

## Research Article

# Seasonal Selection Preferences for Woody Plants by Breeding Herds of African Elephants (*Loxodonta africana*) in a Woodland Savanna

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To evaluate dynamics of elephant herbivory, we assessed seasonal preferences for woody plants by African elephant breeding herds in the southeastern part of Kruger National Park (KNP) between 2002 and 2005. Breeding herds had access to a variety of woody plants, and, of the 98 woody plant species that were recorded in the elephant's feeding areas, 63 species were utilized by observed animals. Data were recorded at 948 circular feeding sites (radius 5 m) during wet and dry seasons. Seasonal preference was measured by comparing selection of woody species in proportion to their estimated availability and then ranked according to the Manly alpha ( $\alpha$ ) index of preference. Animals demonstrated a selection preference in feeding on woody vegetation, and *Grewia hexamita*, *Grewia bicolor*, *Grewia flavescens*, and *Grewia monticola* were selected consistently more over all seasons. In addition, our results indicate that elephant herds have a low preference for at least some of the woody species prone to extirpation and that feeding preferences for woody plants do not account for the association of elephants and riparian fringe habitat.

## 1. Introduction

The transformed and fragmented South African landscape has resulted in a lack of suitably sized protected areas for elephants, thus creating major challenges for managing elephant populations relative to their effects on ecosystem processes, vegetation structure, and species of plants and other animals [1]. Prolonged periods of locally high densities of elephants can alter vegetation structure, and the impact can intensify, especially when animals are confined to small or medium sized fenced reserves [2, 3]. This is especially challenging in fenced reserves smaller than 1000 km<sup>2</sup> to which elephants have been reintroduced by 2001 in South Africa [4, 5]. Subsequent to the introduction of elephant in these small areas, these savannas are exposed to intensive management, and decision makers are increasingly challenged to choose options which can balance needs of locally high elephant

numbers with the maintenance of vegetation and ecosystem diversity.

Elephant feeding behaviour in combination with natural processes, for example, climate and fire, is the architects in different African landscapes and has been the focus of numerous studies describing elephant diet [6–11]. However, many of these studies failed to define selection preferences at the plant species level and only describe preferences at the broad level of growth forms [12, 13]. This gap resulted in incorrectly assigning certain responses in the environment to elephants [14]. White and Goodman [15] used quantitatively collected field data and concluded that differences in the structure and the diversity of woody vegetation in Mkhuzo Game Reserve, South Africa, were unrelated to elephant use. Similarly, Landman et al. [16] used a microhistological analysis of faecal material to determine composition of elephant diet and thereby refuted the popular belief that elephant

herbivory was the major driver of decline of important plants in the Addo Elephant National Park, South Africa.

Food resources are distributed heterogeneously across the landscape and vary in quality and quantity between seasons [14] which might explain elephants altering their selection from green grass during wet seasons to browse foliage during dry seasons [18–20]. Therefore, it could be assumed that elephants might feed through a wide variety of vegetation communities for food species that permit efficient and effective nutrient intake and that specific plants meeting these criteria vary seasonally. Currently, only limited information is available regarding seasonal-dependent variability in food of African elephants, although such information would be important to avoid making suboptimal management decisions.

We describe the seasonal relative availability and species-specific preference for woody vegetation by free-ranging African elephant breeding herds in the southern part of the Kruger National Park (KNP).

## 2. Material and Methods

**2.1. Study Area.** Data were collected from March 2002 to September 2005 in the KNP within the Granite Lowveld, Delagoa Lowveld, Tshokwane-Hlane Basalt Lowveld, Gabbro Grassy Bushveld, and the Northern Lebombo Bushveld [21]. The KNP covers an area of 19000 km<sup>2</sup> and can be longitudinally divided into resistant granites in the west succeeded by Ecca shales, basalt, and rhyolites in the east that give rise to different soil types and associated flora and fauna [22]. Average rainfall varies from 500 to 750 mm/year [23]. From May to July is the early dry season, the late dry season is from August to October, the early wet season is from November to January, and the late wet season is from February to April [24].

**2.2. Study Animals.** We selected, as our focal herd, the first breeding herd of elephants in the southern region of KNP spotted from a helicopter after the take-off. On January 14, 2001, the matriarch was fitted with a VHF radio collar (Africa Wildlife Tracking cc, South Africa) which was replaced in August 2002 with a GPS satellite collar (Africa Wildlife Tracking cc, South Africa) for easier location. We trailed the breeding herds on foot which provided us the means to study patterns of woody plant use in all terrains, thus eliminating the sample bias that would be introduced if elephants were studied only in areas where elephants were regularly seen or areas that were easily accessible by road. To ensure that the collared group's feeding behaviour was not atypical, following the same protocol as above, we recorded selection of noncollared breeding herds randomly sighted in the study area. To avoid collecting from the same breeding herds, we included data from about 20 different herds. Different individuals joined and left the core group from time to time, and contacts with these breeding herds were not continuous throughout the study period. Family groups (breeding herds) are defined as individuals who are seen together more than 70% of the time [25]. We did not collect

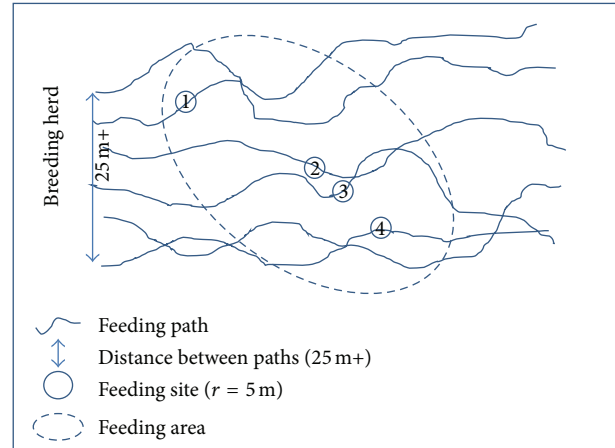


FIGURE 1: A diagram illustrating sampling methodology, that is, feeding paths, feeding area and feeding site.

data of all-male groups or solitary elephant bulls, as sexual dimorphism affects their feeding behaviour [26].

**2.3. Data Collection.** We collected data during two wet seasons and two dry seasons in the early and late phases of each season, commencing in March 2002 and ending in September 2005. Two criteria were used to define a *feeding area* prior to the recording of floristic data (Figure 1).

Firstly, average feeding time measured among at least three individuals in the breeding herd had to exceed 1.5 min. Secondly, the distance between feeding paths within a feeding area had to exceed 25 m. Individual elephants in breeding herds tend to move closer together as a unit when not feeding and especially when crossing open areas or when they perceive imminent danger (J. J. Viljoen, H. C. Reynecke, pers. obs.). Recording data during real-time observations following these criteria eliminated suppositions of the source and nature of the impact due to, that is, chance, accidental, fire, frost, droughts, natural mortality, other herbivores, or elephant bulls [27]. We then identified, using current field guides [28], all woody plants, available to elephants in feeding sites and recorded them as either utilised or not utilised. Feeding sites had a radius of 5 m (area = 78.5 m<sup>2</sup>) measured from the sighting of the first elephant from the herd feeding, assuming that this area would contain the impact of an individual [6, 26].

Once data had been collected at the feeding site observed to have been browsed, an alternative feeding path in the feeding area was followed to limit the chance of collecting data from the same individual's selection. We collected data from four feeding sites selected in the feeding area occupied by a herd to allow for a better representation of the woody species present in the area. Cerling et al. [29] reported that isotope patterns in hairs of different individuals from the same elephant herd were similar which represented dietary preferences and behaviour of the entire group. Similarly, Buss [18] concluded that food habits and other behaviour of individuals within each group were similar based on

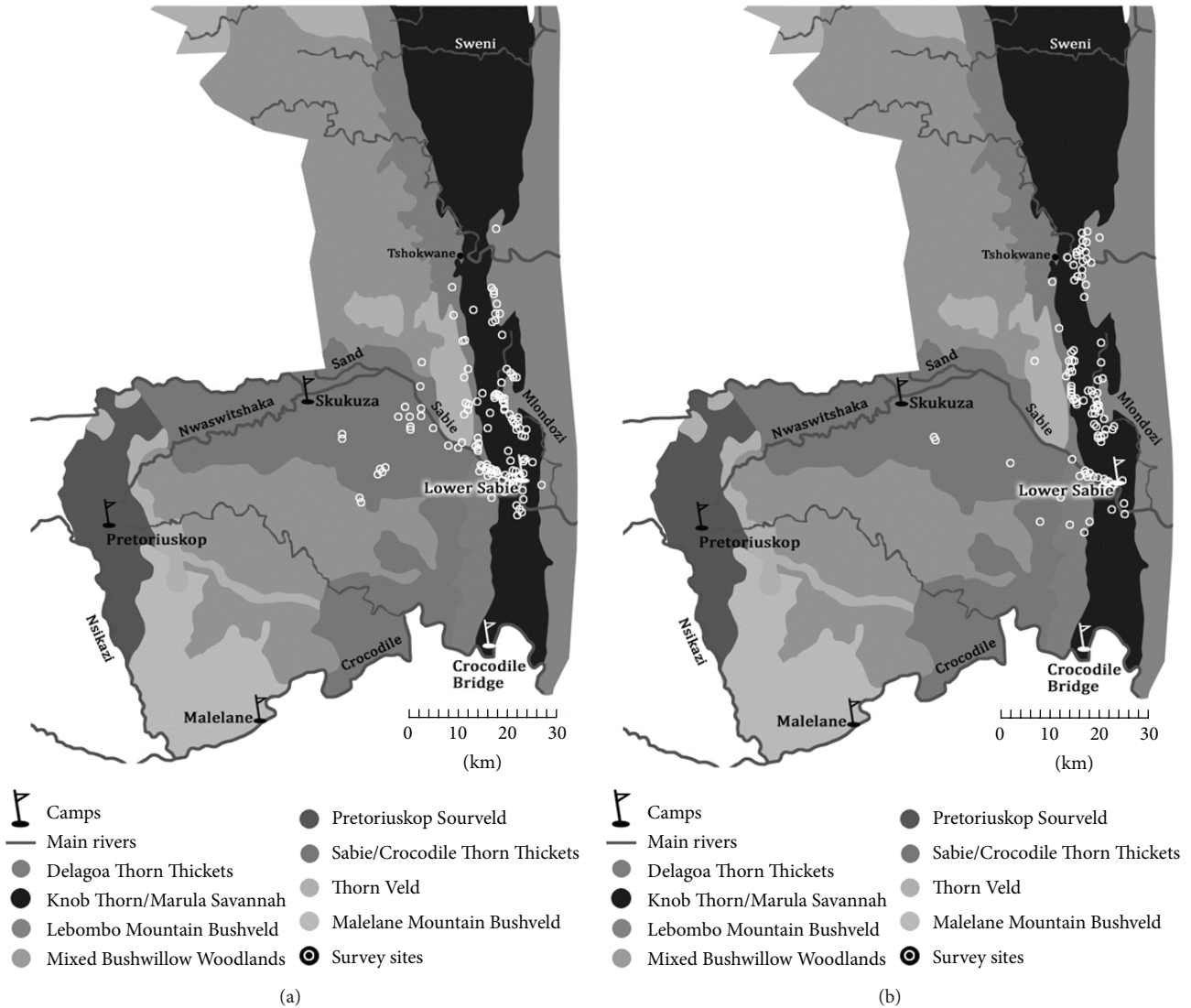


FIGURE 2: The movements of the breeding herds of elephants and location of the survey sites during the wet (a) and dry (b) seasons in the southern Kruger National Park from March 2002 to September 2005. (ecozones ex, Gertenbach [17]).

field observations on feeding behaviour of elephants on the savanna lands in the Murchison Falls National Park region of Uganda.

Field data recording commenced anywhere between 10 and 60 min after a breeding herd had left the observed feeding area. Field crews (at least two observers) maintained a safe distance from the animals to minimize disturbance and always avoided being positioned upwind of the herd to avoid detection. Direct field observations in Uganda on feeding behaviour of elephants indicated that the primary feeding periods occurred most frequently during early morning and only minor or secondary quantities of food were selected at various times of day and night which supplemented their diets [18].

Each elephant within the breeding herd left behind numerous feeding sites on the feeding path, while moving slowly through the feeding area before regrouping and moving towards the next feeding area or to water.

2.4. Data Analysis. An animal which has access to a variety of food items will show preference for some and avoid others [30]. Preference was measured by comparing selection of woody species in proportion to their estimated availability. Seasonal preferences for woody species were then ranked according to Manly’s alpha ( $\alpha$ ) index of preference [30]:

$$\alpha_i = \frac{r_i}{n_i} \left( \frac{1}{\sum r_j/n_j} \right), \tag{1}$$

Where  $\alpha_i$  is Manly’s  $\alpha$  (preference index) for woody species  $i$ ,  $r_i$ ,  $r_j$  is the proportion of woody species  $i$  or  $j$  selected ( $i$  and  $j = 1, 2, 3 \dots, m$ ),  $n_i$ ,  $n_j$  is the proportion of woody species  $i$  or  $j$  in the environment, and  $m$  is the total number of tree species available.

If the index value  $\alpha_i > 1/m$ , then the woody species  $i$  is given preference for selection, whereas if  $\alpha_i < 1/m$ , the woody species  $i$  is neglected.

TABLE 1: Manly's alpha index values of species selected (S) and neglected (N) in the early November–January and late wet seasons (February–April) by African elephant breeding herds in the southern Kruger National Park from March 2002 to September 2005. If  $\alpha > 1/m$ , then the species is considered to be selected, while if  $\alpha < 1/m$ , the species is neglected.

Early wet season ( $1/m = 0.0227$ )			Late wet season ( $1/m = 0.0263$ )		
Species	$\alpha$	Selected/neglected	Species	$\alpha$	Selected/neglected
<i>Manilkara mochisia</i>	0.0866	S	<i>Vachellia nilotica</i>	0.0963	S
<i>Schotia capitata</i>	0.0866	S	<i>Boscia mossambicensis</i>	0.0963	S
<i>Strychnos madagascariensis</i>	0.0866	S	<i>Ozoroa obovata</i>	0.0723	S
<i>Bolusanthus speciosus</i>	0.0577	S	<i>Clerodendrum glabrum</i>	0.0642	S
<i>Peltophorum africanum</i>	0.0469	S	<i>Albizia harveyi</i>	0.0482	S
<i>Carissa bispinosa</i>	0.0433	S	<i>Sclerocarya birrea</i>	0.0482	S
<i>Combretum molle</i>	0.0433	S	<i>Ximenia americana</i>	0.0482	S
<i>Grewia hexamita</i>	0.0408	S	<i>Grewia bicolor</i>	0.0351	S
<i>Boscia albitrunca</i>	0.0371	S	<i>Grewia monticola</i>	0.0341	S
<i>Sclerocarya birrea</i>	0.0371	S	<i>Boscia albitrunca</i>	0.0321	S
<i>Lannea schweinfurthii</i>	0.0334	S	<i>Searsia gueinzii</i>	0.0321	S
<i>Albizia petersiana</i>	0.0289	S	<i>Strychnos spinosa</i>	0.0321	S
<i>Dombeya rotundifolia</i>	0.0289	S	<i>Lannea schweinfurthii</i>	0.0321	S
<i>Ozoroa engleri</i>	0.0266	S	<i>Grewia flavescens</i>	0.0299	S
<i>Cassia abbreviata</i>	0.0217	N	<i>Grewia hexamita</i>	0.0282	S
<i>Mundulea sericea</i>	0.0217	N	<i>Manilkara mochisia</i>	0.0241	N
<i>Cissus cornifolia</i>	0.0204	N	<i>Terminalia prunioides</i>	0.0222	N
<i>Diospyros mespiliformis</i>	0.0200	N	<i>Combretum apiculatum</i>	0.0218	N
<i>Grewia bicolor</i>	0.0192	N	<i>Combretum zeyheri</i>	0.0201	N
<i>Grewia flavescens</i>	0.0164	N	<i>Ziziphus mucronata</i>	0.0186	N
<i>Searsia gueinzii</i>	0.0162	N	<i>Combretum imberbe</i>	0.0161	N
<i>Pterocarpus rotundifolius</i>	0.0156	N	<i>Albizia forbesii</i>	0.0140	N
<i>Ximenia caffra</i>	0.0144	N	<i>Dalbergia melanoxylon</i>	0.0139	N
<i>Euclea divinorum</i>	0.0131	N	<i>Pterocarpus rotundifolius</i>	0.0129	N
<i>Albizia forbesii</i>	0.0124	N	<i>Diospyros mespiliformis</i>	0.0126	N
<i>Combretum zeyheri</i>	0.0124	N	<i>Euclea divinorum</i>	0.0114	N
<i>Dichrostachys cinerea</i>	0.0118	N	<i>Vachellia tortilis</i>	0.0113	N
<i>Ehretia amoena</i>	0.01100	N	<i>Ehretia amoena</i>	0.0098	N
<i>Dalbergia melanoxylon</i>	0.0107	N	<i>Gymnosporia buxifolia</i>	0.0092	N
<i>Vachellia nigrescens</i>	0.0105	N	<i>Gymnosporia senegalensis</i>	0.0089	N
<i>Flueggea virosa</i>	0.0084	N	<i>Dichrostachys cinerea</i>	0.0084	N
<i>Vachellia robusta</i>	0.0081	N	<i>Combretum hereroense</i>	0.0075	N
<i>Combretum collinum</i>	0.0072	N	<i>Vachellia robusta</i>	0.0064	N
<i>Combretum hereroense</i>	0.0069	N	<i>Vachellia nigrescens</i>	0.0057	N
<i>Ziziphus mucronata</i>	0.0064	N	<i>Philenoptera violacea</i>	0.0055	N
<i>Vachellia gerrardii</i>	0.0054	N	<i>Combretum paniculatum</i>	0.0044	N
<i>Gymnosporia senegalensis</i>	0.0052	N	<i>Grewia villosa</i>	0.0040	N
<i>Combretum paniculatum</i>	0.0048	N	<i>Flueggea virosa</i>	0.0019	N
<i>Grewia villosa</i>	0.0040	N			
<i>Vachellia tortilis</i>	0.0036	N			
<i>Combretum apiculatum</i>	0.0029	N			
<i>Euclea undulate</i>	0.0024	N			
<i>Philenoptera violacea</i>	0.0022	N			
<i>Cienfuegosia hildebrandtii</i>	0.0012	N			

TABLE 2: Manly's alpha index values of species selected (S) and neglected (N) in the early May–July and late dry seasons (August–October) by African elephant breeding herds in the southern Kruger National Park from March 2002 to September 2005. If  $\alpha > 1/m$ , then the species is considered to be selected, while if  $\alpha < 1/m$ , the species is neglected.

Early dry season ( $1/m = 0.0161$ )			Late dry season ( $1/m = 0.0145$ )		
Species	$\alpha$	Selected/neglected	Species	$\alpha$	Selected/neglected
<i>Manilkara mochisia</i>	0.093736	S	<i>Boscia mossambicensis</i>	1	S
<i>Searsia gueinzii</i>	0.065615	S	<i>Commiphora mollis</i>	1	S
<i>Grewia monticola</i>	0.06249	S	<i>Croton megalobotrys</i>	1	S
<i>Vachellia xanthophloea</i>	0.056241	S	<i>Grewia occidentalis</i>	1	S
<i>Grewia bicolor</i>	0.04838	S	<i>Peltophorum africanum</i>	0.9286	S
<i>Ozoroa engleri</i>	0.046868	S	<i>Vachellia xanthophloea</i>	0.8571	S
<i>Rhoicissus</i> spp.	0.046868	S	<i>Schotia brachypetala</i>	0.5714	S
<i>Terminalia sericea</i>	0.043263	S	<i>Grewia monticola</i>	0.5616	S
<i>Ziziphus mucronata</i>	0.04166	S	<i>Euclea natalensis</i>	0.5	S
<i>Vachellia gerrardii</i>	0.040534	S	<i>Kigelia africana</i>	0.5	S
<i>Combretum imberbe</i>	0.037494	S	<i>Spirostachys africana</i>	0.5	S
<i>Grewia hexamita</i>	0.036896	S	<i>Terminalia sericea</i>	0.5	S
<i>Dombeya rotundifolia</i>	0.035151	S	<i>Grewia bicolor</i>	0.4901	S
<i>Peltophorum africanum</i>	0.031245	S	<i>Grewia hexamita</i>	0.4419	S
<i>Schotia brachypetala</i>	0.031245	S	<i>Vachellia gerrardii</i>	0.4	S
<i>Lannea schweinfurthii</i>	0.027269	S	<i>Combretum imberbe</i>	0.3636	S
<i>Pterocarpus rotundifolius</i>	0.027102	S	<i>Albizia forbesii</i>	0.2941	S
<i>Vachellia nigrescens</i>	0.024996	S	<i>Grewia villosa</i>	0.2895	S
<i>Albizia petersiana</i>	0.022318	S	<i>Combretum zeyheri</i>	0.2857	S
<i>Vachellia robusta</i>	0.020377	S	<i>Dalbergia melanoxylon</i>	0.2787	S
<i>Diospyros mespiliformis</i>	0.019228	S	<i>Vachellia tortilis</i>	0.25	S
<i>Ozoroa obovata</i>	0.018747	S	<i>Manilkara mochisia</i>	0.25	S
<i>Euclea divinorum</i>	0.017439	S	<i>Mundulea sericea</i>	0.25	S
<i>Combretum hereroense</i>	0.017267	S	<i>Searsia gueinzii</i>	0.25	S
<i>Dalbergia melanoxylon</i>	0.015539	N	<i>Diospyros mespiliformis</i>	0.2143	S
<i>Albizia forbesii</i>	0.013339	N	<i>Euclea divinorum</i>	0.1912	S
<i>Grewia flavescens</i>	0.012226	N	<i>Combretum paniculatum</i>	0.1818	S
<i>Sclerocarya birrea</i>	0.010415	N	<i>Ochna inermis</i>	0.1667	S
<i>Vachellia tortilis</i>	0.008521	N	<i>Vachellia nigrescens</i>	0.1386	S
<i>Dichrostachys cinerea</i>	0.008497	N	<i>Ozoroa engleri</i>	0.125	S
<i>Ximenia caffra</i>	0.006695	N	<i>Grewia flavescens</i>	0.1134	S
<i>Gymnosporia senegalensis</i>	0.006465	N	<i>Vachellia robusta</i>	0.1132	S
<i>Grewia villosa</i>	0.003125	N	<i>Commiphora pyracanthoides</i>	0.1111	S
<i>Flueggea virosa</i>	0.001644	N	<i>Gymnosporia senegalensis</i>	0.1111	S
<i>Ehretia amoena</i>	0.001103	N	<i>Vachellia erubescens</i>	0.1	S
<i>Vachellia erubescens</i>	0	N	<i>Pterocarpus rotundifolius</i>	0.0976	S
<i>Vachellia exuvialis</i>	0	N	<i>Vachellia exuvialis</i>	0.087	S
<i>Bolusanthus speciosus</i>	0	N	<i>Dichrostachys cinerea</i>	0.07	S
<i>Boscia foetida</i>	0	N	<i>Ziziphus mucronata</i>	0.0455	S
<i>Cissus cornifolia</i>	0	N	<i>Ehretia amoena</i>	0.0323	S
<i>Combretum apiculatum</i>	0	N	<i>Combretum apiculatum</i>	0.0313	S
<i>Commiphora mollis</i>	0	N	<i>Combretum hereroense</i>	0.0238	S
<i>Commiphora pyracanthoides</i>	0	N	<i>Boscia foetida</i>	0.0213	S
<i>Croton megalobotrys</i>	0	N	<i>Vachellia grandicornuta</i>	0	N
<i>Ehretia rigida</i>	0	N	<i>Albizia petersiana</i>	0	N
<i>Euclea natalensis</i>	0	N	<i>Balanites maughamii</i>	0	N
<i>Euphorbia ingens</i>	0	N	<i>Berchemia discolor</i>	0	N
<i>Grewia occidentalis</i>	0	N	<i>Bolusanthus speciosus</i>	0	N

TABLE 2: Continued.

Early dry season (1/m = 0.0161)			Late dry season (1/m = 0.0145)		
Species	$\alpha$	Selected/neglected	Species	$\alpha$	Selected/neglected
<i>Gymnosporia buxifolia</i>	0	N	<i>Boscia albitrunca</i>	0	N
<i>Gymnosporia maranguensis</i>	0	N	<i>Carissa bispinosa</i>	0	N
<i>Hyperacanthus amoenus</i>	0	N	<i>Commiphora africana</i>	0	N
<i>Oncoba spinosa</i>	0	N	<i>Ehretia rigida</i>	0	N
<i>Ormocarpum trichocarpum</i>	0	N	<i>Euclea undulata</i>	0	N
<i>Philenoptera violacea</i>	0	N	<i>Flueggea virosa</i>	0	N
<i>Phoenix reclinata</i>	0	N	<i>Gardenia volkensii</i>	0	N
<i>Phyllanthus reticulatus</i>	0	N	<i>Gymnosporia buxifolia</i>	0	N
<i>Senna petersiana</i>	0	N	<i>Lannea schweinfurthii</i>	0	N
<i>Spirostachys africana</i>	0	N	<i>Mystroxydon aethiopicum</i>	0	N
<i>Strychnos madagascariensis</i>	0	N	<i>Oncoba spinosa</i>	0	N
<i>Terminalia phanerophlebia</i>	0	N	<i>Ormocarpum trichocarpum</i>	0	N
<i>Terminalia prunioides</i>	0	N	<i>Philenoptera violacea</i>	0	N
<i>Ximenia americana</i>	0	N	<i>Phyllanthus reticulatus</i>	0	N
			<i>Ptaeroxylon obliquum</i>	0	N
			<i>Schotia caffra</i>	0	N
			<i>Sclerocarya birrea</i>	0	N
			<i>Senna petersiana</i>	0	N
			<i>Strychnos spinosa</i>	0	N
			<i>Terminalia phanerophlebia</i>	0	N
			<i>Ximenia americana</i>	0	N

Data recorded from the woody plant species utilised and not utilised from the collared and noncollared herds were collated according to season. Availability and selection of woody species in the sample sites for all seasons were categorised with a frequency distribution into classes. A woody species with an observed frequency between 0 and 100 in all feeding sites was categorised as rare and with a frequency >100 as common. Similarly, woody species with a selection frequency between 0 and 25 were categorised as low selection and >25 as high selection. Statistica version 7 was used for all analyses [31].

### 3. Results

Average annual rainfall for the Lower Sabie area during the study period measured 549 mm during the wet seasons and 25 mm for the dry seasons. Areas traversed by observed herds during the study period extended from the Sabie and Crocodile River Thickets, Delagoa Thorn Thickets, *Sclerocarya birrea* subsp. *caffra*, *Vachellia nigrescens* Savanna, Mixed *Combretum* Woodlands to the Lebombo Mountain Bushveld. We sampled 237 feeding areas which included 468 wet season feeding sites and 480 dry season feeding sites (Figure 2). We recorded 98 woody species within the feeding areas and of this number; 63 species contributed to the elephant's diet across all seasons.

Based on average percentages of the Manly alpha index values, the woody plants neglected decreased from the wet seasons (65%) to the dry season (41%) (Figure 3). This is

confirmed by the values <0.1 for woody plants in the early wet, late wet, and early dry seasons indicating a low proportion of woody plants being selected (Tables 1 and 2). During the late dry seasons 34 woody plant species had values ranging from 0.1 to 1.0 (Table 2). This change towards a greater proportion of woody species recorded in the dry seasons indicates that the herds selected different vegetation types in the dry season compared to wet seasons. This change might be from the low grass production during the dry season and availability of a diversity of woody plant species in southern KNP [32].

Three *Grewia* species, namely, *Grewia bicolor*, *Grewia flavescens*, and *Grewia monticola* which have a wide distribution in the landscape, were selected in all seasons except in the early wet season, and *Grewia hexamita* was the only woody plant recorded as being highly selected in all four seasons (Table 3). van Wyk and Fairall [33] reported that *Grewia* species were sought after by elephants in the southern region of the KNP. Rarity of occurrence, that is, species occurring at low frequencies (less than 100 individuals in all feeding sites), did not stop elephants from actively seeking out these plants. Of the 63 plants selected across all seasons, only 10 plants were common, and 53 plants were classified as rare (Table 3).

### 4. Discussion

Although it is reported that elephants have a preference for the riparian fringe [34] and are frequently associated with that plant community (Figure 2), our results suggest that they do not have any feeding preference for woody

TABLE 3: Woody species selected (high (h), low (l)) and available (rare (r), common (c)) in the feeding areas during different seasons frequented by African elephant breeding herds in the southern Kruger National Park from March 2002 to September 2005.

Species	Early wet	Late wet	Early dry	Late dry
<i>Grewia hexamita</i>	h, r	h, r	h, r	h, r
<i>Grewia bicolor</i>		h, c	h, c	h, c
<i>Grewia flavescens</i>		h, c	l, r	l, r
<i>Grewia monticola</i>		h, c	h, r	h, r
<i>Searsia gueinzii</i>		h, r	h, r	h, r
<i>Manilkara mochisia</i>	h, r		h, r	h, r
<i>Ozoroa engleri</i>	h, r		h, r	l, r
<i>Peltophorum africanum</i>	h, r		h, r	h, r
<i>Schotia brachypetala</i>	h, r		h, r	h, r
<i>Lannea schweinfurthii</i>	l, r	h, r	h, r	
<i>Sclerocarya birrea</i>	l, r	h, r	l, r	
<i>Vachellia gerrardii</i>			h, r	h, r
<i>Vachellia nigrescens</i>			h, r	l, c
<i>Vachellia robusta</i>			l, r	l, r
<i>Vachellia tortilis</i>			l, r	h, c
<i>Vachellia xanthophloea</i>			h, r	h, r
<i>Albizia forbesii</i>			l, c	h, r
<i>Combretum hereroense</i>			l, r	l, r
<i>Combretum imberbe</i>			h, r	h, r
<i>Dalbergia melanoxylon</i>			l, c	h, r
<i>Dichrostachys cinerea</i>			l, c	l, c
<i>Diospyros mespiliformis</i>			l, r	l, r
<i>Euclea divinorum</i>			l, r	l, c
<i>Grewia villosa</i>			l, r	h, r
<i>Gymnosporia senegalensis</i>			l, c	l, c
<i>Pterocarpus rotundifolius</i>			h, c	l, r
<i>Terminalia sericea</i>			h, r	h, r
<i>Ziziphus mucronata</i>			h, r	l, r
<i>Boscia mossambicensis</i>		h, r		h, r
<i>Ozoroa obovata</i>		h, r	l, r	
<i>Albizia petersiana</i>	h, r		l, r	
<i>Dombeya rotundifolia</i>	h, r		h, r	
<i>Boscia albitrunca</i>	h, r	h, r		
<i>Vachellia erubescens</i>				l, r
<i>Vachellia exuvialis</i>				l, r
<i>Boscia foetida</i>				l, r
<i>Combretum apiculatum</i>				l, r
<i>Combretum paniculatum</i>				l, r
<i>Combretum zeyheri</i>				h, r
<i>Commiphora mollis</i>				h, r
<i>Commiphora pyracanthoides</i>				l, r
<i>Croton megalobotrys</i>				h, r
<i>Ehretia amoena</i>				l, r
<i>Euclea natalensis</i>				l, r
<i>Grewia occidentalis</i>				h, r
<i>Kigelia africana</i>				h, r
<i>Mundulea sericea</i>				h, r
<i>Ochna inermis</i>				l, r
<i>Spirostachys africana</i>				l, r
<i>Ziziphus mucronata</i>				l, r

TABLE 3: Continued.

Species	Early wet	Late wet	Early dry	Late dry
<i>Terminalia sericea</i>				h, r
<i>Flueggea virosa</i>			l, r	
<i>Rhoicissus</i> spp.			h, r	
<i>Ximenia caffra</i>			l, r	
<i>Vachellia nilotica</i>		h, r		
<i>Albizia harveyi</i>		h, r		
<i>Clerodendrum glabrum</i>		h, r		
<i>Strychnos spinosa</i>		h, r		
<i>Ximenia americana</i>		h, r		
<i>Bolusanthus speciosus</i>	h, r			
<i>Carissa bispinosa</i>	h, r			
<i>Combretum molle</i>	h, r			
<i>Schotia capitata</i>	h, r			

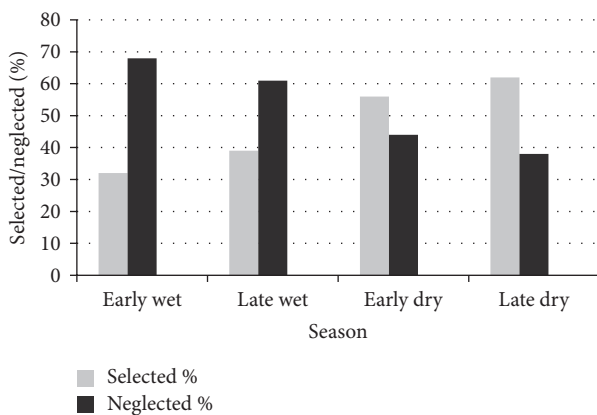


FIGURE 3: Percentage of woody species selected and neglected, based on Manly's alpha values, in the feeding areas selected by breeding herds of African elephants from March 2002 to September 2005 in the southern Kruger National Park.

plants in the riparian fringe. Tree species generally associated with riparian vegetation such as *Ficus sycomorus*, *Breonadia salicina*, and *Nuxia oppositifolia* are commonly found along rivers in the study area. However, the feeding sites actively selected by breeding herds in our study did not contain these woody species. Thus, the association of elephants with riparian fringes might rather be for regulating body temperature and feeding on the reed *Phragmites australis* in the riverbeds (J. J. Viljoen, H.C. Reynecke, pers. obs.).

As there are insufficient quantitative data available, no clear prediction has emerged about which woody species are prone to extirpation and under what circumstances [35]. Kerley et al. [12] made reference to the lack of quantitative studies in terms of species contribution in diet of elephants as well as the plethora of studies that indirectly infer elephant diet from plant-based studies. For example, *Sclerocarya birrea* is a woody plant that is deemed a species susceptible to extirpation [35, 36]; yet, our data show that this plant had a high selection frequency only in the late wet season at a low Manly alpha index value of 0.048. Although present in the

feeding areas in the early dry and late dry seasons, this plant was neglected by the breeding herds of elephants.

To a large degree climatic and biological variability in African savannas explain differences in heterogeneity and productivity of vegetation at landscape and regional scales [14, 35]. These explain the differential use of habitats and seasonal changes in the distribution of elephants [7, 37–44]. This study shows that the selection preference of elephant herds corresponds with seasonal changes [29, 44]. In the feeding areas frequented by the observed elephant breeding herds, 64% of the available woody species were browsed by elephants during the four seasons. This relatively high proportion of sought after woody species suggests that breeding herds select areas that permit efficient and effective nutrient intake [29, 45]. Functional traits of selected woody species, that is, their phenology and life history, probably vary seasonally, which could explain these selection patterns. Future research should investigate the causal mechanisms underlying selection preferences, which might include plant nutrients in the soil, leaves, fruits, and flowers of woody species.

Although our observations were restricted to diurnal hours due to safety issues and visibility, we propose that the woody plant species available and selected during the night did not differ from those selected during daytime [18].

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