Habitat use and diet preference of extralimital giraffes in the Kgalagadi Transfrontier Park

Viljoen, Storme

Supervisor: Dr Edmund C. February

Department of Biological Sciences

University of Cape Town

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Abstract

Extralimital giraffe introductions in the south-western region of Kgalagadi Transfrontier Park, South Africa, may result in changes to the vegetation structure for the region through overutilization of two keystone tree species in the area. In the areas where giraffe density was highest, I determine the relative abundance of giraffe; their diet preference and the potential reasons for this preference. Using both spoor and dung counts as indicators of giraffe presence, transects were carried out over approximately 20 km of the Auob River. Percentage occurrence was plotted onto a map of the river, along with the location of boreholes that supply the only surface water. Little trend could be seen, although occurrence appeared slightly higher near boreholes.

The two trees that most commonly occur in the Auob duneveld, Acacia erioloba and Acacia haematoxylon, were examined for nutritional content, and both chemical and physical defences – all of which are thought to affect herbivore selection. Stable isotope analysis and linear mixing model were used to determine the proportion of each species in the diet of giraffe using the leaves of both species and giraffe dung. The majority of the giraffe's diet consists of A. haematoxylon (mean = 79 %, s.d. = 20.5 %) despite having less crude protein and similar condensed tannin content. Relative lack of physical defences appears to encourage giraffes to exploit A. haematoxylon, which has shorter, weaker thorns. Without management intervention, A. haematoxylon could suffer selective mortality through the impacts of giraffe browsing, resulting in a loss of species and structural diversity of the landscape.

Keywords: *Acacia*, boreholes, condensed tannins, giraffe, isotopes, Kalahari, spinescence.

Introduction

African savannas are among the oldest landscapes in the world, and their ecologies rely on dynamic relationships between vegetation and herbivores that have co-evolved over evolutionary time (Bergstrom 1992). The maintenance of landscape heterogeneity and the conservation of biodiversity is the basis of a large amount of previous ecological research (Rogers 2003). In savannas, trees provide heterogeneity and perform essential ecosystem services, upon which many other organisms depend (Dean *et al.* 1999). Trees, by their nature, are resilient to change, but impacts of high densities of megaherbivores in African savannas have been causally linked to losses of big trees (Bond & Loffell 2001; Kerley *et al.* 2008). When the balance between vegetation and browser is altered, such detrimental changes in species and structural composition can occur.

Alteration of community dynamics is a likely result of the introduction of extralimital animals. Extralimital introductions, which are the movement of animas into an area where they have not historically been distributed, have had undesirable consequences for the environments that animals have introduced to (Bond and Loffell 2001; Parker *et al.* 2003; Jacobs 2009; Cornelius 2010). What was previously considered a conservation tool for extralimital species has now been implicated as a substantial threat to biodiversity in the host environment as the long-term ecological implications of such introductions have only recently emerged. Within South Africa, legislation in the National Environmental Management: Biodiversity Act (Act 10 of 2004) strictly prohibits the introduction of any animal outside of its historical distribution

The rise of ecotourism as a lucrative industry in South Africa also means that there is substantial economic gain to be had from the presence of large, charismatic animals, and so the ecological consequences of their over-stocking or extralimital introduction have often not received adequate consideration (Castley *et al.* 2001). This oversight is particularly unacceptable when one considers how influential megafauna are in shaping ecosystem processes (Owen-Smith 1988; Midgley & Bond 2001; Kerley *et al.* 2008).

The negative impacts of extralimital animal introductions may also be exaggerated when there is no functional similarity between the introduced animal and other animals that occur in that environment. When vegetation is exposed to a herbivore for which it has not adapted to defend itself, this herbivore has the potential to devastate the plant population. The giraffe (*Giraffa camelopardis*) is a good example of a megaherbivore (> 1000 kg, Owen-Smith 1988), that can have substantial impacts on vegetation, particularly in areas outside if its historical distribution (Pellew 1983; Bond & Loffell 2001).

As large browsing ruminant herbivores and foregut fermenters, giraffes require large quantities of food to satisfy their daily energy requirements, which are obtained solely from leaf and branch material (Bell 1971; Pellew 1984). Giraffes are the only exclusively browsing megaherbivore which means that extralimital giraffe introduction are among the most ecologically risky. In South Africa, giraffes have been introduced into protected areas spanning the country, including areas outside of their historical distribution.

Giraffes are the tallest living mammal, with heights averaging between 4.3 and 5.2 m (Skinner & Smithers 1990). This has allowed giraffes to occupy a unique niche as browsers because they can reach above the limit of any other browsing herbivore, with the exception of a large African elephant (*Loxodonta africana*) (Owen-Smith 1988). Feeding height stratification has an important advantage for giraffes, which then do not have to compete interspecifically for food. Their muscular tongue and prehensile upper-lip provides another unique adaptation, whereby a giraffe will grip the distal end of a branch, which it then wraps its tongue around and the giraffe will pull backwards. This action strips the branch of its leaves and the tongue is effectively used to manoeuvre around thorns (Sauer et al. 1977; Sasaki et al. 2001) Consequently, giraffes are less sensitive to the physical defence that thorns provide, which is evident in the fact that spinescent *Acacia* species often make up the majority of a giraffes diet. (Sauer *et al.* 1977; Parker 2004; Milewski & Madden 2006).

African *Acacia* species have evolved under intense herbivory and are often found in semi-arid and arid environments (Rohner & Ward 1997; Midgley & Bond 2001). In such environments, the paucity of water and substrate nutrients results in slow growth rates of woody species. The cost of herbivory is felt more acutely in these habitats because plants draw on finite resources to recuperate biomass losses (Coley *et al.* 1985; Bryant *et al.* 1989; Belsky *et al.* 1993).

Both physical and chemical defences, as well as having low nutrient content, are anti-herbivory strategies that plants employ (du Toit 1990; Lundberg & Astrom 1990; Rohner & Ward 1997). Thorns and related architecture effectively reduce the bite size and slow the feeding rate of ungulate browsers, meaning that they remove less material per unit time, and are less likely to remain on one individual for an extended period of time (Cooper & Owen-Smith 1986).

Secondary metabolites act in a similar way in that they reduce the feeding efficiency of a browser (Robbins et al. 1987). Tannins, including hydrolysable tannins and condensed tannins, act to bind the proteins in the gut of the browser and prevent full digestion. This type of defence is thought to be very useful to plants in stressed environments as they are much less costly to produce, can be rapidly induced and are not a permanent investment, as physical defences are (Young 1987; Bryant *et al.* 1993; Ward & Young 2002).

In the Auob River valley of the Kalahari Desert, the major woody species include *Acacia erioloba* and *Acacia haematoxylon*. These trees are considered keystone species in the Kalahari, and they provide rare services in this sparsely wooded landscape (Dean et al. 1999). Their extensive taproot allows these trees to access deep ground water, which allows their growth to be independent of the erratic Kalahari rainfall (Barnes 1997). Their importance also extends into our conservation ideals because the very limits of the Kalahari have been defined by their presence (Barker 1983).

The historical distribution of giraffes in the southern extent of the Kalahari has never been confirmed. Despite this, it was assumed that the habitat could support giraffes (Hall-Martin & de Graaff 1978) and so in 1991, eight giraffes were translocated from Etosha National Park, Namibia, into an enclosure near the Craig Lockhart borehole on the Auob river (25°51’07.02”S, 20° 05’13.06”E). These giraffe were subsequently released once their population began to increase. (Deacon & Smit *unpubl.*)

Here, I examine the potential effect that the introduction of giraffe may have on the two keystone species for the area, *A. erioloba* and *A. haematoxylon*. I do this by first establishing where giraffes are located at my study site and then make a determination of the relative chemical and physical defences and nutritional quality of the two woody species. I finally use the stable carbon and nitrogen isotope ratios of giraffe dung to establish the relative contribution of each species to the diet of giraffes in the area.

As some the only big tree species in the area, these trees play a critical role in the creation of landscape heterogeneity and the maintenance of patch dynamics upon which other plants and animals are dependent (Dean *et al.* 1999). Additionally, the *A. haematoxylon* population that occurs in the Auob River system is the only population of this species that grows in a large tree form (Ross 1979). The potential effects of giraffe on the vegetation structure of the Auob River are considered with relevance to park management.

Materials and methods

Study site

The study site is located between the Sitzas and Veertiende boreholes on the Auob River, south east of Mata Mata, in the Kgalagadi Transfrontier Park, South Africa (GPS: -25.767122, 20.000138). This park has an area in excess of 80 000km^2, with a boundary that spans across the South Africa-Botswana border (Figure 1). In the southern parts of the Kgalagadi Transfrontier Park (KTP), the geology is deep Aeolian sand and calcrete base layer (Low & Rebelo 1996; Totolo & Chanda 2003). This stretch of river is considered to have the highest density of giraffe in the park (G. Ellis 2013 *pers. comm.*).

KTP receives a mean annual precipitation of around 180 mm (Van Rooyen & Van Rooyen 1998; Stapelberg *et al.* 2008) in its South-western section, which includes the Auob River. Hence, this region is classified as an arid savanna (Van Rooyen & Van Rooyen 1998). Almost all of the rain that it receives is the result of heavy thunderstorms that only occur during the summer period (November to April) (Skarpe 1986). Temperatures during summer can be in excess of 40°C. Winter temperature average around 25°C, with night time temperature often falling below 0°C (Van Rooyen *et al.* 1990).

The hot and dry conditions support sparsely wooded grassland vegetation. Both *A. erioloba* and *A. haematoxylon* are among the species that define the vegetation type of the area (Lubbinge 1999), which forms part of the Kalahari duneveld bioregion (Mucina & Rutherford 2006), The vegetation is an open tree savanna along the Auob River, where fires tend to be either absent or incidental (Menaut *et al.* 1985) as a result of their being minimal fuel load in the form of grass.

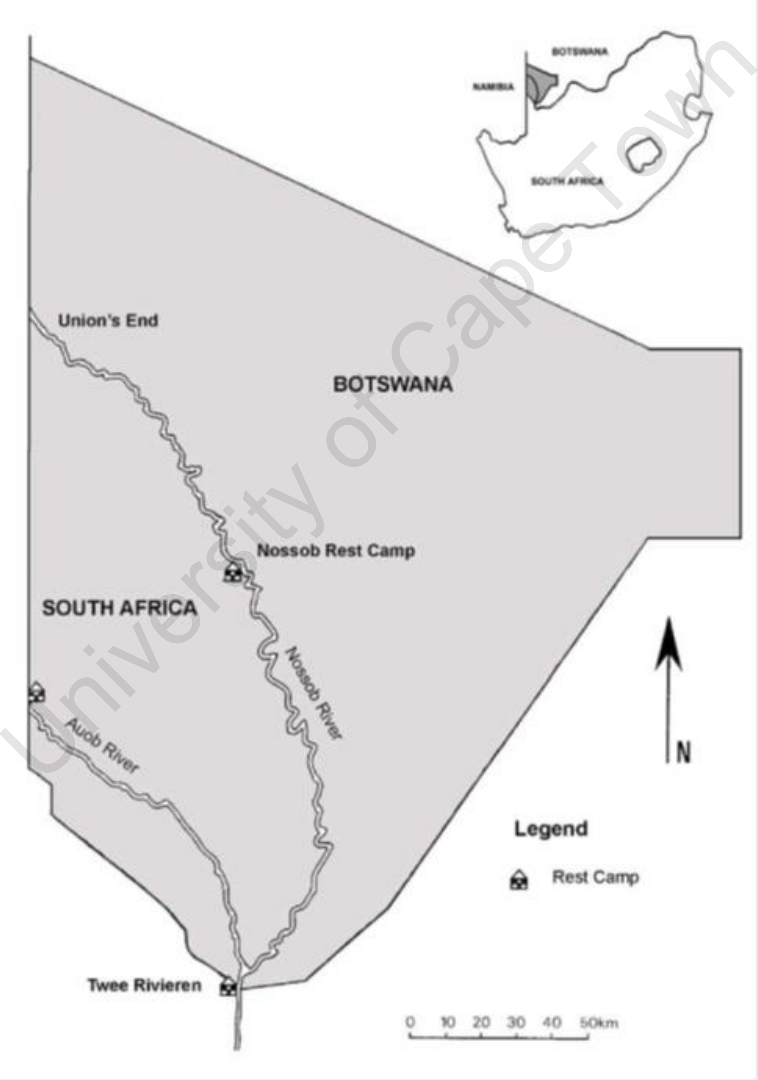

Figure 1: Location of the Kgalagadi Transfrontier Park (shaded area) within southern Africa (Van Rooyen *et al.* 1991)

The Auob River is a dry pan flanked by tall sandy dunes, which only flows episodically after exceptionally heavy rains (G. Ellis *pers. comm.*; Skarpe 1986). However, dry riverbeds still represent an important source of ground water for woody plant species (Rohner & Ward 1997), such as *Acacia erioloba* and *A. haematoxylon*. Boreholes that were constructed at regular intervals of approximately 12.4 km's along the Auob River during the First World War also provide abundant water for herbivores, which tend to concentrate in these riparian areas (Mills & Retief 1984).

Common herbivore species in the study site include springbok (*Antidorcas marsulpialis*), gemsbok (*Oryx gazella*), Ostrich (*Struthio camelus*), and blue wildebeest (*Connochaetes taurinus*) and carnivores such as cheetah (*Acinonyx jubatus*), brown hyena (*Hyaena brunnea*) and black-backed jackal (*Canis mesomelas*). However, unlike these species, the giraffe (*Giraffa camelopardus*) is only a recent feature of the Auob River landscape.

The nutrient-poor soils of the Kalahari duneveld bioregion are thought to have resulted in a vegetation compliment that is well-defended against herbivory. Indeed, both *Acacia* species exhibit spinescence and as well as chemical defence (Seymor & Milton 2003; Shaw 2010). Despite their defences, these trees are heavily targeted and often form a large proportion of the diet of browsers who share the habitat (Leuthold & Leuthold 1972; Midgley & Bond 2001).

Population distribution of giraffe

To ascertain the degree of activity by giraffe at my study site, I made a series of transects for determinations of spoor and dung. I did this in the early dry season, from the 23rd to the 28th of June 2013 along approximately 20 km of the length of the Auob River. Thirty transects running across the river bed were executed in pairs at 150 m intervals along the river valley. The length of each transect was determined by the distance between the midway point on the slope of the dunes that exist on either side of the river, which ranged from 90 to 360 m. Each transect was 10 m wide and was divided into 10m quadrats for which the presence or absence of giraffe dung and spoor was noted. Dung and spoor were both used as indicators of the presence of giraffe; however, these represent different temporal scales with spoor suggesting more recent presence compared with dung which can persist in the landscape for several weeks. Paired transects ran in opposite directions, so that for each pair, the end points were on opposite dunes.

Stable isotope ratios

Based on isotopic composition, the proportion of each acacia species in diet of giraffes in the study area can be determined. Similarity in stable isotope ratios between giraffe dung samples and leaf tissue from A. erioloba and A. haematoxylon is used as a measure of relative dietary proportion.

Leaf material from 10 adult trees (taller than 5 m) was collected for each *Acacia* species occurring near Mata Mata. Only leaves between 2 and 5 m were used as this is within the browse zone that only giraffes can feed in (du Toit 1990). Additionally, only north-facing leaves that would regularly be exposed to the sun were sampled, as leaf orientation, height and exposure to sun are al known to influence leaf chemistry, including the concentration of proanthocyanidins (Waterman and Mole 1994; Mueller-Harvey 2001). Approximately, 100g of leaf material was collected in paper bags and dried in a 60°C oven to a constant weight. These samples were then milled through a 1mm screen, producing homogenous material for determination of condensed tannin concentrations, calorific value and stable isotope analysis.

Twenty giraffe dung samples from different boli were collected opportunistically along transects. Only fresh dung samples were used in order to avoid the chemical effect of prolonged exposure to the sun (Wrench *et al.* 1996). Care should be taken when collecting dung, as pellets closely resemble that of kudu and eland (Norbury &Sanson 1992). Dung samples were dried and milled following the same procedure as for leaf material so that a dry homogenous product could be used for isotopic analysis.

Isotopic analysis of the leaf material for the same 10 trees of each species, as well as the dung samples, was performed at the Stable Isotope Laboratory in the Archaeology Department of the University of Cape Town. Homogenous samples were weighted into tin cups to an accuracy of 1 microgram using a Sartorious/ Mettler Toledo microbalance, which were then folded to enclose the sample. These samples were combusted in a Flash 2000 organic elemental analyser (Thermo Scientific™, Bremen, Germany). The gases from this combustion ware passed to a Delta V Plus Isotope ratio mass spectrometer (IRMS) using a Conflo IV gas control unit (both also made by Thermo Scientific™, Bremen, Germany).

Two in-house standards were used, both of which have been calibrated against International Atomic Energy Agency (IAEA) standards. These standards are Merck Gel, a proteinacious gel produced by Merck™ the leaf material of *Acacia saligna* collected in Glencairn, Western Cape, South Africa. Nitrogen values are expressed relative to atmospheric nitrogen and carbon values expressed in terms of its value relative to the Pee-Dee Belemite (VPDB) standard. Stable carbon and nitrogen isotope ratios were determined relative to a standard which is PDB for carbon and atmospheric N_2 for nitrogen.

Nutritional value

In order to establish which tree species provides the greater nutritive benefit to a giraffe, analysis of the nutritional value of the leaf material was done by ascertaining the percentages of carbon and nitrogen, in addition to and calorific content. The percentage of carbon and nitrogen for each sample was determined by mass spectrometry (as above). Crude protein values were calculated by multiplying the nitrogen content (% N) by a factor of 6.25 (Boyazoglu 1997).

Calorific content was measured using a Bomb Calorimeter (Digital Data Systems Pty Ltd, Randberg, South Africa). This machine is calibrated using 0.5 g of Benzoic acid, upon which the energy released from the pressurized combustion of the sample can be correlated to its calorific value in kilojoules per gram (kJ.g-1). Dry, homogenous leaf material for 10 individuals of each species was analysed in duplicate, with an additional sample being analyses if the difference in calorific content between duplicate samples exceeded 0.9 $kJ.g^{-1}$. This threshold of difference was arbitrarily assigned.

Condensed tannin concentration

Plants may defend themselves chemically against herbivory by having high concentrations of phenolic compounds, such as condensed tannins (Cooper & Owen-Smith 1985). Dry, homogenous leaf material was used to determine the level of chemical defence in the different species. Using the acid-butanol assay for condensed tannins (detailed procedure in Hagerman 2002) with a Sorghum tannin standard, the percentage of condensed tannins was calculated for 10 trees of each species.

While several problems have been found with this colorimetric assay method (Waterman & Mole 1994; Schofield *et al.* 2001; Heil *et al.*2002), which often result in an underestimation of tanniferous capacity of plant tissue, due to it not being able to account for certain insoluble tannins or and hydrolysable tannins. This methods is, however, still commonly used as the most reliable methods of condensed tannin assay (Schofield *et al.* 2001; Scogings *et al.* 2013)

Physical defences

Another defence mechanism of plants is represented by thorns, which provide a physical defence. Thorns act to slow, or prevent, herbivore browsing because they cause discomfort if eaten, and may be very difficult to bite (Cooper & Owen-Smith 1986). Branches from adult *A. erioloba* and *A. haematoxylon* trees were collected and used to take measurements of physical defence. The distal 20 cm of seven randomly locate branches per tree on seven trees per species were used to take thorn measurements. Care was also taken to avoid branches that had been noticeably impacted by insect herbivory, or that of mammal herbivores, as would be indicated by damaged leaves and branches. The length and basal diameter of each thorn, as well as the distance between the tips of paired thorns, distance between sets of paired thorns ('interthorn distance') and the distance from the branch to the tip of and leaves that were associated with a thorn pair was measured using a digital callipers. The number of thorns was per section was also determined.

A thorniness index was used as a measure of how physically defended a branch is against giraffe browsing:

$$TI = \frac{thorn\ length}{leaf\ length} \times interthorn\ distance$$ (adapted from Midgley *et al.* 2001)

Broken thorns, and thorns with a length of less than 5 mm, were excluded from analysis as they would not have contributed to the defence of the branch.

Data analysis

Using ArcGIS™ (2012), graduated symbols representing the dung and spoor percentage occurrence at each GPS data point were overlaid onto a Spot 5 Google Earth™ image (2013) of the study area. The GPS co-ordinate of the end-point of each transect was used so that each graduated symbols did not completely overlap.

A scatterplot of $\delta^{13}C$ versus $\delta^{15}N$ was plotted for samples of *A. erioloba*, *A. haematoxylon* and the giraffe dung samples found in the vicinity of sampled trees, with multiple one-way ANOVAs and post-hoc Tukey HSD tests (Statsoft, Inc. 2012) to assess whether there was significant overlap in the isotopic signals of food sources and dung. Differences in the values of either $\delta^{15}N$ or $\delta^{13}C$ would allow for discrimination of the isotope signals in the dung and indicate the proportion of the diet for each food source (Phillips 2012).

A linear mixing model of the stable isotope ratios of both *Acacia* species and giraffe dung samples was constructed using the 'siar' package in R (Parnell & Jackson 2013). This package uses a Gaussian distribution with a dirichlet prior mixture on the mean to fit a Bayesian MCMC model to the dietary habits of giraffe based on the similarity of isotopic ratios between the food sources and giraffe dung. The model accounts for the isotopic fractionation that occurs during digestion by incorporating trophic enrichment factors for $\delta^{13}C$ (Codron *et al.* 2005) and $\delta^{15}N$ (Sutoh *et al.* 1987) that have been determined during controlled feeding experiments. The concentration of carbon (%C) and nitrogen (%N) for each food source (*A. erioloba* and *A. haematoxylon*) is also incorporated into the model along with the mean and standard deviation of $\delta^{13}C$ and $\delta^{15}N$ values of food sources and dung. Based on this model, the proportion of each food source can be estimated.

The mean value of the replicates was used for statistical analysis. Significant differences between *A. erioloba* and *A. haematoxylon* were tested for using R (R Core Team 2013). Calorific content, concentration of condensed tannins, percentages of carbon and nitrogen, the C:N ratio and the proportion of crude protein were compared between the two species using a T-test after being tested for normality using a Kolmogorov-Smirnoff test.

Thorn length was averaged for each pair and again for each branch. Leaf length and distance between thorn pairs were averaged for each branch. Spinescence indices were calculated for each tree individual. Significant differences between *A. erioloba* and *A. haematoxylon* were tested for using T-tests for mean thorn length, mean basal diameter, leaf length, distance between thorn pairs, the distance between the tips of paired thorns, mean number of thorns and the number of broken thorns per branch. A Mann-Whitney U-test was used to compare to means for the thorniness index, as these data exhibit a non-parametric distribution according to a Kolmogorov-Smirnoff test.

Results

Population distribution of giraffes

Since their introduction, giraffe have not been seen outside of the Auob duneveld. The maximum number of giraffe that have been recorded in the river since February 2012 was 27 individuals, seen in that month. Such high numbers have only ever been recorded during the summer months of December to March, with the mid-year counts being close to zero.

Giraffe activity maps, which used both dung and spoor point data counts as proxies, show little trend in the concentration of giraffe activity in the study site (Figure 2). Percentage spoor occurrence had a greater range than that of dung, with some transects having upwards of 80 % spoor coverage. The middle section of the 20 km site, around Craig Lockhardt borehole, showed very low giraffe activity. However, fewer transects were executed around this site.

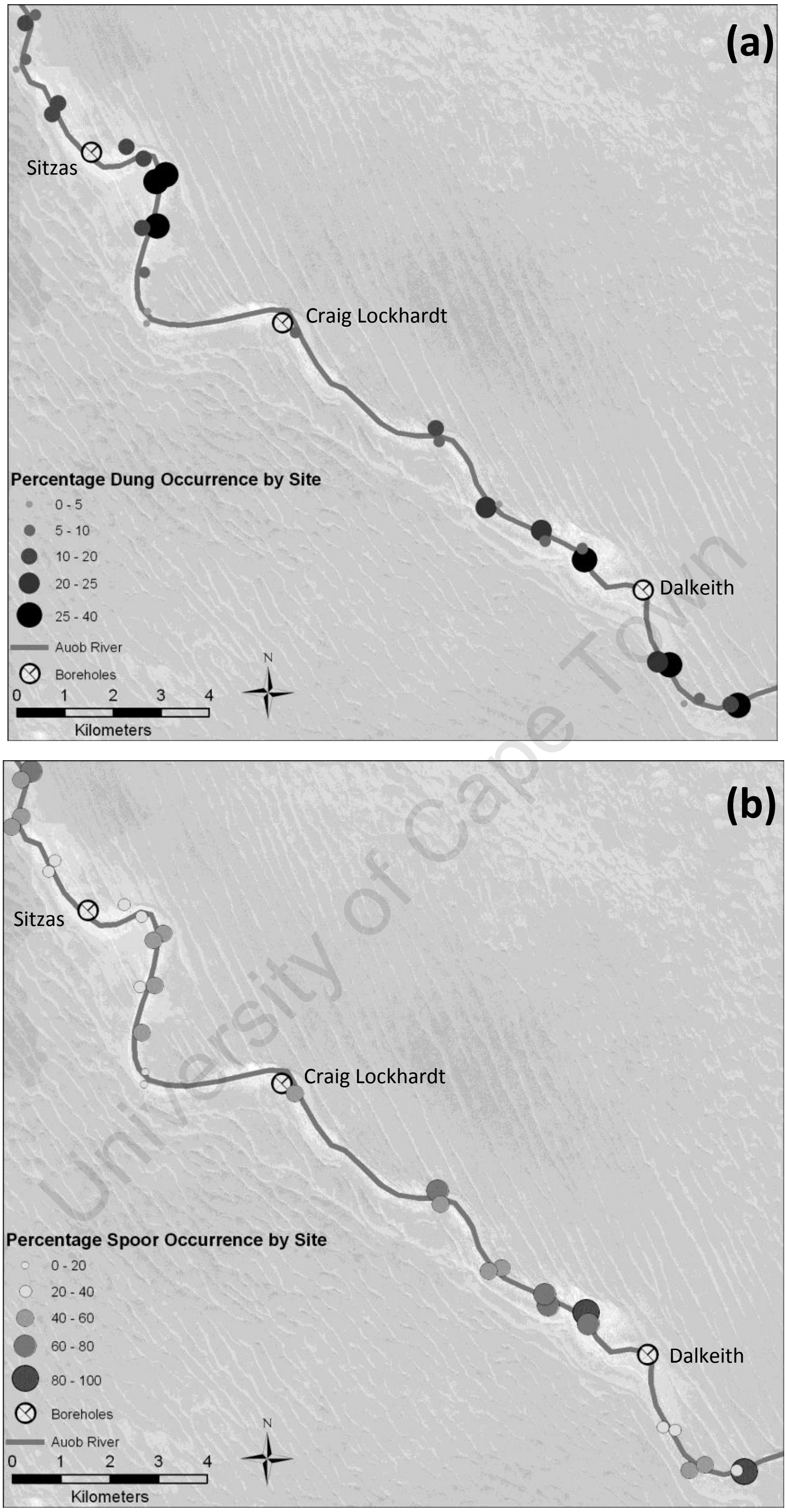

Figure 2: Percentage occurrence of giraffe dung (a) and spoor (b) along a 20 km stretch of the Auob Rover, KTP. Percentage occurrence is calculated as the percentage proportion of the width of the river that contained either giraffe dung or spoor in 10m by 10m quadrats.

Stable isotope ratios

δ^{13}C values for the two *Acacia* species are very similar but they differ significantly in their δ^{15}N values ($T_{(10,2)}$=3.697, $p < 0.01$). The stable isotope ratio of giraffe dung only similar to that of *A. haematoxylon* ($F_{(4,72)} = 11.51$, $p < 0.01$, Tukey HSD: $P < 0.05$) (Figure 3).

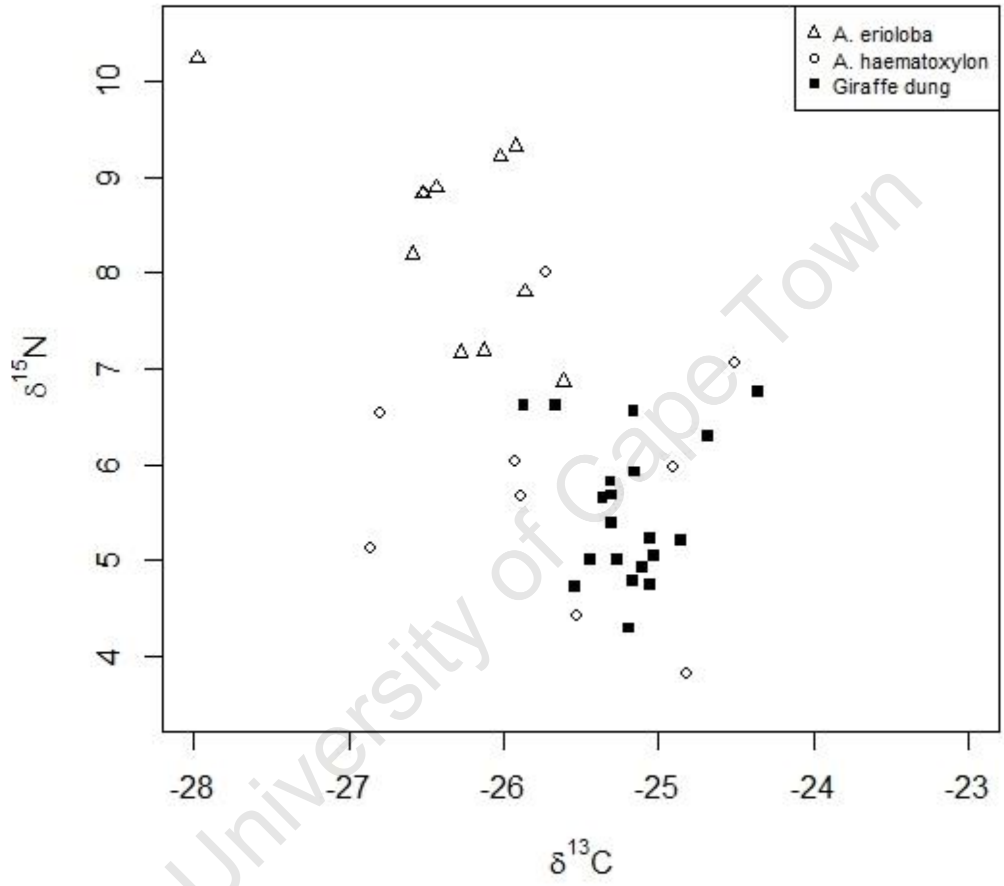

Figure 3: Distribution of δ^{13}C and δ^{15}N isotopic signatures for the leaves of *Acacia erioloba* and *Acacia haematoxylon*, as well as giraffe dung collected in the vicinity of both tree species.

Based on the model, the overlap in isotopic signatures between *A. haematoxylon* and giraffe dung supports by the modelled dietary proportions (Figure 4). Up to 100 % of the diet of the giraffes sampled consisted of *A. haematoxylon* (mean = 79 %, s.d. = 20.5 %), By comparison, very little of a giraffes diet consists of *A. erioloba* (mean = 21 %, s.d. = 20.5 %).

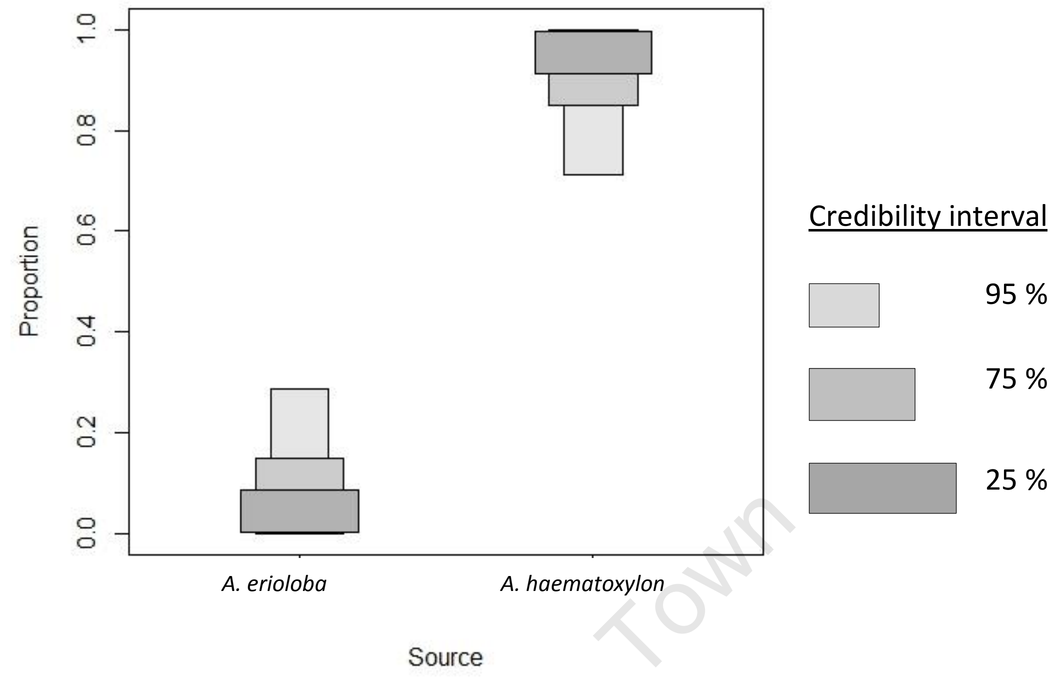

Figure 4: Proportions of *Acacia erioloba* and *Acacia haematoxylon* in the diet of giraffes in the Auob riverbed, Kgalagadi Transfrontier Park. Dietary proportions are derived from a dirichlet MCMC model that accounts for trophic fractionation and concentration dependence of each food source and is based on the δ^{13}C and δ^{15}N values of both food sources and faecal samples from giraffes in the area.

Nutritional value

Although not significant, *A. haematoxylon* has a slightly higher calorific value as well as a lesser percentage of condensed tannins ($T_{(18,2)}$=-1.74, p=0.098) (Table 1). These species do, however, differ in their proportions of carbon and nitrogen. The percentage of crude protein (a factor of percentage nitrogen) is higher in *A. erioloba* ($T_{(10,2)}$=2.745, $p < 0.05$), which also has a lower carbon to nitrogen ratio (C:N)($T_{(10,2)}$=-3.263, $p < 0.01$) . These data suggest that the forage quality of *A. erioloba* is higher than *A. haematoxylon*.

Condensed tannin concentration

These two tree species are very similar in terms of condensed tannin content ($T_{(18,2)}$=0.9145, p=0.37), and are both below the 5 % threshold proposed by Cooper & Owen-Smith (1985). This suggests that neither species is chemically well-defended.

Table 1: Chemical composition values for *Acacia erioloba* and *A. haematoxylon* leaf tissues taken during the early dry season in the Auob riverbed, Kgalagadi Transfrontier Park.

	mean ± s.d.		T-test statistics		
Variable	*A. erioloba*	*A. haematoxylon*	T stat	d.f.	p-value
Condensed tannins (%)	3.3 ± 1.0	2.9 ± 0.9	0.915	18	0.373
Calorie content (kJ.g-1)	19.5 ± 0.9	20.1 ± 0.6	-1.746	18	0.098
Nitrogen (%)	2.2 ± 0.2	2.0 ± 0.2	2.745	10	0.013 *
Carbon (%)	48.5 ± 1.2	49.8 ± 0.8	-2.804	10	0.012 *
C:N	22.1 ± 2.2	25.8 ± 2.8	-3.263	10	0.004 **
Crude Protein (%)	13.8 ± 1.3	12.2 ± 1.4	2.745	10	0.013 *

P < 0.05 = *; P < 0.01 = **; P < 0.001 = ***

Physical defences

Physical defence as spinescence is the most obvious difference between these two species. These species differ in terms of thorn length ($T_{(1049,2)}$=5.386, p < 0.001), but not in leaf length ($T_{(1049,2)}$=0.001, p=0.999); *A. haematoxylon* has a lower average distance between thorn pairs ($T_{(950,2)}$=11.021, p < 0.001) and a greater number of thorns per branch ($T_{(96,2)}$=-6.579, p < 0.01). This suggests that the thorns of *A. haematoxylon* are more densely arranged. Thorn pairs on *A. erioloba* had their thorn tips further apart from one another ($T_{(1049,2)}$=6.659, p < 0.01). The basal thorn diameter is much larger for *A. erioloba* ($T_{(1049,2)}$=31.621, p < 0.01), as its thorns have a swollen base, and will often fuse together. The *A. haematoxylon* branches had a greater proportion of broken thorns per branch ($T_{(96,2)}$=- -3.900, p < 0.001) compared to *A. erioloba*.

Taken together to calculate a spinescence index, *A. erioloba* appears to be significantly more spinescent than *A. haematoxylon* (U = 7.00, p < 0.05) (Figure 5). This suggests that *A. erioloba* has better anti-herbivore physical defences.

Table 2: Measures of physical defence in *Acacia erioloba* and *A. haematoxylon* in the distal 20 cm branches at a height of 3.5 m. Branches were taken from large trees (> 5 m height) in the Auob riverbed, Kgalagadi Transfrontier Park.

	mean ± s.d.		T-test statistics		
Variable	*A. erioloba*	*A. haematoxylon*	T stat	d.f.	p-value
Thorn length (mm)	20.90 ± 11.87	16.90 ± 11.73	5.386	1049	***
Leaf length (mm)	25.34 ± 11.12	25.34 ± 21.85	0.001	1049	-
Distance between thorn pairs (mm)	26.12 ± 18.76	16.58 ± 7.34	11.021	950	***
Distance between thorn pair tips (mm)	29.96 ± 18.17	21.31 ± 22.08	6.659	1049	**
Basal thorn diameter (mm)	2.44 ± 1.33	0.7 ± 0.31	31.621	1049	***
Number of thorns per branch	15.184 ± 2.773	25.837 ± 5.320	-12.428	96	***
Proportion of broken thorns per branch (%)	11.76 ± 13.81	22.43 ± 13.27	-3.900	96	***

$P < 0.05$ = *; $P < 0.01$ = **; $P < 0.001$ = ***

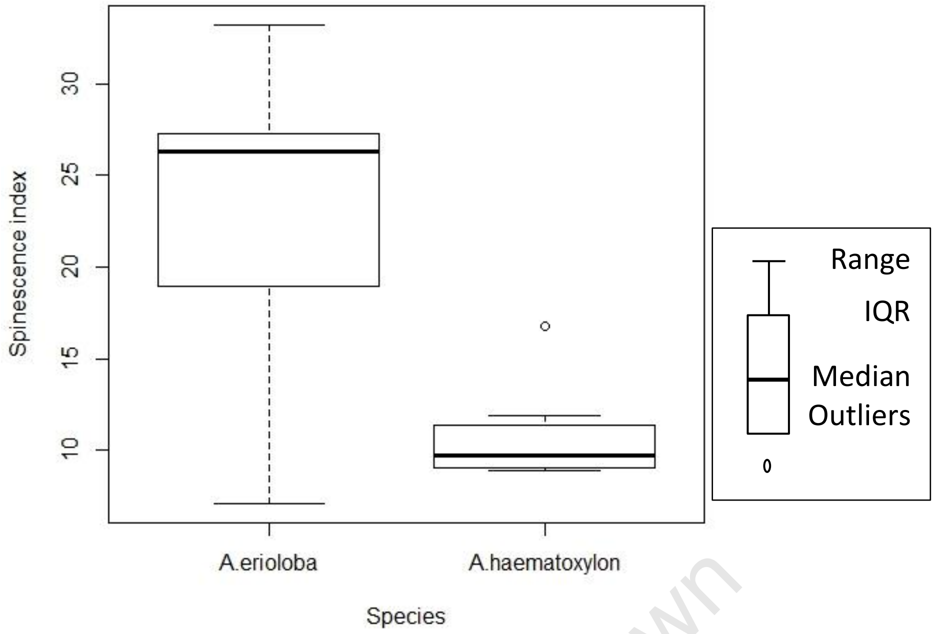

Figure 5: Spinescence indices for distal branches of *A. erioloba* and *A. haematoxylon* in the Auob riverbed, Kgalagadi Transfrontier Park. Spinescence index is calculated as (thorn length/leaf length) * distance between thorn pairs (adapted from Midgley *et al.*2001)

Discussion

As water-dependent ungulates, giraffes are limited as to where they can move in the Kalahari (Van Rooyen *et al.* 1994). In the Auob River valley, giraffes have reliable access to water as a result of the numerous boreholes that occur along the river. Since their release from Craig Lockhardt almost 30 years ago, giraffes have not moved out of the Auob duneveld. These Kalahari giraffes are not exhibiting the migratory behaviour that giraffes have been seen to do in other systems (Du Toit 1990; Le Pendu *et al.* 2000). The sedentary behaviour of giraffes is also supported by how slowly they have spread southwards since their release (G. Ellis *pers. comm*.).

Although Collinson (1983) predicts an increase in non-mobile, water-dependent game species as a consequence of uniformly spaced artificial water points, this had not been seen in the Auob duneveld prior to the introduction of giraffes (Mills & Retief 1984; Knight 1991). Now, while the presence of boreholes does not directly influence the structure of *Acacia* populations (Van Rooyen *et al.* 1994), as these access ground water sources, they may now be suffering from the presence of boreholes due to prolonged giraffe activity in these areas. Giraffes appear to concentrate around the Sitzas and Dalkeith boreholes. However, more thorough study into the dependence of giraffes on Auob river boreholes needs to be done.

Acacia species are the preferred browse for giraffe (Sauer *et al.* 1977; Cooper *et al.* 1988; Caister *et al.* 2003). While there are some *A. mellifera* in the area this would make up only a very small proportion of the diet of giraffe as *A. erioloba* and *A. haematoxylon* are far more common. My results show that approximately 80% of the diet of the giraffes that frequent the Auob riverbed consists of A. haematoxylon rather than *A. erioloba*.

Preference of giraffe for *A. haematoxylon* rather than *A. erioloba* is not due to calorific content as this does not differ between the species. Despite getting roughly the same number of kilojoules per gram of leaves, the difference in C:N makes *A. erioloba* leaves more valuable as a food source. In terms of nutrition, giraffes should prefer *A. erioloba*.

Chemical defences, in the form of condensed tannins (CTs) also do not differ between these species and neither have a concentration that is above 5 % concentration, which Cooper and Owen-Smith (1985) proposed as being they thresholds at which CTs may actually deter a mammalian herbivore. Thus, neither species appears to be chemically defended against herbivory, nor would either one be less attractive to a herbivore based on this alone.

Condensed tannins function to bind to the protein in the cell wall of plant tissue, thus deterring microbial digestion (Cooper & Owen-Smith 1985). To a ruminant, which relies on microbial digestion of its stomach contents to obtain energy, condensed tannins should be strongly avoided. However, few studies have been able to demonstrate this phenomenon in giraffes (see Sauer *et al.* 1982), while Parker (2004) has observed no avoidance of CTs. Proline compounds in the saliva of giraffes, which inhibit the reactivity of tannins is an adaptation that has allowed these animals to consume tanniferous vegetation (Robbins et al. 1987).

The most obvious difference between *A. erioloba* and *A. haematoxylon* is in the extent of their physical defences. The thorns of *A. erioloba* are longer and more robust than those of

A. haematoxylon, while the lengths of their leaves do not differ. Overall, *A. erioloba* is better defended by its thorns according to the higher spinescence index, which accounts for thorn length, leaf length and thorn density. This index has been useful in reconciling the higher thorn density of *A. haematoxylon* with the greater thorn length of *A. erioloba*. The relative importance of these is not considered by the index, but when added to the greater robustness of *A. erioloba* thorns, it becomes clear that the branches of *A. erioloba* do have superior physical defences.

Pellew (1984) and Cooper & Owen-Smith (1986) suggest that giraffes are impervious to physical defences by thorns because of their unique feeding method. However, physical defences seem to be the only explanation for why giraffes have such a high proportion of *A. haematoxylon* in their diet, despite having equal opportunities to exploit both species and *A. erioloba* having a greater nutritional value and having similar chemical defences to *A. haematoxylon*.

Giraffes appear to be less weary of *A. haematoxylon* thorns and will stick their head into the centre of the tree when feeding (*pers. obs.*), which is likely what caused the greater degree of broken thorns on *A. haematoxylon* branches. This contrasts the stance of a giraffe feeding on *A. erioloba*, who will stand at the periphery of the canopy to prune. Field observation of this behaviour needs to be quantified in order to confirm the hypothesis that physical defences substantially alter the feeding behaviour of giraffe between *A. haematoxylon* and *A. erioloba*. This evidence could then substantiate the hypothesis that feeding event of the same duration is far more costly to *A. haematoxylon* than to *A. erioloba* because of the damage done to branch structures closer to the centre of the canopy.

In the Kalahari, giraffes have only a few potential sources of food, and will tend to browse heavily on a single individual (*pers. obs.*). Giraffes can apply intense feeding pressure (Pellew 1984), and are known to reduce the growth rate of food sources (Birkett 2002). Giraffes are preferentially targeting *A. haematoxylon* in a landscape that has both *Acacia* species present because they have to take less care of the weaker *A. haematoxylon* thorns when browsing. This finding should raise concerns about the persistence of *A. haematoxylon* in the Auob duneveld, as Bond & Loffell (2001) found that extralimital giraffes are capable of causing selective mortality in their preferred *Acacia* species.

The tree form of *A. haematoxylon* has most likely never shared their distribution with giraffes, or any functional equivalent. There is thus a lack of co-evolutionary history which would have selected for better defences in *A. haematoxylon*, as are seen in *A. erioloba*. Clearly, *A. haematoxylon* trees in the Auob duneveld, the only place that they occur in tree form (Ross 1979), are facing imminent risk of over-exploitation by sedentary giraffes. With time, this could result in extinction of the *A. haematoxylon* tree form.

The loss of *A. haematoxylon* in the Auob duneveld would mean that giraffes would target *A. erioloba* more heavily and over time, which could lead to a similar fate for both species. However, even if only *A. haematoxylon* is lost from the system, the hybrid species, *A. erioloba x A. haematoxylon*, which is one of only eight endemic species in the Kalahari (Van Rooyen & Van Rooyen 1998), could then become extinct.

These two keystone species provide structural heterogeneity of the landscape, as well as limited sources of food, shade and habitat for many desert animals (Dean et al. 1999). Further biodiversity losses are a likely consequence of extensive damage to these trees, particularly for predatory or social birds that require arboreal nesting habitats. These losses should be of serious concern to park management, as ecotourism in the region relies heavily on the abundance and diversity of many of the species that make direct use of *Acacia* trees in the Auob river bed, which is adjacent to the main tourist roads in south of the park.

In most cases, giraffes do not concentrate their feeding in an area, but will rather traverse great distances (Du Toit 1990; Le Pendu *et al.* 2000). Thus, their impact is spread over the vast areas they are known to traverse and their diet often comprises upwards of 20 plant species (Sauer *et al.* 1977; Leuthold & Leuthold 1972; Parker *et al.* 2003). In areas of high giraffe density, a detrimental impact on vegetation structure has often been observed (Bond & Loffell 2001; Jacobs 2009). The presence of extralimital giraffes in KTP is likely to initiate a change in vegetation structure that would lead to a loss of both structural and plant species diversity, and ultimately harm the integrity and resilience of the ecosystem.

Conclusion

This study highlights the intense browsing pressure that extralimital giraffes are putting on *A. haematoxylon* trees in the Auob river bed. The sedentary behaviour of these giraffes is likely attributed to the presence of boreholes along the Auob riverbed, a relationship that needs further investigation to provide causal linkage. Physical defences appear to the primary mechanism of deterring giraffes from exploiting the more nutritious *A. erioloba*, while neither *A. erioloba* nor *A. haematoxylon* exhibit notable chemical defences as condensed tannins. The majority of the diet of these giraffes consists of *A. haematoxylon*, which seem to suffer substantial damage as a result of this intense feeding pressure. Selective mortality of in the future seems to be very likely if management action is not taken to decrease the browsing pressure of giraffes on this species.

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