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Utilization of termitaria vegetation by translocated Rothschild's giraffes

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Abstract

Patches of high quality resources are important in many African savannahs. A source of this heterogeneity are mounds build by termites (termitaria). The soils and vegetation of termitaria have in many cases been found to be richer in important nutrients, and many studies have shown that termitaria are browsing hotspots for ungulates and megaherbivores. In 2015, 15 Rothchild's giraffes (*Giraffa camelopardalis rothschildi*) were translocated to Lake Mburo National Park in Uganda. I conducted a study to explore to what extent giraffes utilize termitaria vegetation. The giraffe's diet was observed in the dry season from June to August, as well as sampling the vegetation of the study area. Vegetation samples were taken along the feeding transect of the giraffes, perpendicular to the feeding transect, and randomly within the study area. The giraffe's diet preference was analysed in relation to the vegetation available to the giraffes on and off termitaria. Giraffe's were found to browse mainly on savannah vegetation consisting of *Acacia gerrardii* and other *Acacia*, and browsed on termitaria vegetation less than expected. The composition of species browsed on and off termitaria was found to be significantly different from eachother, with some overlap. *Rhus natalensis* and *Carissa spinarum* were browsed more than expected on termitaria, with *R. natalensis* being the most browsed species on termitaria, while *C. spinarum* had few browsing observations and bites associated with it. As the dry season progressed, the giraffes showed increased preference for termitaria vegetation in general, as well as *R. natalensis*. This study shows that for the giraffes of Lake Mburo National Park, while termitaria vegetation is utilized less than expected, it may be an important contributor to diet variability.

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Introduction

The African savannah is one of the most species rich ecosystems on Earth (Mittermeier et al., 1998). The high spatial heterogeneity of the savannah allows a plethora of herbivores to occupy these areas in large numbers. Patches of high quality resources are important in nutrient-poor ecosystems such as many African savannahs (Jouquet et al., 2005; Konaté et al., 1999), where mineral nitrogen and phosphorus are limiting factors for plant productivity (Fynn & O'Connor, 2005; Jacobs et al., 2007). A major source of this spatial and functional heterogeneity is caused by mound-building soil organisms (Konaté et al., 1999; Moe et al., 2009). Among these are the fungus-growing termites (Termitidae, subfamily Macrotermitinae).

Termites are recognized as ecosystem engineers (Jones et al., 1994; McCarthy et al., 1998). In the mounds constructed by termites (henceforth termitaria), termites mineralize soil organic content (Arshad, 1982), which leads to an increase in mineral nutrients such as nitrogen and phosphorus compared to the surrounding soil (Abbadie & Lepage, 1989; Arshad, 1982; Grant & Scholes, 2006). Elevated concentrations of soil minerals may have important consequences for the nutrient availability for plants, which then will affect the productivity of plant communities growing on or near the termitaria (Arshad, 1982). Additionally, termites influence properties such as drainage, hydrology and topography (Sileshi et al., 2010).

The species composition of vegetation growing on termitaria is often significantly different compared to the vegetation of the surrounding area (Arshad, 1982; Jouquet et al., 2004; Moe et al., 2009; Muvengwi et al., 2013). Densities of individuals of woody species has also been shown to be higher on termitaria (Moe et al., 2017). These differences are attributed to soil content, higher level of available nutrients and moisture, and that trees growing on the elevated mounds may escape from ground fires (Joseph et al., 2013; Konaté et al., 1999). The foliar content of woody species growing on termitaria have been found to have higher concentrations of many nutrients except sodium and crude protein compared to inter-mound vegetation (Holdo & McDowell, 2004; Muvengwi et al., 2013). Given the increased nutritional value of termitaria vegetation, it would be expected that termitaria are attractive feeding patches for savannah herbivores (Holdo & McDowell, 2004; Loveridge & Moe, 2004; Mønbæk et al., 2005).

Different sized herbivores exploit vegetation according to nutritional quantity and quality (Geist, 1974). The Jarman-Bell principle states that small herbivores require less food in terms of biomass but of high quality, while large herbivores have higher absolute food requirements, where they require more food in terms of biomass but can tolerate forage of lower quality (Geist, 1974; Jarman, 1974; Owen-Smith, 1992; RHV, 1971; Shipley, 2007; Vesey-FitzGerald, 1960). Still, large herbivores prefer higher quality forage as both medium to large sized ungulates and megaherbivores such as rhino (*Diceros bicornis*) and elephants (*Loxodonta africana*) have been found to graze and browse significantly closer to termitaria than by (Holdo & McDowell, 2004; Loveridge & Moe, 2004; Mobæk et al., 2005)

In July 2015, 15 Rothschild's giraffes (*Giraffa camelopardalis rothschildi*) (11 females and 4 males) were relocated from Murchison Falls National Park (MFNP) in north-western Uganda to Lake Mburo National Park (LMNP) in south-western Uganda. This was done in hopes of controlling the increasing densities of *Acacia* trees in LMNP and in an effort to increase the giraffe's range (Marais et al., 2016). While Brown and Fennessy (2014) did a preliminary assessment of LMNP as a suitable habitat for the Rothschild's giraffe, there has been no further studies to see how the giraffes have adapted to their new environment, specifically in relation to their browsing behaviour and preferences. As both larger ungulates and megaherbivores have been found to prefer termitaria vegetation to inter-mound vegetation, termitaria vegetation might be central to the LMNP giraffe's food choice and ultimately important to their survival in LMNP. To my knowledge there has been no research on how giraffes utilize termitaria vegetation.

The objectives of this study were to determine the feeding preference of the translocated Rothschild's giraffes in LMNP, specifically in relation termitaria vegetation.

I predict that i) giraffes will select for areas with higher densities of termitaria, as ungulates in LMNP have been found to prefer termitaria vegetation (Mobæk et al., 2005), ii) giraffes prefer to feed on termitaria vegetation, as both megaherbivores and ungulates have been found to prefer termitaria vegetation (Holdo & McDowell, 2004; Loveridge & Moe, 2004; Mobæk et al., 2005), iii) giraffes will browse different species on and off termitaria, as species composition in many cases have been found to be different between termitaria and savannah vegetation (Arshad, 1982; Moe et al., 2009), and iv) giraffes will increase their proportional use of termitaria vegetation as the dry season progresses, as this has been found in previous studies (Parker et al., 2003; Pellew, 1984).

Materials and Methods

Study area

The study was conducted in Lake Mburo National Park (LMNP), located in south-western Uganda (between 00° 30'S and 00° 45'S, and 45° 00'E and 31° 05'E) and covers an area of approximately 260 km². The Park is located in the rain shadow between Lake Victoria and the Rwenzori Mountains and receives an average of 800 mm rain in a bimodal annual pattern (February-June and October-December), and has an average recorded temperature of 27.5 °C (Mobæk et al., 2005). The dominant soil types are dystic planosols, ferrasols, histosols, vertisols and dystic leptosols (Blösch, 2002; Blösch, 2008).

The vegetation of the park mainly consists of grass savannah, open tree savannah and open woodland. The mixed woodlands are dominated by a variety of *Acacia* species and thicket clumps, with the most common being *Acacia hockii*, *A. gerrardii*, *Rhus natalensis* and *Grewia* sp. (Blösch, 2008; Mobæk et al., 2005). Another distinct feature in the park are the numerous vegetated termitaria thickets, which are constructed by the termite genus *Macrotermes* (Mobæk et al., 2005; Okullo & Moe, 2012). The density of trees on these termitaria are four times that of the savannah matrix, and the species composition has been found to be more diverse than that of the savannah matrix, commonly consisting of species such as *R. natalensis*, *Scutia myrtina* and *Grewia similis* (Moe et al., 2009; Moe et al., 2017).

The phylogeny of *Acacia* has been proposed reclassified. *Acacia polyacantha* has been suggested to be renamed *Senegalia polyacantha*, while *A. gerrardii*, *A. hockii*, and *Acacia sieberiana* have been suggested to be included in the *Vachellia* genus (Kyalangalilwa et al., 2013). However, as there has been no universal adoption of these proposed changes, the original *Acacia* classification will be used for this paper.

Study species

The Rothschild's giraffe is a subspecies endemic to Kenya and Uganda (Brown & Fennessy, 2014). They have large dark patches that usually have complete margins but spotting seldom reach below the hocks and almost never the hooves. The subspecies is considered endangered, with an estimated 1300 individuals found in the wild (Marais et al., 2016). While it is currently accepted that there exists only one species of giraffe consisting of nine subspecies, a recent paper has suggested that there are four distinct species of giraffe, each consisting of several subspecies (Fennessy et al., 2016). In this new classification, Fennessy et al. (2016) suggests that the Rothschild's giraffe should be subsumed into the nominate Nubian giraffe (*Giraffa camelopardalis camelopardalis*), as a subspecies of the species northern giraffe (*Giraffa camelopardalis*).

Giraffes are almost exclusively browsers, feeding on foliage which is inaccessible to most mammal herbivores, with the exception of elephants (Owen-Smith, 1992). They have been shown to typically select more than 20 plant species in their diet, which is ascribed to the fact that giraffes can traverse large distances within their home range where they encounter and use a wider variety of vegetation types than other browsers (Parker & Bernard, 2005; Skinner & Chimimba, 2005). Although the typical giraffe food is often considered to be *Acacia* (Gordon et al., 2016), their feeding ecology at different locations in Africa provides evidence of substantial dietary diversity (Berry & Bercovitch, 2017). Giraffes have also been found to change feeding preferences between seasons, where they prefer deciduous species (such as many *Acacia*) during the wet season, and switch to more evergreen species during the dry season when their preferred species decline in abundance (Parker et al., 2003).

Data collection

The feeding preference of the translocated giraffes was studied over two months during the dry season, from mid-June to mid-August 2017. The use of vegetation by the giraffes was recorded using focal-animal sampling technique (Altmann, 1974). The giraffes were located using a 4WD car and a spotting scope. Once the giraffes were located, they were followed at a distance of 100-200 m, to reduce disturbance to a minimum. The observations were carried out from 8:00-17:00, with a break during midday as the giraffes would be resting during the hottest hours of the day. The giraffes gathered in groups, which varied daily with a mean size of 9.12 (3.6 SD). When any group of giraffes was located, the first individual observed browsing would be observed for a period of two minutes. If the giraffe continued browsing past those two minutes, a new giraffe was selected for observation. The observation period

would end when the giraffe either moved out of sight or moved away from the plant and did not take a new bite within 5 seconds of the last bite. If the giraffe began browsing 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. To avoid overrepresentation of a single individual, data from the same individual was not collected within 2 minutes of the end of its previous observation period. Number of bites taken per plant species, duration of browsing, tree species browsed, estimated height of browsed tree (highest point of tree, estimated to the nearest 0.5 m) and on or off termitaria browsing was noted within the two-minute observation period.

Vegetation plots ($n=748$) were defined as circles with a 5m radius (total area per plot= 78.54m^2) and were sampled on three different scales using transects (Fig 1). 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. The last tree browsed was determined by different factors; if the tree was more than a kilometre from the starting point, if the giraffes moved out of sight or for other reasons could not be followed, or if they moved more than 200 metres without feeding. A new transect was started from the first point the giraffes observed them browsing after the interruption. The first plot was located at the transect starting point and then a new plot was determined every 100 metres from the initial plot, until the endpoint was reached. Each transect was limited to no more than 11 plots to increase the number of transects and thus the variation in our data material.

Within each plot the tree species, height of the tallest individual of each species and number of individuals of each species were noted. Height was either measured with a 4 m long measuring stick, or if above 4 m, estimated to the nearest 0.5 m. Additionally, if present in the plot, the portion of the plot which was covered by termitaria was estimated and whether each recorded tree was located on termitaria or not. The plots within the transects where the giraffes walked and browsed are called feeding plots ($n=349$). For each feeding plot, an adjacent plot ($n=349$) was alternately assigned 100 m to the left and right of the feeding plot, perpendicular to the transect itself. The same parameters were recorded in the adjacent plots as in the feeding plots. All points, plots and distances were noted and measured using a GPS. In addition to the feeding and adjacent plots, 50 random plots were sampled. These were located in the study area, defined as the area where giraffes were observed to browse. These 50 plots were selected by placing 100 numbered points across a map of the study area, then using a random number generator and selecting 50 plots out of the 100 candidate plots.

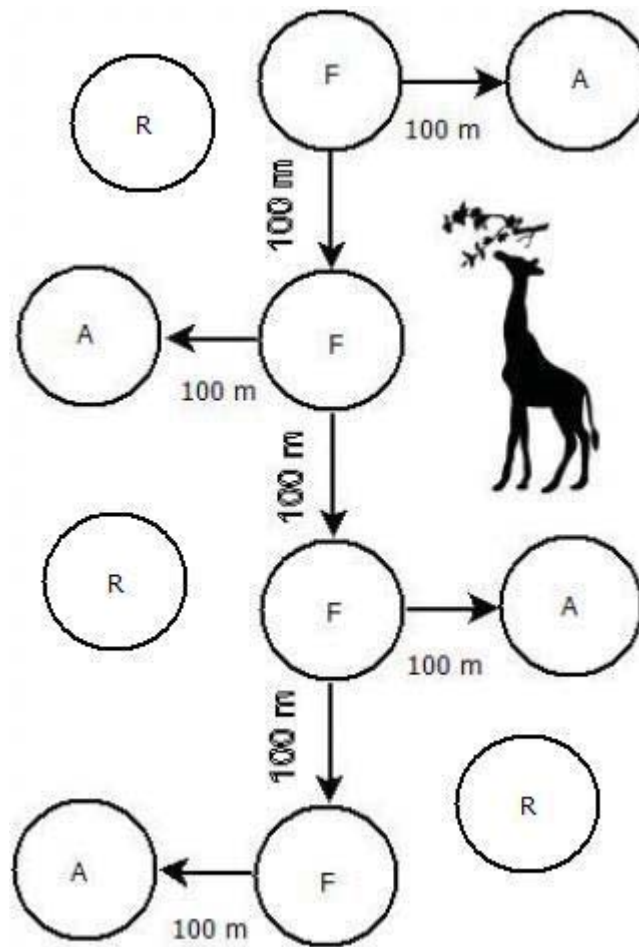


Figure 1. The plots vertical to each other forms the feeding transects (F) where the giraffes were observed browsing, while the plots perpendicular to the feeding plots are the adjacent transects (A). Random plots (R) were randomly distributed in the study area.

Data analysis

All analysis was carried out in R v. 3.4.1 for Windows (R Core Team, 2014). A binomial generalized linear model (glm) was used to analyse whether there was a difference in termitaria presence between the different plot types. The data used was presence/absence of termitaria per plot per transect type where the random plots were used as the control. Statistical significance of the GLM were based on chi square tests against null models.

Differences in the composition of vegetation browsed between termitaria and savannah were tested for using a non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances, followed by ANOSIM using the vegan package, version 2.4-4 (Oksanen et al., 2017).

A chi-square test of goodness of fit was used to test whether giraffes were preferentially feeding on termitaria associated trees. This was done for all browsed species combined, and with the individual species which were browsed more than 50% on termitaria and had five or more feeding observations associated with them both on and off termitaria.

To determine whether there was a change in diet preference over the course of the study (i.e. with a progressively dryer environment), the daily number of bites associated with termitaria vegetation was divided by the sum of all bites per day to get the proportion of daily diet. The same was done with bites associated with savannah vegetation. These daily proportions were aggregated into the mean proportion used per week. Standard error was acquired using the Rmisc package, version 1.5 (Hope, 2013).

Results

Termitaria presence

The mean percentage of plots with termitaria present was 26% (± 44 SD) in the feeding plots, 29% (± 46 SD) in the adjacent plots and 36% (± 48 SD) in the random plots (Table 1).

There was no significant difference in the number of plots where termitaria was present between the different plot types (GLM, $p > 0.1$).

Table 1. List of the total number of plots within the different plot types (feeding, adjacent and random), the total area of those plots consisting of termitaria, and the total percentage of termitaria coverage for each plot type.

Plot type	Total number of plots	Mean percentage (% \pm SD) of plots with termitaria presence
Feeding	349	26 (44)
Adjacent	349	29 (46)
Random	50	36 (48)

Table 2. A complete list of all browsed plant species, how many times each species was observed browsed on and off termitaria (with number of individuals found in feeding plots in parentheses), and the calculated total percentage of feeding observations on termitaria.

Tree species	Number of individuals browsed (recorded in feeding plot) on and off termitaria		Percentage of obs. on termitaria
	Off termitaria	On termitaria	
<i>Abutilon guineense</i>	2 (0)	1 (15)	33%
<i>Acacia gerrardii</i>	770 (878)	4 (11)	0.5%
<i>Acacia hockii</i>	69 (156)	0 (17)	0%
<i>Acacia polyacantha</i>	66 (91)	0 (2)	0%
<i>Acacia sieberiana</i>	223 (170)	2 (2)	0.8%
<i>Allophylus macrobotrys</i>	3 (9)	0 (23)	0%
<i>Asparagus racemosus</i>	0 (0)	1 (2)	100%
<i>Capparis fascicularis</i>	5 (6)	5 (13)	50%
<i>Capparis tomentosa</i>	7 (96)	11 (91)	61%
<i>Carissa spinarum</i>	5 (47)	16 (50)	76%
<i>Cissus quadrangularis</i>	3 (1)	56 (15)	95%
<i>Cyphostemma adenocaula</i>	1 (0)	1 (1)	50%
<i>Dichrostachys cinerea</i>	7 (251)	0 (8)	0%
<i>Flueggea virosa</i>	0 (26)	1 (13)	100%
<i>Gardenia ternifolia</i>	1 (0)	0 (0)	0%
<i>Grewia bicolor</i>	6 (32)	3 (59)	33%
<i>Grewia similis</i>	1 (57)	2 (62)	66%
<i>Lannea schweinfurthii</i>	3 (0)	0 (0)	0%
<i>Maerua angolensis</i>	5 (425)	3 (24)	38%
<i>Maytenus heterophylla</i>	0 (82)	3 (32)	100%
<i>Pappea capensis</i>	5 (6)	0 (4)	0%
<i>Rhipsalis baccifera</i>	4 (1)	0 (1)	0%
<i>Rhus natalensis</i>	44 (191)	50 (97)	53%
<i>Scutia myrtina</i>	13 (36)	37 (141)	74%
<i>Tricalysia niamniamensis</i>	1 (0)	0 (3)	0%
Total	1245 (2561)	196 (686)	13.6%

Termitaria vegetation utilization

From all 1401 recorded feeding observations, 196 (13.6%) were of giraffes browsing on termitaria vegetation (Table 2). Termitaria vegetation was browsed 27.2% less than expected, $X^2(1, N=4868) = 35.53$, $p < 0.0001$.

The giraffes were observed browsing on 26 out of the 46 recorded plant species (Table 2; Table A1). Of all species browsed, 13 were browsed both on and off termitaria, ten only off termitaria and three only on termitaria (Table 2). The species composition of species browsed on and off termitaria was significantly different from each other (Fig 2; ANOSIM $r=0.63$, $p < 0.0001$).

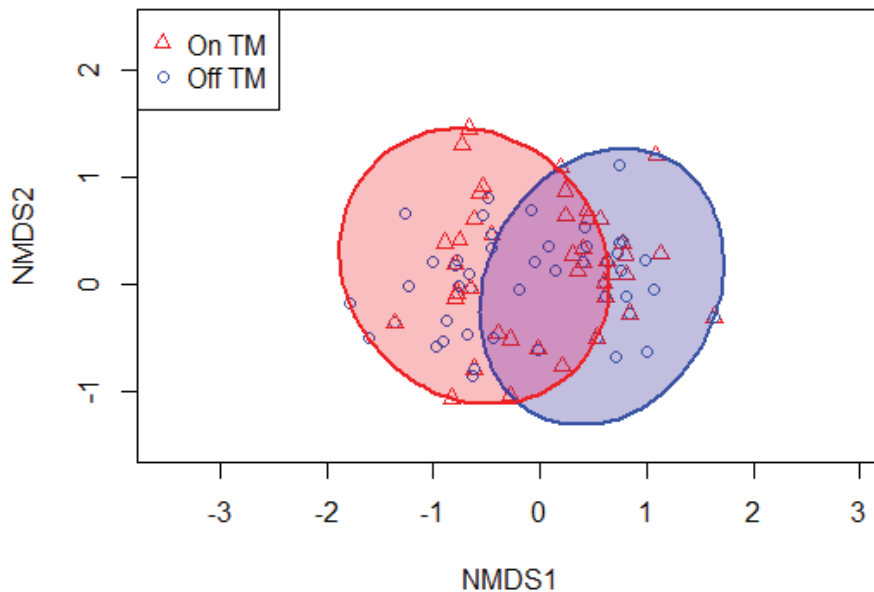


Figure 2. NMDS ordination plot of browsed plant species. Red circle and triangles represents species browsed on termitaria, while blue symbols represent species browsed off termitaria (ANOSIM $r=0.63$, $p < 0.0001$).

The five most browsed species in relation to number of bites were all *Acacia* with the exception of *Rhus natalensis* (Fig 3a). In total 59.8% of all bites were associated with *Acacia gerrardii*, while *Acacia sieberiana* and *R. natalensis* was ranked second and third with 14% and 6.9% of bites associated with them, respectively (Fig 3a; Table A1)). The three most browsed species on termitaria were *R. natalensis*, *Scutia myrtina* and *Cissus quandrangularis* (Fig 3b; Table 2; Table A1). *Capparis fascicularis*, *Capparis tomentosa*, *Carissa spinarum*,

Cissus quadrangularis, *R. natalensis* and *S. myrtina* were browsed between 50% and 95% on termitaria, and of these six only *R. natalensis* and *C. spinarum* yielded significant results in a chi square test. *Cissus quadrangularis* was browsed predominantly (95%) on termitaria and is also generally associated with them (Table 2). Both *R. natalensis* and *Carissa spinarum* were browsed on termitaria significantly more than expected by 36.8%, $X^2(1, N=382) = 11.4$, $p < 0.0001$ and 43.1%, $X^2(1, N=128) = 6.1$, $p < 0.0135$, respectively. *Maytenus heterophylla*, *Flueggea virosa*, *Asparagus racemosus* were browsed exclusively on termitaria, but had below 0.2% of bites and three or less browsing observations associated with them (Table 2; Table A1).

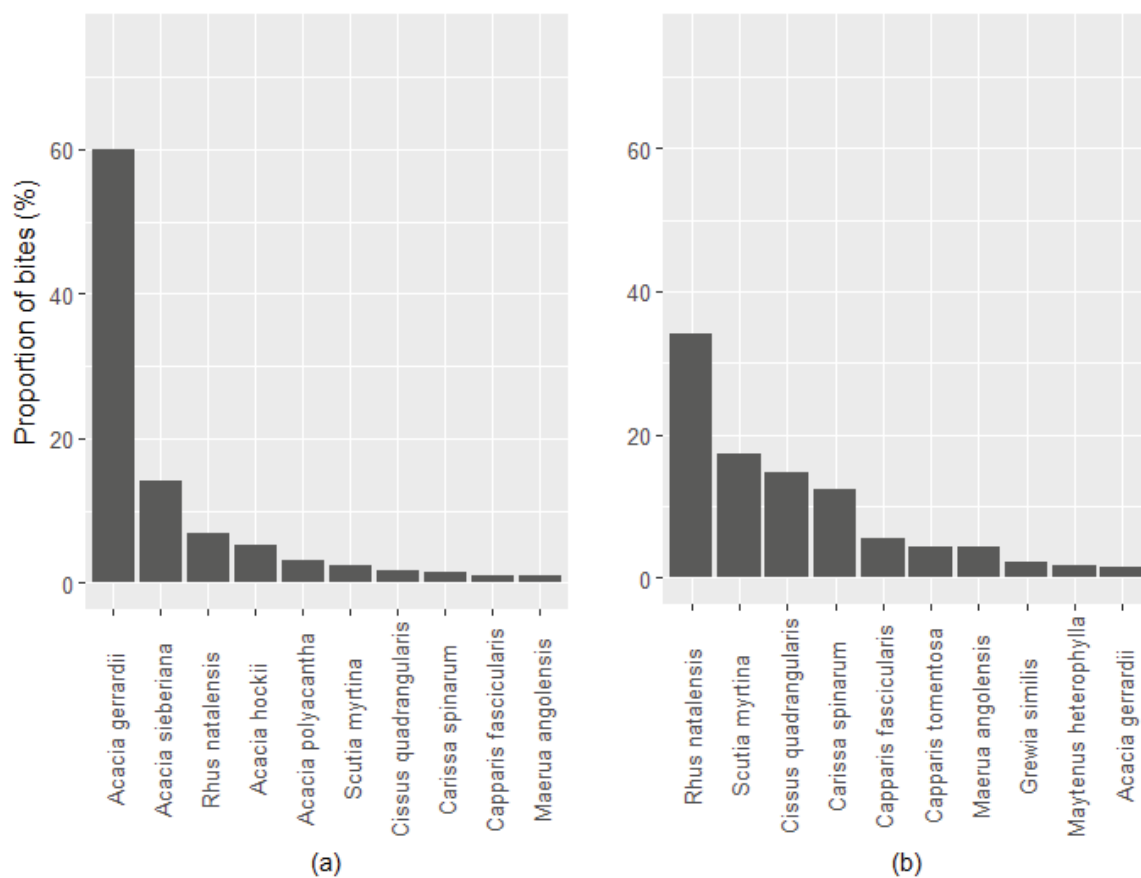


Figure 3. Top ten browsed species by number of bites, ranked from highest to lowest proportion of bites associated with the species, for all species browsed (a) and for bites only on termitaria trees (b).

The use of termitaria vegetation was consistently low, with a mean proportion of 14% (± 6 SD). It was lowest during mid-July at 8.5% of the diet, and peaked at the beginning of August, consisting of 25% of their total diet (Fig. 4a). *R. natalensis* was the third most browsed species overall and the most browsed species on termitaria (Fig. 3). A larger proportion was consumed on termitaria, with a mean proportion of 6% (± 3 SD), and with an increase of approximately 7% at the beginning of August (Fig. 4b). In mid-August, there was a sharp decline of 10%, with a sharp increase of 18 % in the use of savannah *R. natalensis* (Fig. 4b).

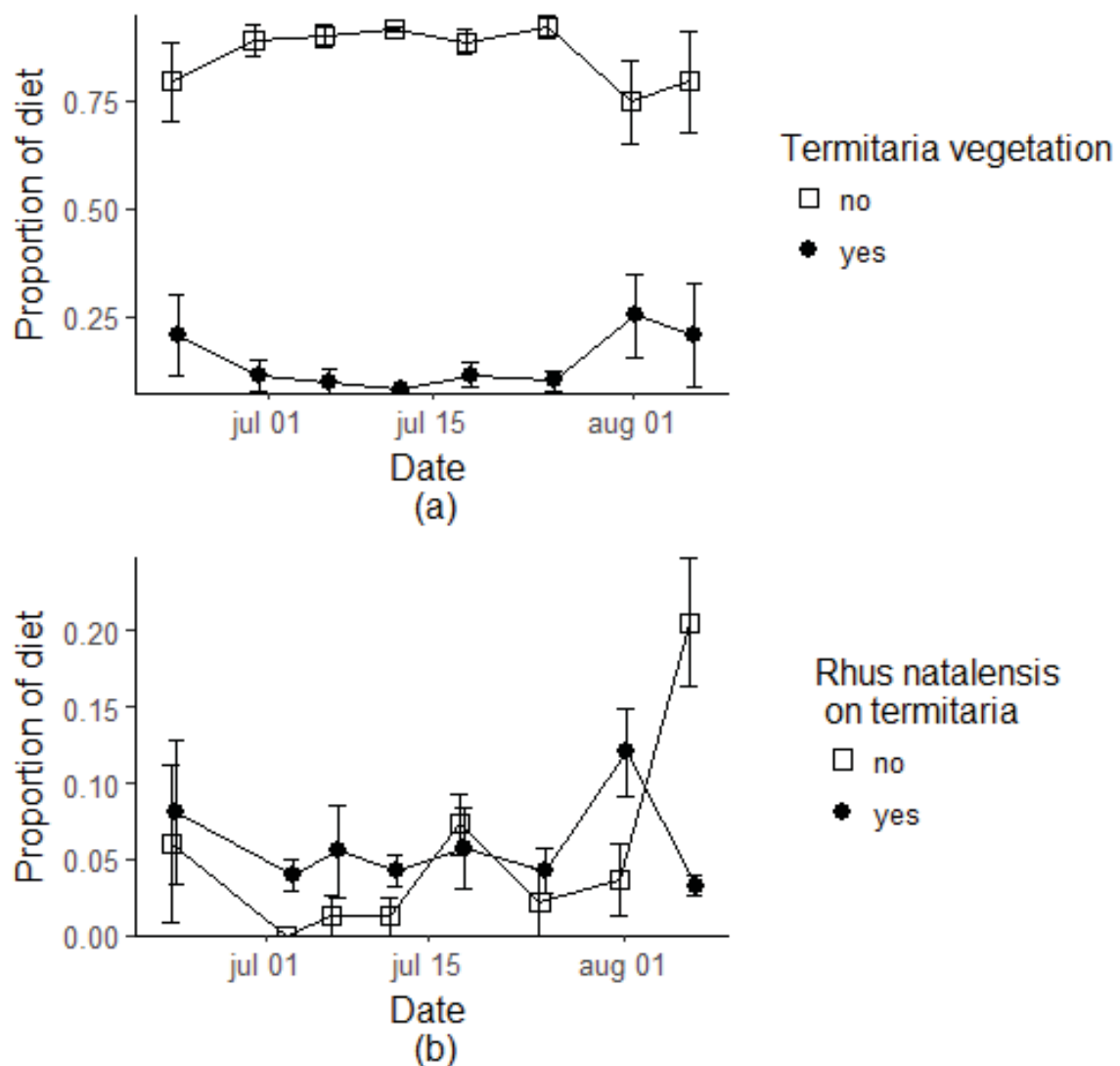


Figure 4. Change in diet composition (proportion of daily diet) over time (weekly means \pm SE) for termitaria vegetation (a) and *Rhus natalensis* (b).

Discussion

Access to and use of termitaria vegetation

I found no difference in the density of termitaria between the different transects, suggesting that the giraffes have equal access to termitaria vegetation throughout the study area, and therefore my first prediction is not applicable. Termitaria vegetation was used significantly less than expected, which contradicts my second prediction. This study clearly documents that while the giraffes of LMNP do utilize termitaria vegetation, it seems to be used as an addition to their main diet of *A. gerrardii*.

Given the abundance of termitaria in the area (Moe et al., 2009) and that termitaria vegetation in many cases have higher concentrations of many important nutrients compared to the adjacent savannah vegetation, especially during the dry season (Holdo & McDowell, 2004; Muvengwi et al., 2013), I would expect the giraffes to browse more on the nutrient rich termitaria vegetation than what we observed. However, Levick et al. (2010) found that while termitaria often cover about 5% of nutrient-poor savannah landscapes, their sphere of influence on vegetation extend to about 20% of the total area where they are found. Therefore, the actual use of termitaria influenced vegetation might be greater than what I found in this study.

Utilization of species on termitaria

The composition of browsed species was significantly different between termitaria and savannah vegetation, supporting my third prediction. It suggests that while giraffes have a strong preference for *A. gerrardii* and other *Acacia* species, they utilize the unique vegetation on termitaria in addition to *Acacia*. However, most species browsed exclusively or primarily on termitaria had few bites and browsing observations associated with them (Table 2; Table A1). Two species, *Rhus natalensis* and *Carissa spinarum*, were browsed significantly more on termitaria than expected and *Cissus quadrangularis* was browsed almost exclusively on termitaria (Table 2). Additionally, it has been found that despite being a smaller part of the diet, *Cissus quadrangularis* had one of the highest selection indices, being used at least three times more often than its availability (Williams, 2018). *R. natalensis* was the most browsed species on termitaria and was ranked third considering all bites combined (Fig. 3; Table A1). Given this, termitaria *R. natalensis* and *Cissus quadrangularis* seems to be important food species to the giraffes, in accordance with other studies (Parker et al., 2003; Parker & Bernard, 2005). While *C. spinarum* was preferred on termitaria, there were few feeding

observations and bites associated with it (Table 2; Table A1), and thus it does not seem to be of significant importance in the diet.

Change in utilization throughout the dry season

The study was conducted during the dry season, which might have several implications on the giraffe's diet. The proportion of termitaria vegetation browsed was generally low throughout the study, except for a peak of 25% in early August (Fig. 4a). This coincided with the end of the dry season, where the vegetation foliage was at its driest and many trees had lost most of their leaves (pers. obs.). Additionally, *A. gerrardii* was found to decrease in relative diet importance at the same time (Williams, 2018). Giraffes have been shown to change their feeding preferences between the dry and wet seasons (Abbadie & Lepage, 1989; Berry & Bercovitch, 2017; Owen-Smith, 1992; Parker et al., 2003; Pellew, 1984). This supports my fourth prediction and suggest that the giraffes increase their use of termitaria vegetation largely at the end of the dry season, when off-mound vegetation might decrease in quality (Parker et al., 2003; Parker & Bernard, 2005). Parker et al. (2003) found that a group of giraffes in South Africa made a switch in their diet from mainly *Acacia karroo* in the wet season to *Rhus sp.* during the dry season, which they attributed to the deciduous nature of *A. karroo*. I did not find *R. natalensis* to be preferred over the various *Acacia* species, which might be explained by *A. gerrardii* being drought resistant and usually evergreen (Kondoh et al., 2006). According to Pellew (1984), giraffes spend more time foraging during the dry season as the amount and quality of available browse is reduced. To fully understand to what extent the giraffes of LMNP use termitaria vegetation, a study during the wet season should be conducted.

Megaherbivore utilization of termitaria and soil properties

Loveridge and Moe (2004) found that termitaria in nutrient-poor miombo woodlands in Zimbabwe were browsing hotspots for megaherbivores, such as the elephant and black rhino. Holdo and McDowell (2004) also found that elephants prefer termitaria vegetation to woodland vegetation. However, other studies have found elephants and other browsers to prefer savannah vegetation to termitaria vegetation, and biomass removal to be higher in savannah plots than termitaria plots (Muvengwi et al., 2013; Plas et al., 2013). It should be noted that in the study by (Muvengwi et al., 2013), while both termitaria soil and vegetation foliage was richer in nutrients than the inter-mound matrix, the study was located in the Zambezi valley, with rich alluvial and basaltic soils. This suggest that large herbivores only

show preference for termitaria vegetation in nutrient-poor environments. However, the soils of LMNP are mainly nutrient-poor (Blösch, 2008), which in this case suggests that the giraffe's preference for savannah vegetation over termitaria vegetation cannot be explained by the nutrient content of the soils alone.

Ungulate utilization of termitaria and competition

Other ungulates in LMNP have been found to prefer vegetation growing close or on termitaria (Mobæk et al., 2005). Bushbuck (*Tragelaphus sylvaticus*), impala (*Aepyceros melampus*), waterbuck (*Kobus ellipsiprymnus*), zebra (*Equus burchelli*), warthog (*Phacochoerus africanus*) and topi (*Damascilus korrigum*) were all feeding significantly closer to termitaria than expected (Mobæk et al., 2005), which suggests that for many of the Parks ungulates, termitaria constitute a major food source, both quantitatively and qualitatively. As I did not find this to be true in the case of giraffes, competition could be a reason for this underutilization of termitaria vegetation.

Given the height of the giraffe, they have access to vegetation which other browsers of LMNP do not (Simmons & Altwegg, 2010). Giraffes have been found to browse at around head height (4-5 m) (Dharani et al., 2009; du Toit, 1990), which held true for the giraffes in LMNP as well (Williams, 2018). *A. gerrardii* trees in the feeding transect had a mean height of 4.1 m (± 2.7 SD) (Unpublished data), whereas most termitaria have available forage from the ground up (pers.obs). Studies have found that in 90% of cases, giraffes would browse out of the height ranges of kudu (*Tragelaphus strepsiceros*) and impala, which mostly browsed below 2m (du Toit, 1990). Cameron and du Toit (2006) found experimental support for the hypothesis that competition with smaller herbivores drives this feeding height stratification in giraffes. This suggests that in LMNP, one of the reasons for giraffes strongly preferring *A. gerrardii* is that other browsers in LMNP both have access to and prefer termitaria vegetation, while giraffes have exclusive access to much of the *Acacia* foliage. This, and the fact that there are no elephants in the park, the giraffes have little competition for *Acacia* food sources. Therefore, the moderate use of termite mound vegetation by giraffes, compared to other ungulates in the park, might be because giraffes face less competition for *A. gerrardii*.

Preference for protein rich foliage

The giraffe's preference for savannah vegetation might be explained by termitaria vegetation being poorer in crude protein compared to the nitrogen fixating *Acacia* (Holdo & McDowell, 2004). Giraffes are known to show preference for *Acacia*, due to the higher

protein and water content of the leaves compared to other vegetation (Cooper et al., 1988; Sauer et al., 1982). Pellew (1984) also found that the amount of crude protein was consistently higher in giraffe diet than that of other African ungulates, particularly in the dry season, and that female giraffes ingest more protein than males. Among other ungulates, Tomlinson (1980) found that waterbuck increased their utilization of termitaria vegetation in the dry season, as their preferred food species had higher crude protein and moisture content on termitaria at this time of year. Protein content of forage thus seems to be an important factor in ungulate forage selection. I have found no research on leaf nutrient content in LMNP, but with *Acacia gerrardii* often being evergreen and possibly higher in crude protein content than termitaria vegetation, giraffes may prefer *Acacia* to termitaria vegetation given the high dietary requirements for protein in giraffe diet.

Female feeding preferences

In LMNP, 11 of the 15 translocated giraffes were female, so while I was unable to correctly ID and gender the giraffes, the majority of our observations was of female browsing behaviour. The giraffe is the only ungulate which breeds throughout the year (Pellew, 1984), but during the two years the giraffes have been in LMNP, no calves have been born. Pellew (1984) stated that breeding females require browse of higher quality and energy, and Mobæk et al. (2005) found that among the ungulates in LMNP, ruminants and female impalas browsed and grazed significantly closer to termitaria than by chance. While the giraffes browsed significantly less on termitaria vegetation, this could change once the giraffes start breeding. Given this, it would be interesting to do further research on this group of giraffes once they start calving.

Translocation and stress

The 15 giraffes in LMNP were translocated from Murchison Falls National Park, but I have not been able to find studies conducted on giraffes and their feeding preferences there. Additionally, translocation is a stressful event which in many cases leads to long-term chronic stress, which might materialize as behavioural changes (Dickens et al., 2010). Given this, it would be interesting to conduct a study to compare the diet of the giraffes in Murchison Falls National Park with that of the translocated giraffes of LMNP.

Conclusion

I found that the group of giraffes in LMNP utilized termitaria less than expected, even with presence of termitaria being equally common between all transects in the study area. *R. natalensis* and *C. spinarum* were browsed more on termitaria than expected. The species composition of termitaria vegetation browsed by the giraffes was significantly different from that of the species browsed in the savannah. There was a change in utilization of termitaria vegetation as the dry season progressed, with the proportion of diet consisting of termitaria vegetation peaking at a quarter of their diet just before the on-set of the wet season. The use of *R. natalensis* on termitaria also increased at the end of the dry season. While most giraffe bites were associated with *A. gerrardii*, termitaria vegetation was used as a supplement to this, especially at the end of the dry season. This suggests that while giraffes do not prefer termitaria vegetation over savannah vegetation, vegetation on termitaria may be an important contributor to diet variability for the giraffes in LMNP.

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Appendix

Table A1. Proportion (%) and rank of species in giraffe diet. Data is based on 1401 feeding observations.

Species	All bites		Bites associated with termitaria	
	Proportion	Rank	Proportion	Rank
<i>Acacia gerrardii</i>	59.98	1	1.60	10
<i>Acacia sieberiana</i>	14.07	2	0.20	14
<i>Rhus natalensis</i>	6.90	3	34.00	1
<i>Acacia hockii</i>	5.25	4	0.00	-
<i>Acacia polyacantha</i>	3.13	5	0.00	-
<i>Scutia myrtina</i>	2.33	6	17.40	2
<i>Cissus quadrangularis</i>	1.58	7	14.70	3
<i>Carissa spinarum</i>	1.51	8	12.40	4
<i>Capparis fascicularis</i>	1.13	9	5.50	5
<i>Maerua angolensis</i>	0.92	10	4.30	7
<i>Capparis tomentosa</i>	0.73	11	4.40	6
<i>Dichrostachys cinerea</i>	0.48	12	0.00	-
<i>Grewia similis</i>	0.39	13	2.30	8
<i>Lannea schweinfurthii</i>	0.30	14	0.00	-
<i>Pappea capensis</i>	0.26	15	0.00	-
<i>Grewia bicolor</i>	0.22	16	0.40	11
<i>Maytenus heterophylla</i>	0.20	17	1.80	9
<i>Rhipsalis baccifera</i>	0.18	18	0.00	-
<i>Abutilon guineense</i>	0.13	19	0.40	12
<i>Tricalysia niamniamensis</i>	0.09	20	0.00	-
<i>Allophyllus macrobotrys</i>	0.08	21	0.00	-
<i>Gardenia ternifolia</i>	0.04	22	0.00	-
<i>Cyphostemma adenocaula</i>	0.04	23	0.20	15
<i>Flueggea virosa</i>	0.03	24	0.30	13
<i>Asparagus racemosus</i>	0.02	25	0.20	16

Table A2 (continued). Proportion (%) and rank of species in giraffe diet. Data is based on 1401 feeding observations.

Species	All bites		Bites associated with termitaria	
	Proportion	Rank	Proportion	Rank
<i>Acalypha psilostachya</i>	0.00	-	0.00	-
<i>Combretum mole</i>	0.00	-	0.00	-
<i>Commiphora africana</i>	0.00	-	0.00	-
<i>Dovyalis sp.</i>	0.00	-	0.00	-
<i>Erythrina abyssinica</i>	0.00	-	0.00	-
<i>Erythrococca bongensis</i>	0.00	-	0.00	-
<i>Euclea racemose</i>	0.00	-	0.00	-
<i>Lannea fulva</i>	0.00	-	0.00	-
<i>Lantana camara</i>	0.00	-	0.00	-
<i>Maytenus senegalensis</i>	0.00	-	0.00	-
<i>Ochna hackarsii</i>	0.00	-	0.00	-
<i>Phyllanthus ovalifolius</i>	0.00	-	0.00	-
<i>Phytolacca dodecandra</i>	0.00	-	0.00	-
<i>Psydrax parviflora</i>	0.00	-	0.00	-
<i>Tarennia graveolens</i>	0.00	-	0.00	-
<i>Vangueria apiculata</i>	0.00	-	0.00	-
<i>Vepris nobilis</i>	0.00	-	0.00	-
<i>Vernonia amygdalina</i>	0.00	-	0.00	-
<i>Ximenia Americana</i>	0.00	-	0.00	-
<i>Zanthoxylum chalybeum</i>	0.00	-	0.00	-
<i>Ziziphus pubescens</i>	0.00	-	0.00	-



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