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The Influence of Body Size on the Foraging Strategy of the Male African Savannah Elephant in Makgadikgadi Pans National Park, Botswana

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Abstract

Differences in feeding behaviour and species selection, due to the difference in body size, between the sexes for the African savannah elephants (*Loxodonta africana*) is well documented. However, there are also substantial body size differences within male elephants due to their two significant growth periods and continues growth. Therefore, the main objective was to explore how body size influences the foraging strategy between male elephants. Differences in feeding behaviour, selection of woody plant species and feeding patch choices of male African savannah elephants, according to sex and physical condition were examined during the dry season in Makgadikgadi Pans National Park in Botswana. Behavioural observations of feeding bouts were used to investigate the duration of the feeding bout, number of mouthfuls, the part of plant species eaten, foraging intensity index, feeding height and plant height. Vegetation sampling, using both a feeding plot and a control plot, where used to determine the woody species selection and the feeding patch choice. The youngest elephants (10-20 years) exhibited more selective feeding behaviour than older elephants (21-25 and 26+ years), as indicated by the lower foraging intensity index score, selection of smaller branches, browsing for a shorter amount of time, a lower number of mouthfuls, and a higher bite rate. The oldest males (26+ years) had the least diverse diet of woody plant species, with a small number of species dominating the diet, whereas the elephants 21-25 years of age had the widest range in their diet in term of woody plant species and a positive selection for *Philenoptera violacea* and *Dichrostachys cinerea*. The oldest elephants (26+ years) selected patches that offered the highest density of edible species, whereas the younger elephants (10-20 and 21-25 years) focused on patches with the largest number of preferred species and with a high richness of woody species present. These results suggest that body size is a vital factor in understanding dietary differences within male African elephants in terms of feeding behaviour, selection of woody plant species as well as feeding patch choices. This is consistent with the foraging hypothesis, which states that a larger body size enables consumption and digestion of higher quantities of low-quality forage while still obtaining sufficient nutritional benefits to match their energy demands.

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Introduction

The African savannah elephant (*Loxodonta africana*, henceforth termed elephant) exhibit pronounced sexual segregation, meaning that the males and females live apart outside the breeding season, which is commonly associated with body size dimorphism (Conradt, 1998; Stokke & Du Toit, 2002; Shannon et al., 2006b; Evans & Harris, 2012). Male elephants leave their natal herd, to roam alone or join a bull society, between 10 and 19 years of age, while female elephants remain in family units with their offspring (Lee & Moss, 1986; Evans & Harris, 2008). There are three main hypotheses that have been proposed to explain this sexual segregation (Main et al., 1996; Ruckstuhl & Neuhaus, 2000; Ruckstuhl, 2007): i) The predation risk hypothesis states that males are less vulnerable to predation due to their large size (Bleich et al., 1997; Ruckstuhl & Neuhaus, 2000). Therefore, male elephants tend to select habitats primarily for foraging opportunities in order to maximise productivity and growth, as well as reproductive potential (Duffy et al., 2006). ii) The indirect competition hypothesis (also called the scramble hypothesis) predicts that adult male elephants will be outcompeted by females in the collection of resources, resulting in a clear segregation in feeding location (Clutton-Brock & Harvey, 1978; Stokke & du Toit, 2000; Ruckstuhl, 2007). iii) The foraging hypothesis predicts that size dimorphism leads to sexual segregation due to different nutritional requirements (Mysterud, 2000; Shannon et al., 2006b), this hypothesis has generally received the most support (Stokke & du Toit, 2000; Shannon et al., 2006b; Mramba & Mlingi, 2021).

From birth onwards male elephants grow faster than females and at around 17 years, male elephants have already reached the same size as females of > 40 years (Lee & Moss, 1995; Evans & Harris, 2008). The male elephants have not only an additional significant increase in both height and weight between 20 and 30 years old, before completing the majority of their structural growth (Poole, 1994; Lee & Moss, 1995; Evans & Harris, 2008), but also a delayed fusion of their bones, allowing them to grow, though slowly, throughout their lives (Poole, 1994). Resulting not only in significant height difference between males and females, but also within the males. Numerous studies show that larger herbivores can subsist on forage of lower quality than smaller herbivores (e.g. Ruckstuhl & Neuhaus, 2000; Wilmshurst et al., 2000), based on the Jarman-Bell principle (Bell, 1971; Jarman, 1974). The Jarman-Bell principle states that body size influences feeding behaviour in terms of metabolic rate, the gut size and the time food remains in the digestive tract. Body size has a substantial influence on energy requirements due to the different growth rates, where the gut capacity remains a constant portion of the body mass, the absolute metabolic needs and retention period increases with body mass, but the metabolic rate decreases. This means that larger individuals have a reduced energy requirement per kg of body mass, which enables larger individuals to consume and digest higher quantities of low-quality forage and still obtain sufficient nutritional benefit from it to match their energy demands (Bell, 1971; Jarman, 1974). Therefore, the benefit of abundance will outweigh the costs of searching for high-quality forage, and thus larger individuals (i.e. older elephants) are predicted to choose quantity over quality in times of scarcity. Conversely, the smaller individuals (i.e. younger elephants) forage more selectively for high-quality food, both in times of scarcity and plenty (Du Toit & Cumming, 1999; Stokke & du Toit, 2000; Smit et al., 2007; Woolley et al., 2011).

Different requirements for nutrients and energy demands will lead to differences in the ways of obtaining the needed nutrients and the selection of plants (Ruckstuhl & Neuhaus, 2000; Woolley et al., 2009). The consumer's feeding behaviour theory, states that feeding behaviour can be classified into a series of decisions; i) where to search for food, ii) which food sources to select, and iii) how long to continue feeding on a food item before moving to another food source or continuing to search (Owen-Smith & Novellie, 1982; Stokke, 1999). These series of decisions result in their feeding behaviour being either i) non-selective, ii) frequency dependent or iii) frequency independent (Greenwood & Elton, 1979; Stokke, 1999). Non-selective feeding means that the different plants are eaten in proportion to their abundance. Frequency dependent can be either positive (i.e. abundant plant species are overrepresented in the diet) or negative (i.e. rarer plants species are used intensively). Therefore, when the common or rare species are exploited, it meets criteria ii and a situation where one particular species is always selected is described by criteria iii. Consequently, the effect of body size, age, and life-history stages drive foraging decisions, but also influence their use of the environment. For example, male elephants have the tendency to explore new areas, especially when there is a lack of resources. This explorative elephant behaviour increases the likelihood of conflict with humans and increases the management challenges (Osborn, 2004; Evans & Harris, 2012).

Although several studies have focused on foraging behaviour (Stokke & du Toit, 2000; Shannon et al., 2006b; Owen-Smith & Chafota, 2012; Mramba & Mlingi, 2021), habitat selection (Stokke & Du Toit, 2002; Shannon et al., 2006a; Evans & Harris, 2012), and species selection (Stokke, 1999; Owen-Smith & Chafota, 2012; Viljoen et al., 2013) of the African savannah elephant, there are still knowledge gaps. First, all studies, except the one by Evans & Harris (2012), focus on differences between female and male elephants only. Second, although the study from Evans & Harris (2012) looked at the effect of age, and thus size, on habitat selection of male elephants, it has been suggested that the focus of diet selection should be shifted from the broad scale of forage types towards the plant species level, as plant species vary considerably in their physical properties, chemical composition, and nutritional values (Hanley, 1997; Stokke, 1999). In other words, there is little attention given to the foraging behaviour and species selection within males, despite their explorative behaviour that causes management problems. Makgadikgadi Pans National Park (MPNP) is well suited to explore the foraging behaviour and the woody plant species selection within the male elephants populations, since the elephant population comprise of 98% males, either as single bulls or bull groups (Evans, 2019). Therefore, the goal of this study is to explore the influences of age and physical condition on the foraging strategy of the male African savannah elephant.

Following the foraging hypothesis, I predict that younger elephants and elephants with poorer physical condition will forage more selectively. Meaning that they, in order to minimise fibre intake, target thinner branches, eat for a shorter amount of time, take fewer bites per plant, and have a higher bite rate. According to the indirect competition hypothesis, I predict that the older elephants should target taller plants and feed higher than the younger elephants to avoid competition.

A woody species selection analysis will provide insights into the woody species selection patterns of male elephants across different age classes, both in terms of diet and habitat preferences. By comparing the analysis results for all age classes combined and for separate age classes, I expect to observe that younger elephants show a positive selection for a greater number of woody species due to the selection of foraging sources with the priority of quality over quantity based on the foraging hypothesis.

Furthermore, according to the foraging hypothesis, younger elephants are expected to consume a wider range of woody plant species to meet their dietary requirements and energy demands because of their selective feeding behaviour to minimise fibre intake. Finally, I predict that the younger elephants are more sensitive to the spatial distribution of resources in their environment compared to the older elephants. As a result, they are anticipated to adopt a frequency-dependent strategy, selecting feeding patches with the priority of quality of food over quantity.

Methods

Study area

Makgadikgadi Pans National Park (MPNP) is located in North-Eastern Botswana, between S19°32’-20°50’and E24°16’-25°07’, covering an area of 7,300 km^2. The climate is hot and dry for most of the year, with the dry season running from March till November and the rainy season from November till April. The regional average annual rainfall is 450 mm (Meynell & Parry, 2002). The park is connected to the Okavango Delta in the north, through the Boteti River which runs along the western boundary of the park and forms a sharp border with the community lands. After the resurgence of the Boteti River in 2009, having been dry for 19-years (Evans, 2019), MPNP has seen an increase in the number of elephants. Due to the irregular precipitation pattern in this area, this river is the major water source and therefore of great importance for the wildlife inhabiting the national park. The vegetation differs greatly throughout the park, in the west there is dense *Vachellia* and *Senegalia* dominated riparian forests and when moving towards the east, the woody species become sparser, resulting in grassland dominating areas on the eastern side.

The elephant population in MPNP is dominated by male elephants, comprising 98% of the total population and primarily consists of individuals aged between 10 and 35 years, with only a few individuals older than 36 years. These older males have reached reproductive age and often disperse from the area in search of mating opportunities when in must. While the breeding herds' numbers have been slowly increasing with the return of the Boteti River, the progress remains limited thus far. The density of elephants in the park varies throughout the year due to seasonal changes. During the dry season, when water is scarce, elephant herds tend to gather around the remaining water sources, resulting in a higher density of elephants in this area. However, as soon as the first rains arrive, the elephants disperse into the surrounding grasslands where there is a higher concentration of water and vegetation, leading to a decrease in their density in the area. The density of the elephant population in MPNP is also influenced by the migratory corridor the park is part of. The elephants move through this corridor in search of food and water, and their movement can be affected by a number of factors such as rainfall pattern and vegetation growth, which can vary from year to year.

Data collection

Data was collected over a period of four months, from mid-July to mid-November 2022. The elephants were located and observed from a 4WD vehicle by the principal researcher, with at least one research assistant present. Elephants where actively searched for in the area of the park, opposite the village of Khumaga (Figure 1), an area that has a high density of elephants, due to the accessibility to the Boteti River. In 2021 the fence on a part of the western border of MPNP got rebuilt. This fence crosses the Boteti River in several locations to allow access to the river for both wildlife and local communities. When an elephant, or group of elephants, was located within 150 m of the road they were observed for a few minutes to establish if they were alarmed or moving away. If they foraged calmy, data collection was started. The position of the observer was recorded with a GPS and the distance to the elephant(s) measured, using a range finder, to ensure they were within 150 meters of the road, before a focal individual was selected.

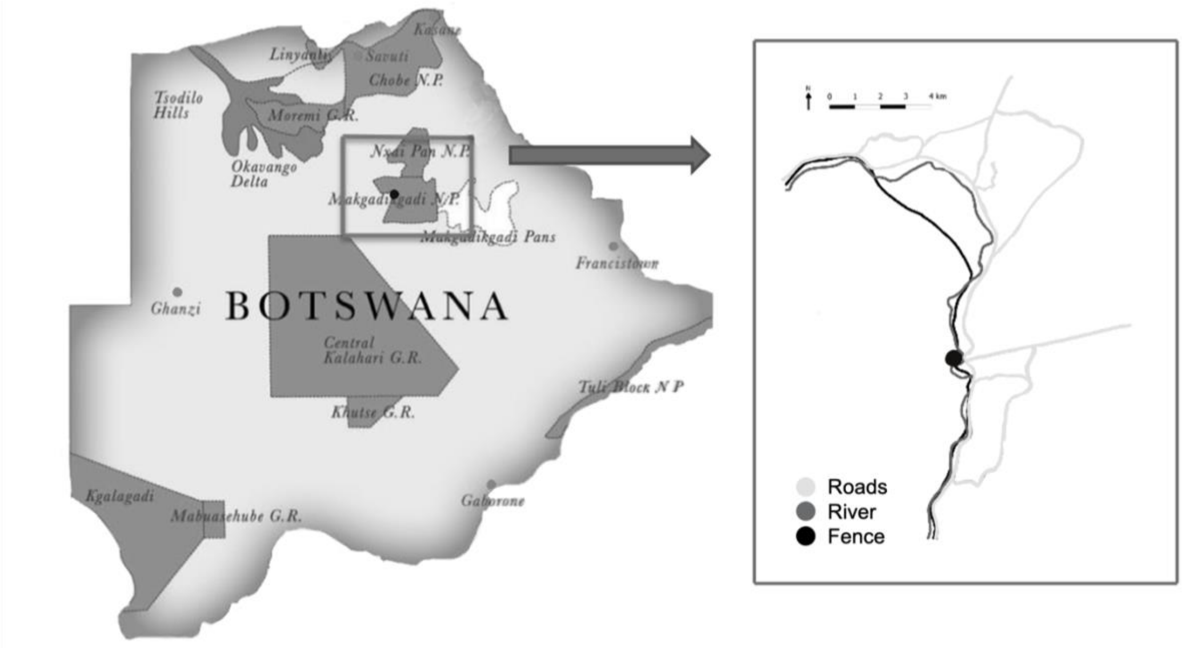

Figure 1: Map of Makgadikgadi Pans National Park's location in Botswana, with a zoomed in map of the Khumaga area. The black dot on each map represents Khumaga village.

The focal individual was selected based on visibility; the principal researcher observed the elephant with the best visibility. If a group of elephants was observed, in contrast to a single bull, the research assistant would collect data and observe the elephant with the next best visibility simultaneously. Whenever possible, the choice of focal individual was also influenced by the age of the elephant(s), in such a way that all age classes would be represented as equally as possible in the dataset. For the selected focal individual(s), the age (Table 1, Appendix 1) and physical condition (Table 2, Appendix 2) were noted. The age classes used in this study were carefully chosen to account for body size as accurately as possible. The first age group, consisting of individuals aged 10-20 years, comprises elephants that have recently attained independence from their herd, and are similar in size to adult female elephants. The second group, ages 21-25 years, includes elephants in their second significant growth phase and therefore exhibit a steep increase in body size. The last group, contained elephants aged 26 years and above, includes the largest individuals who have completed their significant growth phase and considered sexually mature.

Table 1: Age classification of male elephants (Adapted from Western et al., 1983; Lee & Moss, 1986; Moss, 1996;).

Age (yrs.)	Height (cm)	Description
10 – 20	204 – 243	Male rounded head shape starts to become noticeable.
21 – 25	244 – 275	Height increases significantly, head still slender and narrow.
26+	> 276	Hourglass-shaped head starts to form, circumference at the lip strikingly greater than younger males.

Table 2: Physical condition of each elephant based on body shape attributes (Adapted from Pitfield, 2017).

Class	Description
Thin to moderate	Shoulder blades, pelvic bone and full backbone are visible.
Moderate	Shoulder blades, pelvic bone and part of the backbone are visible.
Moderate to good	Shoulder blades, pelvic bone and no backbone are visible.

Data collection started with the first feeding bout on a woody species, which was defined as the period of time during which the elephant actively consumed parts of the woody plant. The observation period (feeding bout) started when the first bite was taken of a new woody species. During this feeding bout the plant species, as well as the part of the plant eaten, were noted. This included: i) only leaves, ii) both leaves and twigs, iii) branches, iv) fruits or seedpods, v) bark and vi) roots. Grazing was not included since it was three months into the dry season and thus no grass was available to forage. The feeding height and the height of the plant they were eating were estimated by extrapolating the estimated height of the elephant. The number of mouthfuls was counted, where each mouthful was the event of the trunk delivering food to the mouth. The foraging intensity was determined following a five-point index (Table 3) using the number of mouthfuls, an estimate of biomass removed as well as the duration of the feeding bout, modified according to the size of the plant that was eaten.

Table 3: The five-point scale foraging intensity index. Based on Shannon et al. (2006b).

Foraging intensity	Description
Highly selective	1-4 small mouthfuls of small branches and leaves, <10% of canopy removed and <1 min in duration.
Selective	5-10 mouthfuls of small branches and leaves, <10% of canopy removed and 1-3 min in duration.
Moderate	>10 mouthfuls, removal of some medium branches and 3-5 min in duration.
Intensive	>10 large mouthfuls, breaking of large branches and >5 min in duration.
Highly intensive	Removal of more than 50% of canopy, tree pushed over or debarked.

To ensure consistency, each focal individual was observed for a period of no more than 30 minutes. If the elephant moved too far away or the observation period was exceeded, a new individual was chosen for observation. Feeding bouts were considered complete if the elephant stopped feeding, which was indicated by the absence of chewing or reaching for new forage for over 30 seconds, or if the elephant moved away from the plant. If the 30-min observation period ended while the elephant was still feeding, the observation would continue until the feeding bout was completed, and only then would a new focal individual be selected for observation. Data was discarded if the focal individual showed any signs of disturbance due to the presence of the observers or other human sources.

Vegetation plots were used to determine the selection of woody plant species and feeding patches. These plots were circular with a radius of 5 m and were used to measure the available species composition. Two types of vegetation plots were used in the study. The first type, a feeding plot, was positioned with the recently browsed tree at the centre. Additionally, a control plot was established 50 m away from the feeding plot, positioned at a 90° or 270° angle, as determined by a compass, from the location where the elephant was observed feeding. The preferred angle was opposite to the direction from which the elephant left the feeding area unless obstacles prevented the control plot from being positioned there (Figure 2).

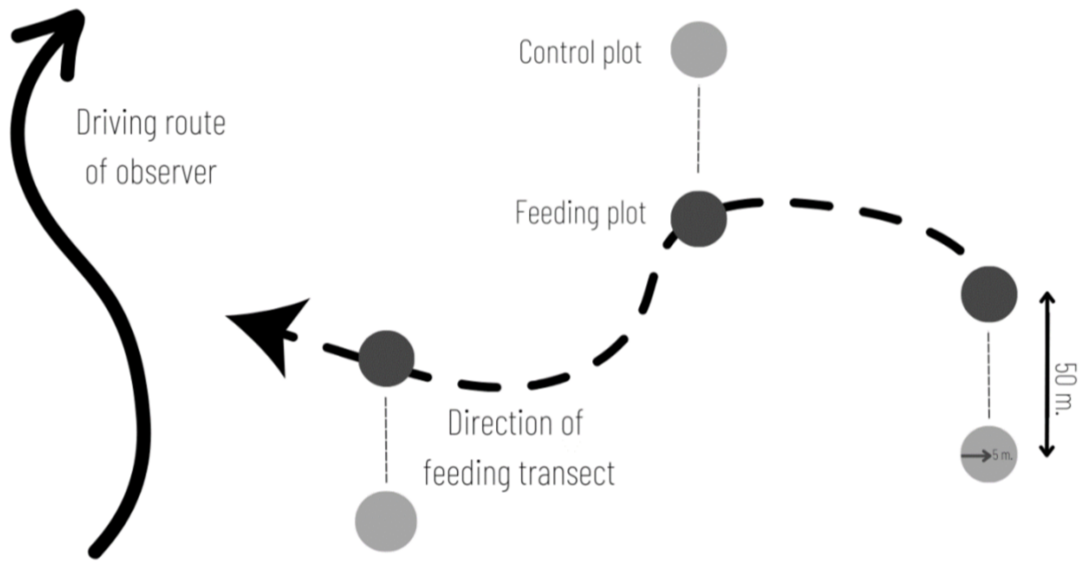

Figure 2: The study design illustrating the feeding plot (dark grey) and the control plot (light grey) in relation to the feeding transect of male elephants. Each plot had a radius of 5 m. The first feeding plot of the feeding transect had the same position as the first feeding observation. Adjacent plots were 50 m from their corresponding feeding plot at right angles of the transect path, alternatingly left or right. Each feeding plot was situated at least 50 m from the previous one with a recently browsed tree as centre point. Distances between plots were centre-to-centre distances. The figure is not drawn to scale.

When the elephant had been observed for sufficient time, the path it took, from start to finish, while feeding was marked as the feeding transect. Additional feeding and control plots were placed along the transect, with a recently browsed tree as the centre point (Figure 2). The corresponding control plots were then alternated in the direction of the previous control plots. These vegetation plots were ideally sampled directly after the elephant left the area. If this was not possible due to safety, they were sampled within 48 hours after the collection of the feeding data for the corresponding transect.

Statistical analysis

General Linear Mixed Models, using the lme4 package in R (Bates et al., 2015), were used to test whether age and physical condition affect the feeding height, the height of the plant eaten, the duration of the feeding bout, the bite rate, the number of mouthfuls, the part of species eaten, and the foraging intensity index. The elephant's ID was added as a random factor to account for pseudo-replications and an interaction between age and physical condition was included. The most parsimonious model was selected by starting with the full model and then dropping one variable at a time with backwards elimination. The different models generated were then compared to each other, with the use of the analysis of variance test (ANOVA), and the model with the lowest AIC value was selected as the optimal and final model. Tukey post hoc test was used to test for significant differences between different age classes.

To comprehensively examine the influence of body size on the woody species selection of male elephants, I conducted a species selection test using all age categories combined to identify common plant species preferred by male elephants of all body sizes using the Ivlev's electivity index was used according to the following formula.

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

Where u is the relative abundance of species i in the diet (use), and a is the relative abundance of species i in the environment (availability, Ivlev, 1961). The Ivlev's electivity index was chosen because it does not assume resource depletion and is bounded between -1 and +1. A value of 0 indicates a species consumed at the same proportion as its availability (Lechowicz, 1982). Any plant species that did not occur in the diet but did occur in the vegetation plots will have an electivity value of -1.0. Similarly, species that occurred in the diet but did not occur in the vegetation plots will have an electivity value of +1.0. Rare species, that only occur in the diet or vegetation plots, may be a due to sampling errors rather than actual selection by the elephants (Lechowicz, 1982). To prevent the chance of sampling errors, these rare species were excluded from the analysis. To test if the species were eaten differently from their available proportion, I used the chi-square goodness of fit test, which was followed by the Bonferroni-adjusted confidence intervals. The conditions to be able to use this test is that the expected frequencies should be five or more (Warner, 2012). Because several expected frequencies where below this threshold, six woody plant species that were utilised by the elephants were excluded from this analysis.

To test the woody species selection of the different age classes, I used the proportion of available units (availability) and samples of used resource units (use) per age class according to Manly's selection index, after which a standardised selection standardised selection index of woody plant species preferences, that adds up to one, can be calculated (Manly et al., 2007). The selection index chosen in this study was preferred to Ivlev's electivity index, as it provides a standardized selection index and avoids negative values that may hinder comparisons across different age groups. The standardised selection index (*B*i) was calculated according to the following formula.

$$Bi = \frac{wi}{\sum_{i=0}^{n} wi}$$

Where *wi* is the Manly's selection index and is obtained by dividing the proportion of the sample of woody plants used that belonged to species *i*, by the proportion of woody plant species *i* in the population. This selection index is defined as the estimated probability that a category *i* resource unit would be the next one selected if all types of resource units were equally available (Manly et al., 2007). A bootstrap algorithm was applied to compare the slope of the selection ratios between the different age classes (Stokke, 1999). An application written in Visual Basic was used to generate 1000 random bootstrap samples per category of size n from the empirical data set of the same size. For each bootstrap sample a new set of selection indices was generated, and a linear regression line was fitted. The slope value from this regression is a bootstrap replication of the original slope value representing the empirical data set. Thus, in total 3000 bootstrap replications were produced for the different age classes (Stokke, 1999). Finally, the values from each category were tested pairwise for any difference between the categories using the Kruskal-Wallis test.

The feeding site attractiveness value (FSAV) was used to determine if the different elephant age classes select for either quality or quantity in their feeding strategy (Stokke, 1999).

$$FSAV = \sum_{\mathrm{i}=0}^{\mathrm{n}} Pi * Bi$$

Where *Pi* is the proportion of *species i* and *Bi* is the standardized selection index for species *i* as calculated by the Manly selection index (Manly et al., 2007). As it is a comparison between two interdependent plot types, only the woody plant species that were actually consumed by the elephants were included. 'Empty' control plots (meaning $\Sigma \mathrm{pi} = 0$) were recorded in eight cases and they were excluded from this analysis, together with the corresponding feeding plots. To test for differences in sensitivity to resource distribution, I analysed the frequency distribution of FSAV values between the corresponding elephant feeding and control plots for the different age classes. As described above, a bootstrap algorithm was applied and for each bootstrap sample a new set of FSAV values were generated for both the feeding plots and control plots. The values, for the feeding plots and control plots from each age class, were then tested to determine whether they differed from each other using a two-tailed t-test. Finally, the slope of the FSAV values was tested to see if they differed from 1. All statistical tests were done in R version 4.1.2 (R Core Team, 2021).

Results

Feeding behaviour

The youngest elephants (10-20 years) foraged more selectively, targeting leaves and small branches, took fewer bites and spent a short amount of time at each woody plant (mean ± SE foraging intensity index 2.01 ± 0.10), while older elephants (21-25 and 26+ years) foraged more less selectively, commonly targeting medium-sized branches, took more bites and spent more time at each woody plant (21-25 years, mean ± SE foraging intensity index 2.35 ± 0.11 and 26+ years, 2.55 ± 0.14, Table 4, Figure 3A). The oldest males (26+ years) exhibited more intensive feeding behaviour than the youngest elephants (10-20 years), with 13% of the feeding bouts being categorised as highly intensive, by the foraging intensity index, for the oldest elephants and 2% for the youngest elephants ($X^2 = 6.50$, df = 2, $p < 0.05$). The oldest elephants (26+ years) consumed branches more often than the youngest elephants (10-20 years), with 47% of their feeding bouts categorized as branches, compared to 19% for youngest elephants ($X^2 = 12.15$, df = 2, $p < 0.01$). When the height of the plant increased, the foraging intensity decreased, and highly intensive feeding behaviour increased when roots were consumed (Table 4).

Table 4: Parameter estimates for the minimum adequate model (selected with AIC) of the effect of age, height of plant and, part of plant on the foraging intensity. The effect of age on the number of mouthfuls and the effect of age, feeding height and part of plant on the bite rate. The models are mixed effect models, with the Elephant ID as random factor to account for pseudo-replications. No significant effect of physical condition or interaction between age and physical condition of the male elephants for any of the models.

Fixed effects	**Estimate**	**SE**	**t value**	**P value**
Foraging intensity				
Intercept	0.862	0.165	5.212	< 0.001
Age 21-25	0.240	0.105	2.298	0.022
Age 26+	0.255	0.117	2.173	0.030
Height of plant	-0.049	0.013	-3.721	< 0.001
Part of plant	0.309	0.036	8.552	< 0.001
Mouthfuls				
Intercept	3.870	0.240	16.101	< 0.001
Age 21-25	-0.623	0.346	-1.807	0.263
Age 26+	-0.762	0.388	-1.965	0.036
Bite rate				
Intercept	6.604	0.485	13.622	< 0.001
Age 21-25	-0.164	0.285	-0.577	0.564
Age 26+	-0.351	0.319	-1.666	0.050
Feeding height	-0.583	0.140	-4.173	< 0.001
Foraging intensity	-0.567	0.123	-4.589	< 0.001
Part of plant	-0.583	0.116	5.004	< 0.001

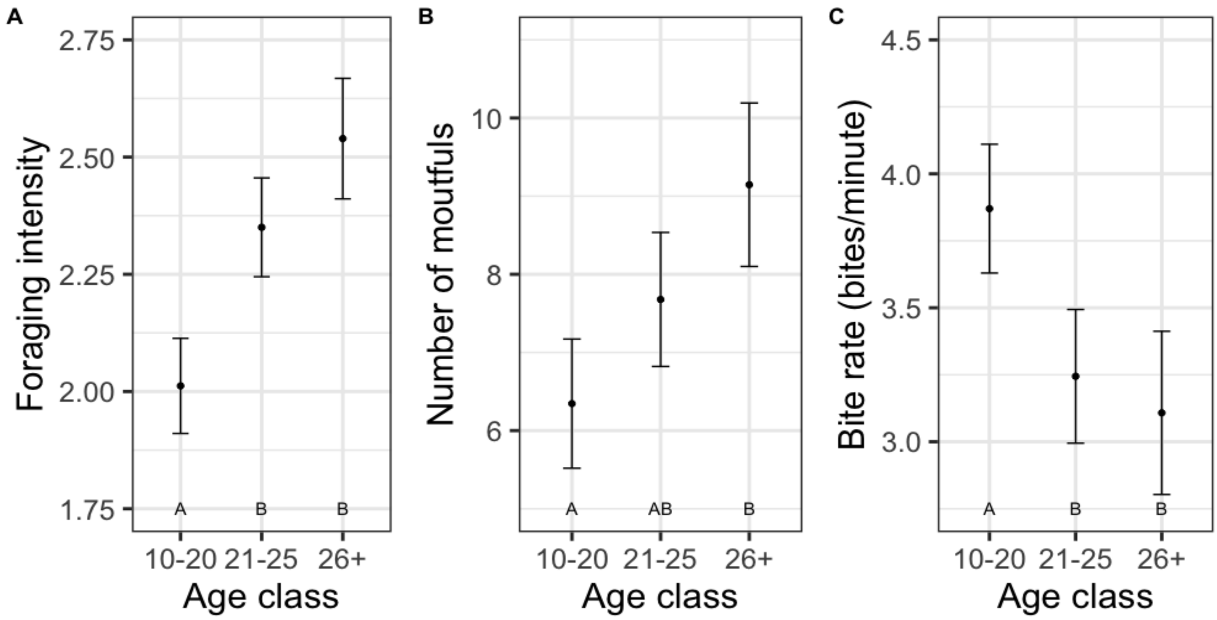

Figure 3: Mean (± SE) of the effect of age of male elephants on A) foraging intensity, B) number of mouthfuls and C) bite rate, with the ID of the elephants as random effect to account for pseudo-replications, extracted from the models. Different letters indicate significant differences (Tukey post hoc tests P < 0.05).

The youngest elephants (10-20 years) took fewer bites per plant (mean ± SE number of mouthfuls 6.35 ± 0.83) than the oldest elephants (26+, mean ± SE number of mouthfuls 9.15 ± 1.04, $p < 0.05$, Table 4, Figure 3B). The youngest elephants (10-20 years) had a higher bite rate (mean ± SE bites per minute 3.87 ± 0.24) than the oldest elephants (26+, mean ± SE bites per minute 3.11 ± 0.30, $p < 0.05$, Table 4, Figure 3C). The bite rate decreased when the feeding height increased, decreased when the intensity of the feeding bout increased and is lowest when roots were being consumed (Table 4).

Duration of feeding bout, plant height, feeding height, physical condition and interaction between age and physical condition was not included in any of the most parsimonious models (Table 4).

Woody species selection

Terminalia prunoides, *Vachellia nilotica*, *Grewia flava*, *Searsia tenuiervis*, *Dichrostachys cinerea* and *Senegalia mellifera* were consumed at a significantly higher proportion than they were available and *Gymnosporia senegalensis* and *Combretum* spp. were consumed at a significantly lower proportion than its availability (Figure 4A). The *Combretum s*pp. results should be interpreted with caution since it could only be identified to genus level. Despite their relative low diet ranks, based on the number of times they were consumed, *Terminalia prunoides* (9) and *Vachellia nilotica* (10) were the two species with the highest selection indexes, being browsed over three times more than availability (Appendix 3). *Dichrostachys* *cinerea* was the most commonly browsed species, comprising 40% of all the feeding bouts. Yet it only had an electivity index of 0.15, indicating the frequent occurrence of this species in the landscape (Appendix 3). Comparing the diet with control plots, the elephants selected areas with a dominance of the species with *Terminalia prunoides* and *Ximenia americana* (Figure 4B). *Vachellia nilotica* showed an electivity index of 1, this is because the species was only found in the diet and feeding plots and should therefore be interpreted with care. Areas with a dominance of the species *Combretum* spp*., Gymnosporia senegalensis,* and *Vachellia erioloba* seems to be unfavourable for feeding purposes (Figure 4B).

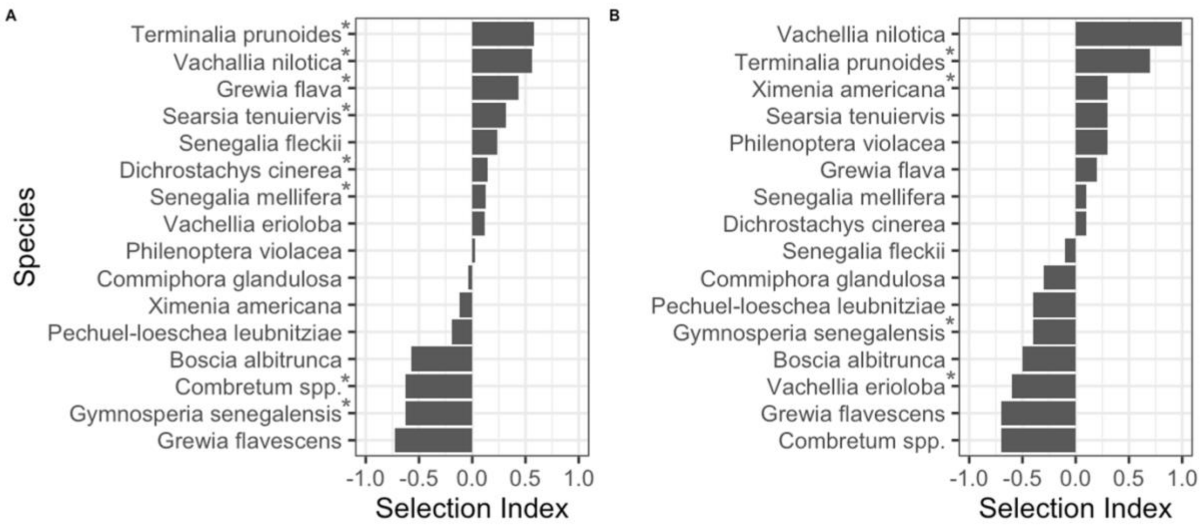

Figure 4: Ranked Ivlev's electivity selection index for plants comparing diet of male elephants with feeding plots (A) and diet with control plots (B). Rare species, eaten less than 5 times, were excluded from the analyses. Differences between proportional abundances of species in diet and plot types were tested using Pearson's chi-squared test with 10.000 permutations. (A: x^2 = 215.42, df = 15, P < 0.001; B: x^2 = 225.7, df = 15, p < 0.001. Stars after the species names indicate significant (p < 0.05) based on the Bonferroni corrections of p-values.

Of all the woody plant species that were included in the preference analysis, the youngest elephants (10-20 years) utilised 19 woody plant species, the elephants aged 21-25 years utilised 21, and the oldest elephants (26+ years) utilised 17 woody plant species. Elephants aged 21-25 years exploited a wider range of woody plant species than the other two age classes (Figure 5, Appendix 4), with preferences for *Philenoptera violacea and Dichrostachys cinerea* and selecting against *Gymnosporia senegalensis*. The youngest elephants (10-20 years) showed the second widest range of woody plant species being exploited, without showing a preference for any of the plant species and selecting against *Gymnosporia senegalensis*. The oldest elephants (26+ years) exploited the smallest range of woody plant species, also without significantly preferring any of the species and selecting against *Gymnosporia senegalensis (*Figure 5, Appendix 4, bootstrap replications, Kruskal-Wallis chi-squared = 2658.5, df = 2, p-value < 0.001).

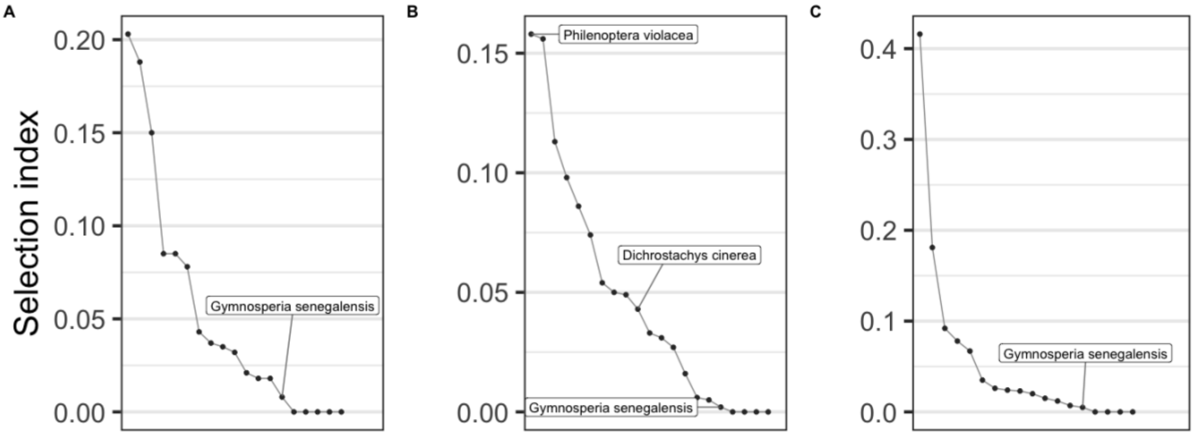

Figure 5: Ranked standardised electivity selection index for woody plants recorded for the three different male elephant age classes. A = 10-20 years. B = 21-25 years, C = 26+ years. Bootstrap replications, Kruskal-Wallis chi-squared = 2658.5, df = 2, p-value < 0.001. Species added as a label are significantly preferred or avoided. Steep slopes indicate high dominance of a few species in diet.

Feeding patch choice

The oldest elephants (26+ years) exhibited significant tenacity in selecting quality over quantity indicated by the lower slope value (Figure 6A, slope = 0.70, t = 72.98, $p < 0.001$), in contrast to the younger elephants who selected quantity over quality, indicated by the higher slope values. (Figure 6A, 10-20 years; slope = 0.88, t = -23.07, $p < 0.001$ and 21-25 years; slope = 0.85, t = -41.82, $p < 0.001$). All age classes had significant differences between the FSAV values for feeding plots vs control plots (Figure 6B, 10-20 years, t = -3.66, $p < 0.001$ and 21-25 years; -6.96, $p < 0.001$ and 26+ years; t = 9.10, $p < 0.001$) but the oldest elephants (26+ years) are the only age class that had higher FSAV values in the feeding plot compared to the control plots (Figure 6B, mean ± SD FSAV value 0.027 ± 0.016 and 0.025 ± 0.016. However, these values were also significantly lower than the FSAV values of the younger elephants (Figure 6B, 10-20 years; mean ± SD FSAV values 0.038 ± 0.018 and 0.039 ± 0.035 and 21-25 years; mean ± SD FSAV values 0.037 ± 0.018 and 0.038 ± 0.021).

The oldest elephants had a higher density of woody plant species in the feeding plots compared to control plots (26+ years, mean ± SE density 23.46 ± 3.32 vs 12.03 ± 3.44, F value = 5.74, $p < 0.05$, Figure 7A). The younger elephants (10-20 years and 21-25 years) had no significant difference between the number of available species between the feeding and control plots (10-20 years: F value = 0.21, p = 0.65 and 21-25-years: F value = 1.97, p = 0.16, Figure 7A). The density of the species in the feeding plots did not differ significantly between the different age groups (F value = 2.80, p = 0.06). For the younger age classes (10-20 and 21-25 years), the feeding plots had a higher richness of woody plant species compared to the control plots (10-20 years: mean ± SE richness 3.67 ± 0.19, vs 2.93 ± 0.19, F value = 7.22, $p < 0.05$ and 21-25 years: mean ± SE richness 3.90 ± 0.23 vs 3.23 ± 0.24, F value = 4.04, $p < 0.05$, Figure 7B). Species richness did not differ significantly between the feeding plots and control plots for the oldest elephants (26+ years, F value = 0.58, p = 0.45, Figure 7A), and the species richness in the feeding plots did not vary significantly across the different age classes (F value = 0.33, p = 0.72, Figure 7B).

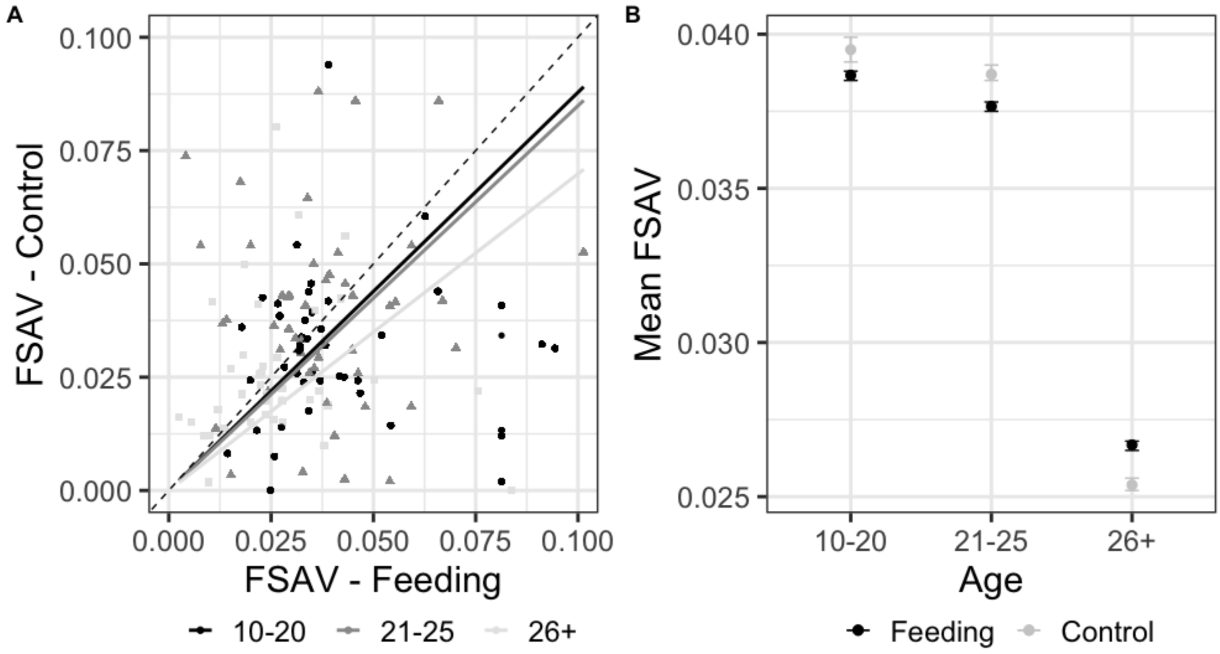

Figure 6: A) Comparison between the feeding site attractiveness values (FSAV) for feeding plots and control plots for the different age categories of male elephants. The dashed black line notes equal allocation of resources in the two plot types according to the FSAV method. The graph is zoomed in to improve the readability. B) Mean (± 95% CI) FSAV values for feeding plots and control plots for different age classes of male elephants.

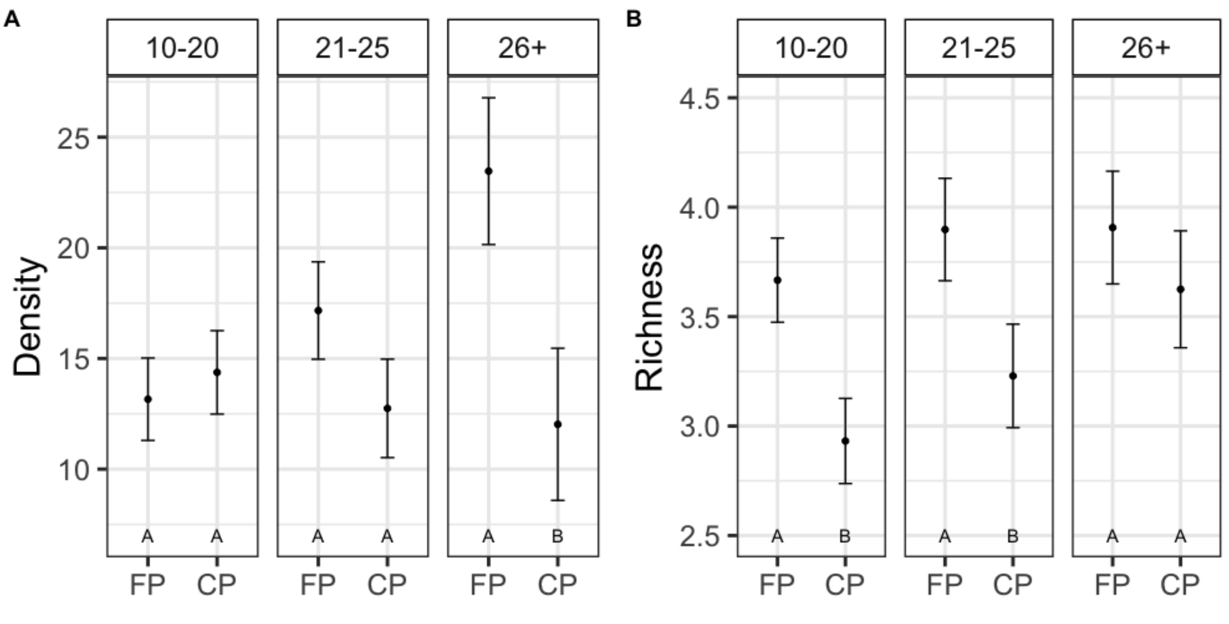

Figure 7: A) Mean (± SE) density of woody plant species per feeding plot (FP) and control plot (CP) for different age classes of male elephants. B) Mean (± SE) species richness of woody plants per feeding plot and control plot for different age classes of male elephants. Different letters indicate a significant difference. No significant difference between density or richness in feeding plots between the different age classes.

Discussion

In this study all the age classed showed feeding behaviour, woody species selection and feeding patch patterns that were qualitatively distinct from each other. The youngest elephants (10-20 years) were observed to feed more selectively compared to the older elephants (21-25 and 26+ years). The elephants in the age class 21-25 years consumed the most diverse diet with the least number of dominant species. Young elephants (10-20 and 21-25 years) maximised quality over quantity, in contrast to the oldest elephants (26+) who appeared to select quantity over quality.

Following the prediction that the foraging hypothesis is also relevant for male elephants, younger elephants and elephants with a poorer condition should forage more selectively to obtain enough qualitative forage to meet their energy demands. The oldest elephants (21-25 and 26+ years) foraged more intensively (i.e. a higher foraging intensity index score) and thus less selective than the youngest elephants (10-20 years). A study about the bite and break diameter by Stokke and du Toit (2000) also demonstrated that older male elephants forage less selective than younger males, by breaking off and foraging on resources with a larger diameter. The youngest elephants have a similar body size to that of female elephants and are therefore expected to show similar feeding behaviour. The study conducted in the Pongola Game Reserve and Phinda Private Game Reserve in South Africa supports this observation, revealing that female elephants exhibited selective feeding behaviour twice as much as males, while engaging in highly intensive feeding behaviour three times less often than males, according to the foraging intensity index. (Shannon et al., 2006b).

In addition to the lower foraging intensity index score, the youngest elephants (10-20 years) also took fewer bites per plants and had a higher bite rate, in contrast to the older elephants (21-25 and 26+ years) who took more bites and had a lower bite rate. The combination of fewer bites and a higher bate rate suggest that the younger elephants took smaller bites, indicating a more selective feeding approach. When looking at sexual differences, Stokke and du Toit (2000) and Shannon et al. (2006b) found similar results, where the females have a higher bite rate than the larger males. A higher bite rate is believed to reflect a higher relative energy demand, as a study done by Ruckstuhl et al. (2003) on big-horn sheep *(Ovis canadensis)* showed that lactating females had higher bite rates than adult males and non-lactating females.

In line with the indirect competition hypothesis, I predicted that the older elephants and elephants with a better physical condition target taller plants and feed higher than the younger elephants because the younger males outcompeted them. However, there was no significant difference in the feeding height of plants or height of plant they are feeding on in different age or physical condition classes, indicating that there is no indirect competition between these groups. This contradicts the findings of Stokke and Du Toit (2000), who found that sub-adult males do feed higher than adult males, but that the plants they are feeding on are similar in height. However, this finding contradicts the indirect competition hypothesis, which predicts that adult males should feed higher than sub-adults. Different studies find mixed results for sexual differences in feeding height among elephants. In the Serengeti National Park in Tanzania, Mramba and Mlingi (2021) found that the males were feeding higher than females, while in the Chobe National Park in Botswana and in the Pongola Game Reserve and Phinda Private Game Reserve in South Africa, two other studies showed no significant difference between the feeding heights of males and females (Stokke & du Toit, 2000; Shannon et al., 2006b). The similarity in feeding height between the different age classes can a result of the high abundance of low-quality forage that is available in Makgadikgadi Pans National Park. The availability of forage for the elephants during the study period might have remained above the level at which inter-age group competition would have an effect and low inter-age group competition may permit the smaller and larger individuals to forage at similar heights to meet their energy demands (Stokke & du Toit, 2000; Shannon et al., 2006b).

The Elephants in MPNP show a preference for the woody species *Terminalia prunoides*, *Vachellia nilotica, Grewia flava, Searsia tenuiervis, Dichrostachys cinerea, and Senegalia mellifera*, meaning they were all eaten at a higher rate than their availability. The preference, or presence, of *Dichrostachys cinerea* in the diet of the elephants has been observed in multiple studies and in different areas (De Boer et al., 2000; Makhabu, 2005; O'Kane et al., 2011; Woolley et al., 2011; Biru & Bekele, 2012; Owen-Smith & Chafota, 2012; Shrader et al., 2012; Seloana et al., 2018). Seloana et al. (2018) believes that the preference for *Dichrostachys cinerea* is not solely to its availability and high regrowth capacity, but also due to the low tannin concentration and high crude protein levels that *Dichrostachys cinerea* has. Where *Dichrostachys cinerea* accounts for 40% of all the feeding bouts and has a positive selection index score in my study, Stokke (1999) found a similar high selection index score for *Dichrostachys cinerea,* but in his study the species were eaten in accordance with their availability and Viljoen (2013) even reported a negative selection for *Dichrostachys cinerea*. Similar patterns are revealed for *Terminalia prunoides*, Stokke (1999) found a high selection index score, but the species was only eaten according to its availability. In contrast, Viljoen (2013) found a negative selection index. As indicated by numerous studies reporting frequent consumption of Vachellia nilotica and Senegalia mellifera (O'Kane et al., 2011; Shrader et al., 2012; Mramba et al., 2017; Seloana et al., 2018), Vachellia and Senegalia species appear to be favoured widely (Ruggiero, 1992; De Boer et al., 2000). Seloana et al. (2018) believes that the preference for *Vachellia nilotica* comes not only from its high nutritional quality but also because of its high palatability:tannin ratio, meaning it has a high proportion of palatable components (protein, fats, and sugar in the form of glucose, fructose, and sucrose) and a low proportion of tannins. Only one other study has documented consumption of *Grewia flava* and this study also reported a preference for this species (Seloana et al., 2018). Lastly, I found a negative selection for *Gymnosporia senegalensis*, which coincides with the findings of Shrader et al. (2012) and Viljoen et al. (2013). Having multiple species that are consumed at a significantly higher or lower proportion than their availability in the elephants' diet is comparable to the findings of other studies (Shrader et al., 2012; Viljoen et al., 2013; Seloana et al., 2018).

By comparing the woody species selection analyses for all age classes combined and for separate age classes, I expect to observe that younger elephants show a positive selection for a greater number of woody species due to the priority of selecting foraging sources with the priority of quality over quantity. The results revealed both similarities and differences in the species selection patterns of male elephants between the analyses conducted with all age categories combined and those conducted separately for each age category. Notably, *Philenoptera violacea* was not selected negatively or positively by all age classes combined, whereas the elephants 21-25 years old showed a high selection for this species, mainly exploiting the species for its leaves. The leaves of *Philenoptera violacea* were found to have a high level of nitrogen, indicating it is a good source of crude protein (Gama et al., 2019). *Dichrostachys cinerea* was also positively selected only by the age class 21-25 years, even though it does show a positive selection for all age classes combined. *Dichrostachys cinerea* also contains a high level of crude protein as well (Seloana et al., 2018), which is a crucial nutrient for growth, thus justifying the logical choice of a positive selection for these species. All three age classes showed negative selection, consistent with the results of the woody species selection analysis conducted with all age classes combined.

Following the foraging hypothesis, I predicted that the younger elephants (10-20 years) would have the widest range of woody plant species in their diet and the oldest elephants (26+ years) the smallest. The oldest elephants utilised the lowest number of woody plant species and their diet was strongly dominated by a few species as predicted. However, the youngest elephants had the second lowers number of woody plant species, and the age category 21-25 years had the widest range of woody plant species in their diet with a low number of dominant species. This is contradicting the prediction that the youngest age class would have the highest diversity and the least number of dominant species in their diet. A potential explanation for this unpredicted outcome could be that elephants in the age class 21-25 years are in a strong and significant growth period (Poole, 1994; Lee & Moss, 1995; Evans & Harris, 2008). While the youngest age class elephants show an average growth of 40 cm in 10 years, the 21-25 years old elephants can grow up to 30 cm in just 4 years (Lee & Moss, 1986; Moss, 1996; Western et al., 1983). To account for this high growth rate, it is likely that they will be selective for higher quality forage or specific nutrients to accommodate this growth by incorporating more species into their diet. The higher number of species in their diet suggest that they remove less biomass per plant and thus minimise fibre intake, but this is only partially true, as they foraged more intensively than the youngest elephants, suggesting they are seeking out nutrient rich food and minimise fibre intake.

Lastly, I predicted that the younger elephants were more sensitive to the spatial distribution of resources in their environment compared to the older elephants. Therefore, I anticipated that they would adopt a frequency-dependent strategy, selecting feeding patches with the priority of quality of food over quantity. Initial results indicate that the oldest elephants (26+ years) selected feeding patches with higher-quality plants than the younger elephants (aged 10-20 and 21-25 years). However, when analysing the average quality of the feeding patches, it became apparent that the oldest elephants had much lower quality values compared to the youngest elephants. Therefore, the prediction is supported in that that the youngest elephants (10-20 and 21-25 years) are actively seeking out feeding patches with a higher concentration of preferred plant species. Moreover, they showed a preference for locations within these patches that had greater species diversity of woody plant species, potentially indicating a strategy to maximize their access to a variety of nutrients in their diet. Unlike the younger elephants, the older elephants (26+ years) appeared to prioritize the overall quantity of plants in their choice of feeding patches, rather than the specific species or diversity of species within the patch. Meaning that the youngest elephants were more concerned with the quality of their food, while the oldest elephants were more focused on quantity. While it is true that large-bodied herbivores can tolerate low-quality food, it does not necessarily mean that they prefer it over high-quality food (Bell, 1971), In fact, the food plots selected by the oldest elephants (26+ years) contained a greater number of high-quality plant species compared to their control plots. This suggests that the oldest elephants still prioritize quality even though they initially seek out larger quantities of food.

Conclusion

In summary, this study emphasises the significance of body size in feeding behaviour, woody species selection and feeding patch choice within male African savannah elephants. The oldest elephants (26+ years) were less selective feeders, targeted larger branches, browsed for a longer time, took more bites per plant, and had lower bit rates, indicating that they take larger bites, compared to the younger elephants (10-20 and 21-25 years). The oldest elephants (26+ years) had a smaller range of woody species in their diet and their feeding patches had a lower quality with a higher density of woody plant species, in contrast to a wide range of woody species and feeding patches with a higher quality and higher species richness for the younger elephants (10-20 and 21-25 years). Indicating that the oldest elephants approach their foraging strategy to select for quantity over quality and the younger elephants select for quality over quantity. These results indicate that the foraging hypothesis can be useful in predicting foraging behavioural differences among different age groups of male African savannah elephants.

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Appendixes

Appendix 1. Photo guide for age classification

10-20 yrs. - Male rounded head shape starts to become noticeable

21-25 yrs. - Height increases significantly, head still slender and narrow

26 + yrs. - Hourglass shape head starts to form, circumference at the lip strikingly greater than younger males.

Appendix 2: Photo guide for physical condition classification

2.5 - Thin to moderate: Shoulder blades, pelvic bone visible and full backbone are visible

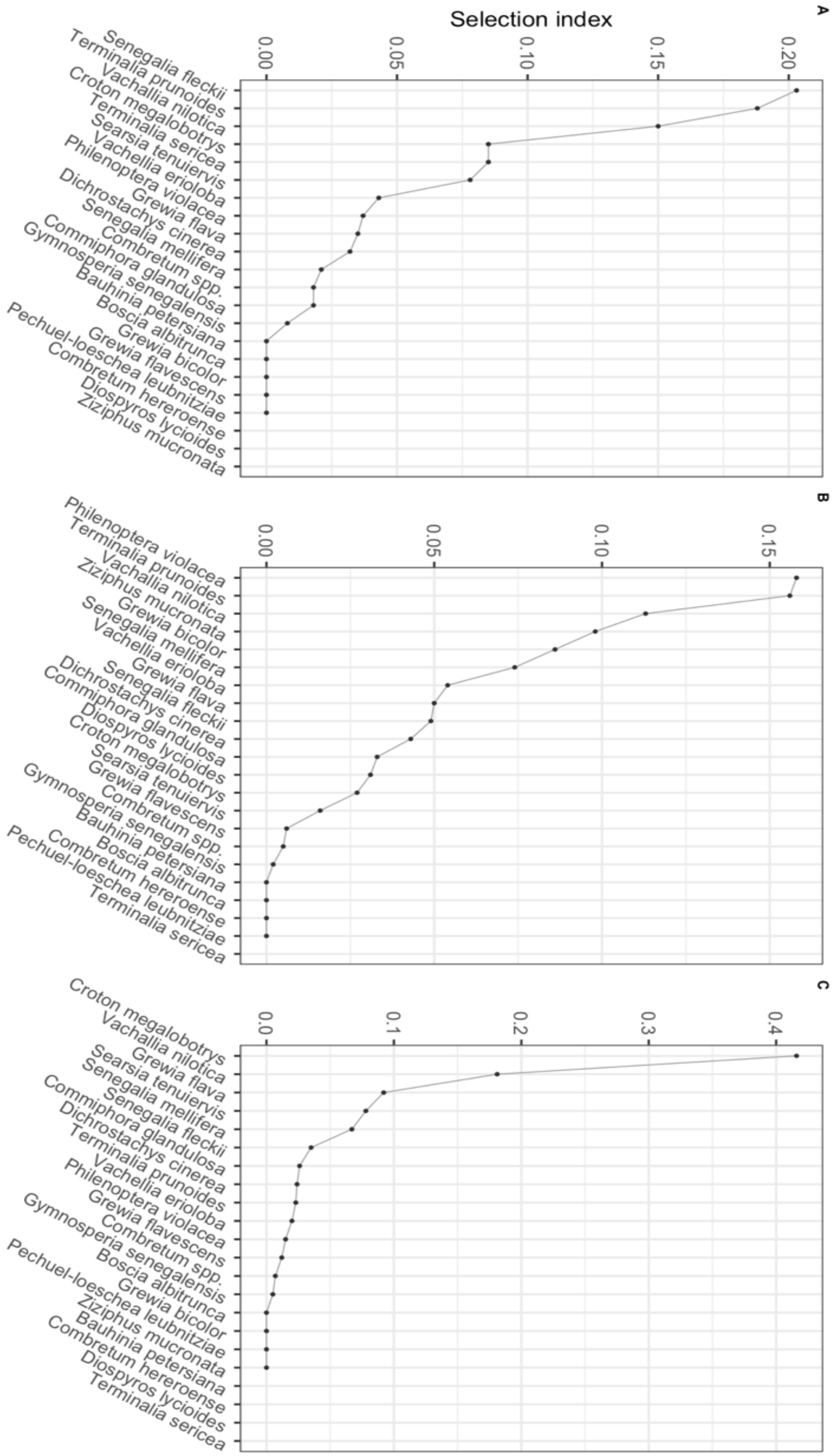
3 - Moderate: Shoulder blades, pelvic bone and part of backbone are visible

3.5 - Moderate to Good: Shoulder blades, pelvic bone and no backbone are visible

Appendix 3: Proportion (%) and rank, based on the number of times it is consumed, of species in elephant diet and vegetation plot types in alphabetical order.

	Diet		**Feeding plot**		**Control plot**	
	%	Rank	%	Rank	%	Rank
Bauhinia petersiana	-	-	0.4 %	20	0.7 %	17
Boscia albitrunca	0.3 %	20	5.2 %	6	4 %	12
Catophractes alexandri	-	-	-	-	0.2 %	20
Combretum imberbe	-	-	-	-	0.2 %	21
Combretum hereroense	-	-	0.2 %	24	-	-
Combretum spp.	0.8 %	14	6.1 %	4	6.1 %	6
Commiphora glandulosa	1.3 %	12	3.8 %	12	4.9 %	10
Croton megalobotyrs	0.7%	16	1 %	18	0.2 %	22
Dichrostachys cinerea	42 %	1	16 %	1	16.3 %	1
Diospyros lycioides	0.7 %	17	0.4 %	21	0.2 %	23
Gardenia volkensii	-	-	-	-	0.2 %	24
Grewia bicolor	0.8 %	15	2.7 %	16	0.9 %	16
Grewia flava	8.0 %	3	5.2 %	7	6.5 %	4
Grewia flavescens	0.3 %	21	5.3 %	5	5.4 %	7
Gymnosporia senegalensis	5.7 %	5	5.2 %	8	4.9 %	11
Pechuel-loeschea leubnitziae	1.6 %	11	4.8 %	11	6.5 %	5
Philenoptera violacea	5.1 %	6	3.2 %	13	4 %	13
Searsia tenuiervis	6. 1%	4	7.3 %	3	7.5 %	3
Senegalia fleckii	1.3 %	13	2.5 %	17	3.3 %	14
Senegalia mellifera	4.3 %	7	5 %	10	5.4 %	8
Terminalia prunoides	3.8 %	9	3.2 %	14	2.6 %	15
Terminalia sericea	0.2 %	11	0.4 %	22	0.7 %	18
Vachellia nilotica	2.6 %	10	3.1 %	15	-	-
Vachellia erioloba	9.7 %	2	13 %	2	13.5 %	2
Ximenia americana	4.1 %	8	5.2 %	9	5.1 %	9
Ziziphus mucronate	0.7 %	19	0.8 %	19	0.7 %	19
'Unknown'	0.7 %	18	0.4 %	23	-	-

Appendix 4: Ranked selection index with woody plant species names.



Ranked standardised electivity selection index for woody plants recorded for the three different elephant age classes. A = 10-20 years. B = 21-25 years, C = 26+ years. Bootstrap replications, Kruskal-Wallis chi-squared = 2658.5, df = 2, p-value < 0.001.

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