosser, A. (2003). Female tannin avoidance: a possible explanation for habitat and dietary segregation of giraffes (Giraffa camelopardalis peralta) in Niger. *African Journal of Ecology*, 41 (3): 201-210.

Cameron, E. Z. & du Toit, J. T. (2006). Winning by a neck: tall giraffes avoid competing with shorter browsers. *The American Naturalist*, 169 (1): 130-135.

Cao, Y., Larsen, D. & Thorne, R. S.-J. (2001). Rare species in multivariate analysis for bioassessment: some considerations. *Journal of the North American Benthological Society*, 20 (1): 144-153.

Chao, A. (1984). Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of statistics*: 265-270.

Chao, A. (1987). Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*: 783-791.

Chao, A. & Jost, L. (2012). Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. *Ecology*, 93 (12): 2533-2547.

Chao, A., Ma, K. H. & Hsieh, T. C. (2015). *SpadeR: Species Prediction and Diversity Estimation with R*. 0.1.0 ed.

Chritz, K. L., Blumenthal, S. A., Cerling, T. E. & Klingel, H. (2016). Hippopotamus (H. amphibius) diet change indicates herbaceous plant encroachment following megaherbivore population collapse. *Scientific reports*, 6: 32807.

Coetsee, C., Gray, E. F., Wakeling, J., Wigley, B. J. & Bond, W. J. (2013). Low gains in ecosystem carbon with woody plant encroachment in a South African savanna. *Journal of Tropical Ecology*, 29 (01): 49-60.

Dalle, G., Maass, B. L. & Isselstein, J. (2006). Encroachment of woody plants and its impact on pastoral livestock production in the Borana lowlands, southern Oromia, Ethiopia. *African Journal of Ecology*, 44 (2): 237-246.

Dharani, N., Kinyamario, J., Wagacha, P. W. & Rodrigues, A. J. (2009). Browsing impact of large herbivores on Acacia xanthophloea Benth in Lake Nakuru National Park, Kenya. *African Journal of Ecology*, 47 (2): 184-191.

Doughty, C. E., Faurby, S. & Svenning, J. C. (2016). The impact of the megafauna extinctions on savanna woody cover in South America. *Ecography*, 39 (2): 213-222.

du Toit, J. (1990). Feeding-height stratification among African browsing ruminants. *African Journal of Ecology*, 28 (1): 55-61.

du Toit, J. T., Bryant, J. P. & Frisby, K. (1990). Regrowth and palatability of Acacia shoots following pruning by African savanna browsers. *Ecology*, 71 (1): 149-154.

Eldridge, D. J., Bowker, M. A., Maestre, F. T., Roger, E., Reynolds, J. F. & Whitford, W. G. (2011). Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters*, 14 (7): 709-722.

Fennessy, J., Bidon, T., Reuss, F., Kumar, V., Elkan, P., Nilsson, M. A., Vamberger, M., Fritz, U. & Janke, A. (2016). Multi-locus analyses reveal four giraffe species instead of one. *Current Biology*, 26 (18): 2543-2549.

Fennessy, J. T. (2004). *Ecology of desert-dwelling giraffe Giraffa camelopardalis angolensis in northwestern Namibia*. PhD. Sydney, Australia: University of Sydney.

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 (3): 247-253.

Fornara, D. & du Toit, J. (2007). Browsing lawns? Responses of Acacia nigrescens to ungulate browsing in an African savanna. *Ecology*, 88 (1): 200-209.

Fryxell, J. M., Hazell, M., Börger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., McIntosh, T. & Rosatte, R. C. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences*, 105 (49): 19114-19119.

Furstenburg, D. & Van Hoven, W. (1994). Condensed tannin as anti-defoliate agent against browsing by giraffe (Giraffa camelopardalis) in the Kruger National Park. *Comparative Biochemistry and Physiology Part A: Physiology*, 107 (2): 425-431.

Gandiwa, E., Magwati, T., Zisadza, P., Chinuwo, T. & Tafangenyasha, C. (2011). The impact of African elephants on Acacia tortilis woodland in northern Gonarezhou National Park, Zimbabwe. *Journal of Arid Environments*, 75 (9): 809-814.

Giraffe Conservation Foundation. (2017). *Africa's Giraffe: A Conservation Guide*. Eros, Namibia.

Gordijn, P. J., Rice, E. & Ward, D. (2012). The effects of fire on woody plant encroachment are exacerbated by succession of trees of decreased palatability. *Perspectives in Plant Ecology, Evolution and Systematics*, 14 (6): 411-422.

Gordon, C. E., Eldridge, D. J., Ripple, W. J., Crowther, M. S., Moore, B. D. & Letnic, M. (2017). Shrub encroachment is linked to extirpation of an apex predator. *Journal of Animal Ecology*, 86 (1): 147-157.

Gordon, C. N., Eichenberger, L., Vorster, P., Leslie, A. J. & Jacobs, S. M. (2016). Diet and seasonal dispersal of extralimital giraffe at Sanbona Wildlife Reserve, Little Karoo, South Africa. *Koedoe*, 58 (1): 1-6.

Gray, E. F. & Bond, W. J. (2013). Will woody plant encroachment impact the visitor experience and economy of conservation areas? *Koedoe*, 55 (1): 00-00.

Hagenah, N., Munkert, H., Gerhardt, K. & Olff, H. (2009). Interacting effects of grass height and herbivores on the establishment of an encroaching savanna shrub. *Plant ecology*, 201 (2): 553-566.

Hall-Martin, A. (1974). Food selection by Transvaal lowveld giraffe as determined by analysis of stomach contents. *South African Journal of Wildlife Research-24-month delayed open access*, 4 (3): 191-202.

Hill, M. O. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54 (2): 427-432.

Horn, H. S. (1966). Measurement of" overlap" in comparative ecological studies. *The American Naturalist*, 100 (914): 419-424.

Hsieh, T., Ma, K. & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7 (12): 1451-1456.

Infield, M., Duli, E. M., Mugisha, A. R. & Rubagyema, P. (2008). How protection took the beauty from the land; conflicting values and meanings of Lake Mburo National Park, Uganda. In Mallarach, J.-M. (ed.) *Protected Landscapes and Cultural and Spiritual Values. Volume 2 in the series Values of Protected Lands-capes and Seascapes, IUCN, GTZ and Obra Social de Caixa Catalunya*, pp. 132-145. Heidelberg: Kasparek Verlag.

Ivlev, V. (1961). *Experimental feeding ecology of fishes*: Yale University Press, New Haven, Conn.

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, 88 (10): 2427-2439.

Jost, L., Chao, A. & Chazdon, R. (2011). Compositional similarity and beta diversity. In *Biological diversity: frontiers in measurement and assessment*, pp. 66-84.

Kiffner, C., Rheault, H., Miller, E., Scheetz, T., Enriquez, V., Swafford, R., Kioko, J. & Prins, H. H. (2017). Long-term population dynamics in a multi-species assemblage of large herbivores in East Africa. *Ecosphere*, 8 (12).

Kondoh, S., Yahata, H., Nakashizuka, T. & Kondoh, M. (2006). Interspecific variation in vessel size, growth and drought tolerance of broad-leaved trees in semi-arid regions of Kenya. *Tree physiology*, 26 (7): 899-904.

Kyalangalilwa, B., Boatwright, J. S., Daru, B. H., Maurin, O. & Bank, M. (2013). Phylogenetic position and revised classification of Acacia sl (Fabaceae: Mimosoideae) in Africa, including new combinations in Vachellia and Senegalia. *Botanical Journal of the Linnean Society*, 172 (4): 500-523.

Lechowicz, M. J. (1982). The sampling characteristics of electivity indices. *Oecologia*, 52 (1): 22-30.

Leuthold, B. M. & Leuthold, W. (1972). Food habits of giraffe in Tsavo National Park, Kenya. *African Journal of Ecology*, 10 (2): 129-141.

Lock, J. (1993). Vegetation change in Queen Elizabeth National Park, Uganda: 1970–1988. *African Journal of Ecology*, 31 (2): 106-117.

Loehle, C. & Rittenhouse, L. R. (1982). An analysis of forage preference indices. *Journal of Range Management*: 316-319.

MacArthur, R. H. & MacArthur, J. W. (1961). On bird species diversity. *Ecology*, 42 (3): 594-598.

Mahenya, O., Mathisen, K. M., Andreassen, H. P. & Skarpe, C. (2016a). Hierarchical foraging by giraffe in a heterogeneous savannah, Tanzania. *African Journal of Ecology*, 54 (2): 136-145.

Mahenya, O., Ndjamba, J. K., Mathisen, K. M. & Skarpe, C. (2016b). Giraffe browsing in response to plant traits. *Acta Oecologica*, 75: 54-62.

Marais, A. J., Fennessy, S., Brown, M. B. & Fennessy, J. (2016). *Country Profile: A rapid assessment of the giraffe conservation status in the Republic of Uganda*. Windhoek, Namibia: Giraffe Conservation Foundation.

Mayor, S. J., Schneider, D. C., Schaefer, J. A. & Mahoney, S. P. (2009). Habitat selection at multiple scales. *Ecoscience*, 16 (2): 238-247.

Milewski, A. V. & Madden, D. (2006). Interactions between large African browsers and thorny Acacia on a wildlife ranch in Kenya. *African Journal of Ecology*, 44 (4): 515-522.

Moe, S. R., Mobæk, R. & Narmo, A. K. (2009). Mound building termites contribute to savanna vegetation heterogeneity. *Plant Ecology*, 202 (1): 31.

Mugasi, S., Sabiiti, E. & Tayebwa, B. (2000). The economic implications of bush encroachment on livestock farming in rangelands of Uganda. *African Journal of Range and Forage Science*, 17 (1-3): 64-69.

Nackley, L. L., West, A. G., Skowno, A. L. & Bond, W. J. (2017). The Nebulous Ecology of Native Invasions. *Trends in ecology & evolution*.

Namara, J. (2017). *Climate change impacts on rangelands in Lake Mburo National Park - Uganda*. IAIA, Montreal.

O'Connor, T. G., Puttick, J. R. & Hoffman, M. T. (2014). Bush encroachment in southern Africa: changes and causes. *African Journal of Range & Forage Science*, 31 (2): 67-88.

O'Kane, C. A., Duffy, K. J., Page, B. R. & Macdonald, D. W. (2011). Are the long-term effects of mesobrowsers on woodland dynamics substitutive or additive to those of elephants? *Acta oecologica*, 37 (5): 393-398.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., et al. (2017). *Vegan: Community Ecology Package*. 2.4-4 ed.

Olsen, M. (2016). *Effect of vegetation encroachment on Macrotermes subhyalinus (Rambur) activity and associated mound vegetation, in Lake Mburo National Park, Uganda*. MSc. Ås: Norwegian University of Life Sciences, Department of Ecology and Natural Resource Management. 38 pp.

Or, K. & Ward, D. (2003). Three–way interactions between Acacia, large mammalian herbivores and bruchid beetles-a review. *African Journal of Ecology*, 41 (3): 257-265.

Owen-Smith, N. (1987). Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology*, 13 (3): 351-362.

Owen-Smith, N. (1989). Megafaunal extinctions: the conservation message from 11,000 years BP. *Conservation Biology*, 3 (4): 405-412.

Owen-Smith, N. (2008). Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos*, 117 (4): 602-610.

Parker, D., Bernard, R. & Colvin, S. (2003). The diet of a small group of extralimital giraffe. *African Journal of Ecology*, 41 (3): 245-253.

Parker, D. & Bernard, R. (2005). The diet and ecological role of giraffe (Giraffa camelopardalis) introduced to the Eastern Cape, South Africa. *Journal of Zoology*, 267 (2): 203-210.

Pellew, R. A. (1980). The production and consumption of Acacia browse and its potential for animal protein production. *Browse in Africa: the current state of knowledge. International Livestock Centre for Africa, Addis Ababa, Ethiopia*: 223-231.

Pellew, R. A. (1984a). The feeding ecology of a selective browser, the giraffe (Giraffa camelopardalis tippelskirchi). *Journal of Zoology*, 202 (1): 57-81.

Pellew, R. A. (1984b). Food consumption and energy budgets of the giraffe. *Journal of Applied Ecology*: 141-159.

Pierce, B. M., Bowyer, R. T. & Bleich, V. C. (2004). Habitat selection by mule deer: forage benefits or risk of predation? *Journal of Wildlife Management*, 68 (3): 533-541.

Pringle, R. M., Goheen, J. R., Palmer, T. M., Charles, G. K., DeFranco, E., Hohbein, R., Ford, A. T. & Tarnita, C. E. (2014). Low functional redundancy among mammalian browsers in regulating an encroaching shrub (Solanum campylacanthum) in African savannah. *Proceedings of the Royal Society of London B: Biological Sciences*, 281 (1785): 20140390.

Prins, H. H. & van der Jeugd, H. P. (1993). Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology*: 305-314.

R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rannestad, O. T., Danielsen, T., Moe, S. R. & Stokke, S. (2006). Adjacent pastoral areas support higher densities of wild ungulates during the wet season than the Lake Mburo National Park in Uganda. *Journal of tropical ecology*, 22 (06): 675-683.

Ratajczak, Z., Nippert, J. B. & Collins, S. L. (2012). Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, 93 (4): 697-703.

Redfern, J., Grant, C., Gaylard, A. & Getz, W. (2005). Surface water availability and the management of herbivore distributions in an African savanna ecosystem. *Journal of Arid Environments*, 63 (2): 406-424.

Riginos, C. & Young, T. P. (2007). Positive and negative effects of grass, cattle, and wild herbivores on Acacia saplings in an East African savanna. *Oecologia*, 153 (4): 985-995.

Riginos, C. & Grace, J. B. (2008). Savanna tree density, herbivores, and the herbaceous community: Bottom-up vs. top-down effects. *Ecology*, 89 (8): 2228-2238.

Roques, K., O'connor, T. & Watkinson, A. (2001). Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, 38 (2): 268-280.

Ruess, R. & Halter, F. (1990). The impact of large herbivores on the Seronera woodlands, Serengeti National Park, Tanzania. *African Journal of Ecology*, 28 (4): 259-275.

Sauer, J., Theron, G. & Skinner, J. (1977). Food preferences of giraffe Giraffa camelopardalis in the arid bushveld of the western Transvaal. *S. Afr. J. Wildl. Res*, 7 (2): 53-59.

Sauer, J. (1983a). A comparison between Acacia and Combretum leaves utilized by giraffe. *South African Journal of Animal Science*, 13 (1): 43-44.

Sauer, J. (1983b). Food selection by giraffes in relation to changes in chemical composition of the leaves. *South African Journal of Animal Science*, 13 (1): 40-43.

Sirami, C., Seymour, C., Midgley, G. & Barnard, P. (2009). The impact of shrub encroachment on savanna bird diversity from local to regional scale. *Diversity and Distributions*, 15 (6): 948-957.

Skowno, A. L., Midgley, J. J., Bond, W. J. & Balfour, D. (1999). Secondary succession in Acacia nilotica (L.) savanna in the Hluhluwe Game Reserve, South Africa. *Plant Ecology*, 145 (1): 1-9.

Smart, N., Hatton, J. & Spence, D. (1985). The effect of long-term exclusion of large herbivores on vegetation in Murchison Falls National Park, Uganda. *Biological conservation*, 33 (3): 229-245.

Smit, I. P., Grant, C. C. & Devereux, B. J. (2007). Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, 136 (1): 85-99.

Smit, I. P. & Prins, H. H. (2015). Predicting the effects of woody encroachment on mammal communities, grazing biomass and fire frequency in African Savannas. *PloS one*, 10 (9): e0137857.

Staver, A. C., Bond, W. J., Stock, W. D., Van Rensburg, S. J. & Waldram, M. S. (2009). Browsing and fire interact to suppress tree density in an African savanna. *Ecological applications*, 19 (7): 1909-1919.

Stevens, N., Lehmann, C. E., Murphy, B. P. & Durigan, G. (2017). Savanna woody encroachment is widespread across three continents. *Global Change Biology*, 23 (1): 235-244.

Strauss, M. K. & Packer, C. (2015). Did the elephant and giraffe mediate change in the prevalence of palatable species in an East African Acacia woodland? *Journal of Tropical Ecology*, 31 (01): 1-12.

Strauss, R. E. (1979). Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society*, 108 (4): 344-352.

Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M. & Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, 92 (2): 398-407.

Uganda Wildlife Authority. (2015). Lake Mburo Conservation Area - General Management Plan (2015-2025).

USAID. (2017). Climate risks to conservation in Uganda: An assessment of selected regions: USAID.

Valeix, M., Fritz, H., Matsika, R., Matsvimbo, F. & Madzikanda, H. (2008). The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. *African Journal of Ecology*, 46 (3): 402-410.

Valeix, M., Loveridge, A., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D. (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, 90 (1): 23-30.

Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming, D. & Duncan, P. (2011). Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biological Conservation*, 144 (2): 902-912.

Van Beest, F. M., Mysterud, A., Loe, L. E. & Milner, J. M. (2010). Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *Journal of Animal Ecology*, 79 (4): 910-922.

van Bommel, F. P., Heitkönig, I. M., Epema, G. F., Ringrose, S., Bonyongo, C. & Veenendaal, E. M. (2006). Remotely sensed habitat indicators for predicting distribution of impala (Aepyceros melampus) in the Okavango Delta, Botswana. *Journal of tropical ecology*, 22 (1): 101-110.

Van de Koppel, J. & Prins, H. H. (1998). The importance of herbivore interactions for the dynamics of African savanna woodlands: an hypothesis. *Journal of Tropical Ecology*, 14 (5): 565-576.

Van Langevelde, F., Van De Vijver, C. A., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L. & Bond, W. J. (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84 (2): 337-350.

Waldram, M. S., Bond, W. J. & Stock, W. D. (2008). Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. *Ecosystems*, 11 (1): 101-112.

WallisDeVries, M. F., Laca, E. A. & Demment, M. W. (1999). The importance of scale of patchiness for selectivity in grazing herbivores. *Oecologia*, 121 (3): 355-363.

Wigley, B., Bond, W. & Hoffman, M. (2009). Bush encroachment under three contrasting land-use practices in a mesic South African savanna. *African Journal of Ecology*, 47 (s1): 62-70.

Wronski, T. (2002). Feeding ecology and foraging behaviour of impala Aepyceros melampus in Lake Mburo National Park, Uganda. *African Journal of Ecology*, 40 (3): 205-211.

Young, T. P. & Isbell, L. A. (1991). Sex differences in giraffe feeding ecology: energetic and social constraints. *Ethology*, 87 (1-2): 79-89.

Zinn, A., Ward, D. & Kirkman, K. (2007). Inducible defences in Acacia sieberiana in response to giraffe browsing. *African Journal of Range and Forage Science*, 24 (3): 123-129.

Appendix

Table A1. Proportion (%) and rank of species in giraffe diet and vegetation plot types. Data based on 1401 feeding observations, 349 feeding plots, 349 adjacent plots, and 50 random plots.

	Diet		Feeding plot		Adjacent plot		Random plot	
	%	Rank	%	Rank	%	Rank	%	Rank
Acacia gerrardii	59.98	1	26.00	1	19.76	1	11.21	1
Acacia sieberiana	14.07	2	5.03	8	2.83	12	7.64	5
Rhus natalensis	6.90	3	8.42	3	8.76	3	7.47	7
Acacia hockii	5.25	4	5.06	7	6.92	5	2.72	14
Acacia polyacantha	3.13	5	2.72	12	2.16	13	3.57	10
Scutia myrtina	2.33	6	5.18	6	6.05	7	9.51	2
Cissus quadrangularis	1.58	7	0.47	21	0.60	21	1.36	18
Carissa spinarum	1.51	8	2.84	11	3.43	10	8.15	4
Capparis fascicularis	1.13	9	0.56	19	0.85	18	1.36	18
Maerua angolensis	0.92	10	13.13	2	13.20	2	8.49	3
Capparis tomentosa	0.73	11	5.47	5	5.93	8	5.60	8
Dichrostachys cinerea	0.48	12	7.58	4	6.32	6	4.75	9
Grewia similis	0.39	13	3.48	9	3.24	11	3.06	12
Lannea schweinfurthii	0.30	14	0.00	-	0.00	-	0.00	-
Pappea capensis	0.26	15	0.29	24	0.09	31	0.00	-
Grewia bicolor	0.22	16	2.66	13	3.59	9	7.64	5
Maytenus heterophylla	0.20	17	3.33	10	7.82	4	2.89	13
Rhipsalis baccifera	0.18	18	0.06	29	0.00	-	0.00	-
Abutilon guineense	0.13	19	2.11	14	1.54	14	3.57	10
Tricalysia niamniamensis	0.09	20	0.09	27	0.18	27	0.17	26
Allophyllus macrobotrys	0.08	21	0.94	16	1.01	15	1.19	20
Gardenia ternifolia	0.04	22	0.00	-	0.05	35	0.00	-
Cyphostemma adenocaule	0.04	23	0.03	32	0.05	35	0.00	-
Flueggea virosa	0.03	24	1.14	15	0.92	17	1.87	16
Asparagus racemosus	0.02	25	0.06	29	0.11	30	1.19	20
Acalypha psilostachya	0.00	-	0.03	32	0.34	23	0.00	-

Table A1 (continued). Proportion (%) and rank of species in giraffe diet and vegetation plot types. Data based on 1401 feeding observations, 349 feeding plots, 349 adjacent plots, and 50 random plots.

	Diet		Feeding plot		Adjacent plot		Random plot	
	%	Rank	%	Rank	%	Rank	%	Rank
Combretum molle	0.00	-	0.00	-	0.64	20	0.00	-
Commiphora africana	0.00	-	0.50	20	0.94	16	0.85	22
Dovyalis sp.	0.00	-	0.09	27	0.14	29	0.17	26
Erythrina abyssinica	0.00	-	0.79	17	0.07	33	0.00	-
Erythrococca bongensis	0.00	-	0.00	-	0.71	19	1.70	17
Euclea racemosa	0.00	-	0.03	32	0.09	31	0.00	-
Lannea fulva	0.00	-	0.47	21	0.18	27	0.17	26
Lantana camara	0.00	-	0.32	23	0.00	-	0.00	-
Maytenus senegalensis	0.00	-	0.00	-	0.05	35	0.00	-
Ochna hackarsii	0.00	-	0.00	-	0.00	-	0.34	24
Phyllanthus ovalifolius	0.00	-	0.00	-	0.02	39	0.00	-
Phytolacca dodecandra	0.00	-	0.00	-	0.02	39	0.00	-
Psydrax parviflora	0.00	-	0.00	-	0.07	33	0.00	-
Tarenna graveolens	0.00	-	0.12	26	0.21	24	0.00	-
Vangueria apiculata	0.00	-	0.00	-	0.05	35	0.00	-
Vepris nobilis	0.00	-	0.03	32	0.21	24	2.04	15
Vernonia amygdalina	0.00	-	0.03	32	0.00	-	0.00	-
Ximenia americana	0.00	-	0.06	29	0.02	39	0.17	26
Zanthoxylum chalybeum	0.00	-	0.18	25	0.21	24	0.34	24
Ziziphus pubescens	0.00	-	0.73	18	0.60	21	0.85	22

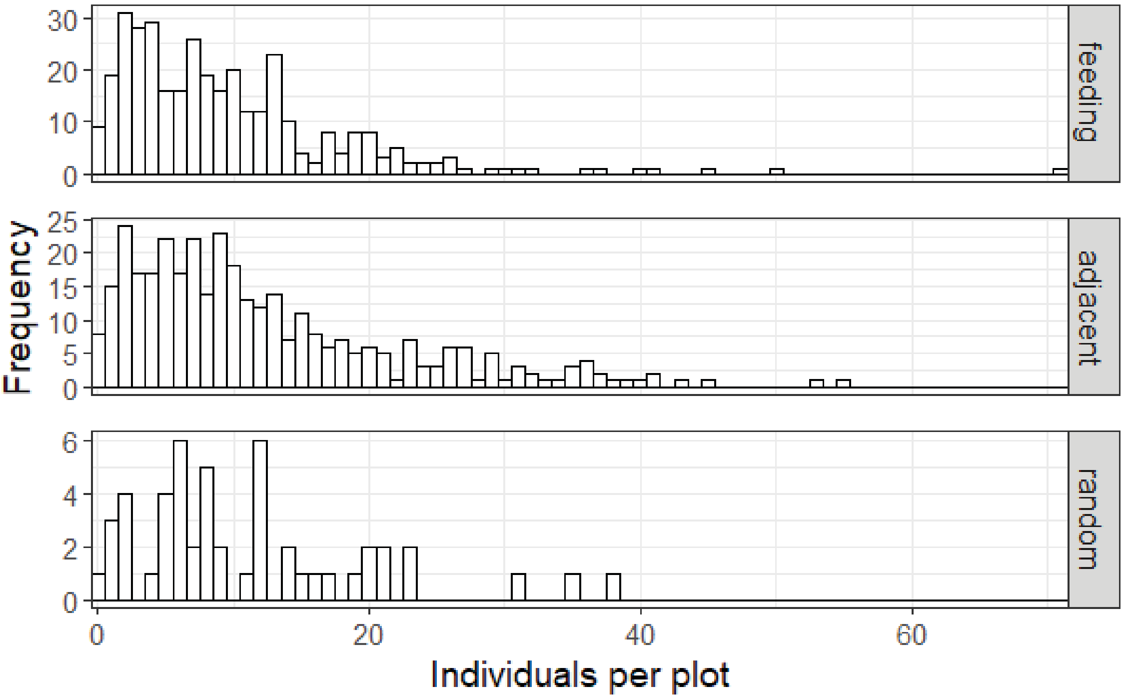

Figure A1. Frequency histogram of density of woody species in feeding (n=349), adjacent (n=349), and random (n=50) plots.

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