

Utilisation of Woody Plants by the Cape Porcupine in Mesic Savannas in South Africa

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Herbivory plays a fundamental role in determining the structure of savannas. The impacts of small and medium-sized mammalian herbivores on trees in savannas remain poorly understood because most research attention focuses on large herbivores such as elephants whose destructive effects on trees can be pervasive at landscape scales. On the other hand, feeding activities of generalist herbivores such as Cape porcupines on woody plants can lead to tree mortality. The study was aimed at investigating the utilisation of woody plants by the Cape porcupine in three mesic savanna sites in South Africa. We determined the woody plant diet of the porcupine for the early and late dry seasons at Roodeplaas Farm in Gauteng Province, and at Goss Game Farm and Bisley Valley Nature Reserve in KwaZulu-Natal Province. Thirty and twenty randomly located quadrats (30 m × 30 m) were laid at Roodeplaas and Goss, respectively, while 10 smaller quadrats (10 m × 10 m) were laid at Bisley. We measured stem diameter and the length and width of bark scars made by porcupines on stems of woody plants. We collected ten dung samples from each study site in the wet and dry seasons for quantification of woody material in porcupine diet. Porcupine foraging behaviour impacted different tree species at each site: *Vachellia robusta* at Roodeplaas, *Spirostachys africana* at Goss and *Vachellia nilotica* at Bisley. Each of these trees was dominant at each site. More scarring and tree mortality were recorded at Bisley with almost 70% tree sapling mortality occurring on trees which porcupine fed on. The size of bark scars was greater at Goss ($P < 0.01$) than at Roodeplaas and Bisley, which were similar. Area of bark damage on *S. africana* trees

differed significantly by stem diameter size class ($P = 0.007$) and was greater for small stems (size class < 7.1 cm) than the larger stems (size classes 7.1–14 cm and 14.1–21). For all the study sites, dung samples revealed that woody material contributed over 80% of the porcupine diet in the dry season, but was lower at 35% during the wet season for Roodeplaar although it was consistently high for Bisley at 79%. Porcupine foraging activities substantially contributed to tree mortality at each site. We posit that porcupine induced mortality on dominant tree species at each site may contribute to structural heterogeneity in woody plant vegetation in mesic savannas.

Key words: Bark damage, Dry season diet, Herbivory, Mesic savanna, Ring-barking.

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BACKGROUND

The extent of mammalian herbivory varies greatly depending on the type of ecosystem among other factors (Maron and Crone 2006; Marquart et al. 2019). This may be influenced by the type(s) and densities of herbivore species. Large herbivores may have considerable impacts on the landscape, such that herbivory is considered a major determinant of savanna structure (Sankaran et al. 2005 2008). As such, without herbivory and fire, most mesic savannas could develop into closed woodlands (Bond 2008; Stevens et al. 2016). The influence of herbivores on vegetation is evident for extensively studied species such as the African elephant (*Loxodonta africana*) (e.g., O'Connor et al. 2007; Stevens et al. 2016), but are poorly understood for less charismatic and cryptic species such as the Cape porcupine (*Hystrix africaeaustralis*). As such, the utilisation of woody vegetation by such animals is understudied in African savannas.

Seasonality in African savannas is associated with changes in vegetation. The dry season is characterised by decreased availability and quality of grasses and deciduous trees whereas evergreen trees tend to be available (Aide 1992; Duru and Ducrocq 2000). The decrease in forage quality and quantity results in food scarcity for herbivores, more so for grazers because grass quality declines more strongly in the dry season. To deal with the changes in forage availability, some ungulates and other mammals such as elephants migrate (Fryxell and Sinclair 1988; Fryxell et al. 1988; Canney 2021). Others feed on less nutritious foods in their habitats but struggle to meet their dietary requirements while mixed feeders simply shift to incorporate a greater portion of woody plants in their diet during the dry season (Codron et al. 2007).

Cape porcupines are generalist herbivores that occur throughout southern Africa (van Aarde, 1987) and they feed on natural vegetation and cultivated plants (Bragg et al. 2005; Hafeez et al. 2011). Their diet is mainly made up of tubers, corms, roots, and tree bark, and the foraging activities of porcupines may lead to death of the plants that are impacted (Bruno and Riccardi 1995; Mohamed 2011). Because tubers and rhizomes of herbaceous plants are less available during the dry season, porcupines utilise other food sources such as seeds and the bark as well as roots of certain tree species (Hafeez et al. 2011). Damage of the tree bark makes the trees susceptible to fire as well as diseases which may come about due to attack by insects (*e.g.*, ants) and pathogenic bacterial and fungal attack (Vospornik 2006; Wigley et al. 2019). Apart from herbivory and fire, trees may be damaged by natural processes such as wind action, which may also result in bark stripping as branches fall. On individual trees, debarking by mammals may be pervasive so that the trunk is ringbarked. The removal of the bark and cambium does not impact on the movement of water and nutrients in plants as most trees possess enough carbohydrate reserves to continue growth but may die over time as the reserves become depleted (Hölldt et al. 2006). The lack of carbohydrate in plants may negatively influence water and nutrient uptake, which then results in the death of the tree (Cleary and Holmes 2011). Ringbarking may thus fast track and facilitate the death of trees.

Porcupines are nocturnal, territorial and solitary foragers, although they can occasionally be found foraging in groups of two to three animals (Coppola et al. 2019; Viviano et al. 2020). Their nocturnal activity patterns hinder direct studies on their feeding behaviour, but evidence of their feeding can be seen in the wild as some trees have porcupine bite marks on the trunk. The foraging behaviour of porcupines is also indicated by their digging through the soil for subterranean plant parts. Through their feeding and foraging activities, porcupines have trophic and landscape level effects on terrestrial ecosystems (Sharma and Prasad 1992; Alkon 1999; Mori et al. 2017 2018). Extensive excavation of holes and burrows by such organisms leading to modification or creation of habitats for other organisms is known as ecosystem or soil engineering (Jones et al. 1997). Such animals modify resource availability for other organisms (Alkon 1999; Haussmann et al. 2018; Grossman et al. 2019). Unfortunately, the engineering aspects such as digging by porcupines and other animals are seen as a problem particularly in farming systems and commercial forestry. Porcupines are thus viewed as pests in these systems, as they interfere with crop production and harvest (Alkon and Saltz 1985; Khan et al. 2000; Mushtaq et al. 2010; Laurenzi et al. 2016). Although effects of foraging activities of the Cape porcupine on woody vegetation have been investigated in the *Burkea africana* savanna at Nylsvley (see Yeaton 1988; de Villiers and van Aarde 1994), quantification of the amount of bark stripped off individual trees has not been undertaken. Resource availability may influence the utilisation of the landscape by porcupines

(Alkon 1999). The effects of porcupine foraging behaviour in agriculture show that they may have potential to deal with problem plants even if it is at a smaller scale than larger herbivores. A higher density of porcupines may have greater and negative effects on plants.

In this study, the utilisation of woody plants as porcupine food during the wet and dry seasons, and the foraging activities of porcupines were monitored at three geographically distant sites in South Africa. The study was aimed at quantifying the extent of herbivory by the porcupines on target trees during the wet and dry season in savannas. We hypothesised that woody plants feature in Cape porcupine diets according to the season due to availability of preferred plants. We predicted: (1) an increase in the dry season contribution of woody plants in the porcupine diet compared to the wet season when there is greater availability of herbaceous plants; and 2) greater preference for dominant woody plants at each site because the animal is a generalist herbivore. We used dung samples to determine and quantify plant materials consumed by porcupines during the wet and dry seasons. We also quantified the extent of bark damage by porcupines on target trees at each site and related bark damage to woody plant constituents in the dung for each study site.

MATERIALS AND METHODS

Study sites

The study was conducted at three locations: the Roodeplaat Experimental Farm (25°36'26"S, 28°33'40"E, altitude 1220 m above sea level) of the Agricultural Research Council (ARC) located in northern Gauteng, Goss Game Farm (27°33'22"S, 31°44'46"E, 340 m asl) near Pongola in northern KwaZulu-Natal and at Bisley Valley Nature Reserve (29°39'41"S, 30°23'05"E, 750 m asl) near Pietermaritzburg, also located in KwaZulu-Natal, South Africa (Fig. 1). Although the sites were far apart (> 300 km) and of different sizes, the common aspect amongst them was woody plant encroachment.

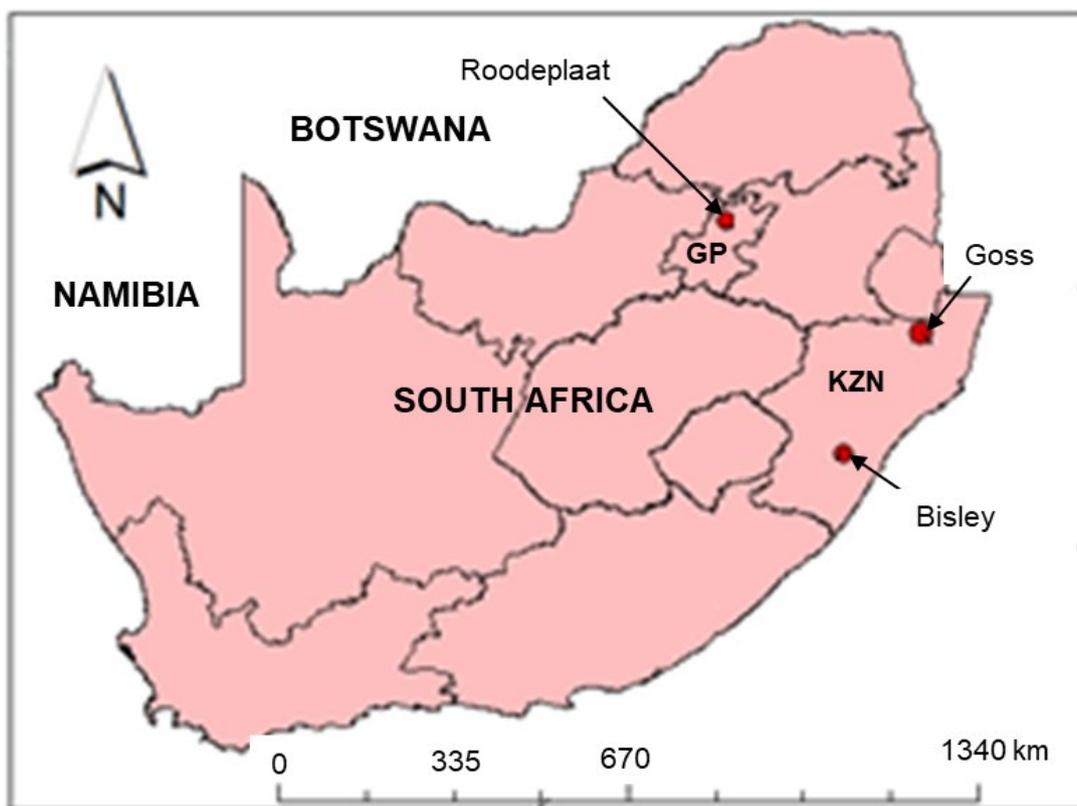


Fig. 1. Map of South Africa showing the three study sites located at Roodeplaatt in Gauteng (GP) Province, and Bisley and Goss in KwaZulu-Natal (KZN) Province.

The three sites are in semi-arid to mesic savannas with minor differences in mean annual precipitation (Roodeplaatt: 646 mm; Bisley: 694 mm; Goss: 543 mm) which largely occurs during the summer months (November-April). The vegetation at Roodeplaatt is described as Marikana Thornveld, which consists of open *Vachellia karroo* woodland occurring in valleys, undulating plains and lowland hills (Mucina and Rutherford 2006). The mean maximum temperature in summer can reach 29°C and mean minimum temperatures in winter can drop to 2°C with frost occurring during the winter months (Mkhize et al. 2018). The common tree species that occur in Roodeplaatt Farm include *V. nilotica*, *V. tortilis*, *V. robusta* subsp. *heteracantha* and *Ziziphus mucronata*. *Grewia flava*, *Searsia pyroides* var. *pyroides*, *Diospyros lycioides* subsp. *guerkei* are among some of the tall shrubs occurring in Roodeplaatt Farm. The grasses include *Melinis nerviglumis*, *Elionurus muticus*, *Heteropogon contortus* and *Fingerhutia africana*. Some herb species found there are *Hermannia depressa*, *Ledebouria revoluta* and *Ipomoea obscura*. Large herbivores at Roodeplaatt consist of mainly cattle (*Bos taurus*) and low densities of zebra (*Equus burchelli*), kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*). The vegetation type at Goss Game Farm is classified as Northern Zululand Sourveld, which occurs in most parts of northern KwaZulu-Natal. The vegetation is characterised by wooded grasslands and dense bushveld thickets, with tall shrubs of *Gardenia volkensii* and *Gnidia caffra* (Mucina and Rutherford 2006). Goss Game Farm lies in a hot, semi-arid to mesic region, with mean temperatures reaching a

maximum of 38.5°C in summer and a mean minimum of 7°C in winter (Mucina and Rutherford 2006). Common trees in the area include *Spirostachys africana*, *Sclerocarya birrea*, *Z. mucronata*, *V. robusta*, *V. tortilis*, *V. nilotica*, *V. caffra*, and *V. karroo*. The common grasses found in Goss Game Farm are *Eragrostis curvula*, *Panicum maximum* and *Themeda triandra*. This is utilised by a large mammalian fauna that includes impala, zebra, kudu, giraffe (*Giraffa camelopardalis*), and warthog (*Phacochoerus africanus*).

The vegetation at Bisley Valley Nature Reserve (Bisley) is categorised as a transition zone between KwaZulu-Natal Hinterland Thornveld (savanna) and Ngongoni Veld (grassland) and is thus susceptible to invasion by woody plants (Ward et al. 2017). Bushveld thickets are common along the main drainage channels. Bisley experiences hot summers with a mean maximum of 26.4°C and mild winters with a mean minimum of 8.8°C. The common trees that occur in this area are *V. nilotica*, *V. sieberiana*, *Searsia dentata* and *Coddia rudis* while *V. karroo* occurs near the major streams. The herbaceous layer is characterised by several grasses such as *E. curvula*, *P. maximum* and *Sporobolus* spp. Other plants in the herbaceous layer include *Hypoxis* spp., *Justicia flava* and *Aloe pruinosa*, an endemic restricted to the Pietermaritzburg surrounds. Here, large mammals consist of giraffe, zebra, wildebeest and impala. The main growing season for all sites is summer, and the dry season starts in May and peaks in July. All three sites are normally dry in winter with lower availabilities of forage, and most of the available food for large mammalian browsers (> 4 kg, *sensu* Bragg et al. 2005) is derived from shrubs and trees (Mucina and Rutherford 2006).

Field sampling

Sampling was undertaken during the dry season between July and October 2019. Revisits were made to the sites during the wet season (January–March 2020). Quadrats were randomly laid out according to the size of the site. At Roodeplaat, porcupine diggings were mainly for lower parts of the trunk of *Vachellia robusta*, in addition to digs made for bulbous herbaceous plants. Using thirty 30 m × 30 m quadrats, stem diameters of all *V. robusta* trees were measured at a height of 0.5 m, which is consistent with the height to which porcupine bark damage occurred (Fig. 2). We also measured the length and width of scars on the bark and roots made by the porcupines. At Goss, porcupine tree damage was mainly on the stems of *Spirostachys africana* (Fig. 2), so tree diameter was measured at 0.5 m above ground using twenty 30 m × 30 m quadrats. At Bisley, porcupines dug to reach a portion of the main root of *V. nilotica* seedlings and saplings. The diameter of the dug-out tree stem was also measured in 10 smaller quadrats of 10 m × 10 m. To cater for different sizes of targeted trees, we used larger quadrats (30 m × 30 m) at the sites where mature trees were

damaged, while smaller quadrats (10 m × 10 m) were used at the site where porcupines only utilised seedlings and saplings. The number of quadrats was also influenced by the area of porcupine activities, which was much larger at Roodeplaat (5–8 ha; 30 quadrats) than Goss (< 5 ha, 20 quadrats) and at Bisley (approx. 3 ha; 10 quadrats). In some instances, portions of the tree stem cut out from the roots were found near the foraging hole. The diameter of these stems was also recorded and used in the final analysis. Trees were divided into stem diameter size classes (*i.e.*, small, < 7.1 cm; medium, 7.1–14 cm; and large, 14.1–21 cm) for *S. africana* and (small, < 4.5 cm; medium, 4.5–8.5 cm; and large, 8.6–14 cm) for *V. robusta*. Finally, *V. nilotica* comprised of only one size class of seedlings and saplings with a diameter of < 2.5 cm. Faecal samples were collected at each site for the dry season (August–October) and at Bisley and Roodeplaat for the wet seasons (January–March) to identify components of the diet derived from woody plants. Due to logistical constraints, collection for the wet season was not possible at Goss.



Fig. 2. Tree bark damage on (a) *Vachellia robusta* at Roodeplaat and (b) *Spirostachys africana* at Goss.

Debarking by porcupines was identified by marks on the bark of trees where signs of debarking were categorised as new and old. Bark damage by porcupines is characteristic of the animal, and is widely identifiable by landowners (*e.g.*, at Goss), wildlife rangers (at Bisley) and the authors. The literature (*e.g.*, Yeaton 1988; de Villiers and van Aarde 1994; Bragg et al. 2005) provides additional descriptions that link the porcupine to the observed bark damage. In addition, no other large mammalian species that is known to feed substantially on tree bark from ground level to

0.5 m occur at the three sites. New bark damage was estimated to have occurred approximately a few weeks to a few months (less than 3 months) prior to sampling. Old bark damage was more than 3 months old and was distinguished from the new by the change in colour of the scar to brown for all damaged trees. The data were pooled to include both new and old scars because we wanted to determine utilisation of the woody plants by Cape porcupines and the extent to which this was done. We regarded old scars just as important as new because they both compromise the health of the plant, and may potentially lead to the death of the plant. Some trees, through possession of old and new scars, showed repeated use by porcupines. The length and width of bark scars caused by porcupines were measured for each tree. We also took note of whether tree seedlings or saplings were completely dug out and destroyed, or they were damaged but remained alive.

Faecal analysis

Porcupine droppings are easily identifiable as they form a stack of elongate pellets. Identification was also based on the size, colour, and contents (*e.g.*, ground tree bark, tree roots, leaves of herbaceous plants) of the pellets including places where they were deposited, which mainly occurred on game trails and feeding locations. Faecal samples were collected along the quadrats and opportunistically from all three sites and oven-dried (60°C, 48 h) for storage before later analysis of diet composition. Ten samples were analysed for each site per season, based on the assumption that constituents of these samples were representative of other dung samples not collected at each site. The dung samples were first weighed and then cut into smaller pieces and a representative portion of the whole dung sample was then analysed. The sample was washed in 70% ethanol to separate the different components and then air-dried, sieved through a 1-mm sieve and weighed again. The different diet components were then grouped according to their categories (*e.g.*, woody material, herbaceous material and seeds of both woody and herbaceous plants) on the basis of weight, and then examined under a dissecting microscope.

Data analysis

All statistical analyses were carried out in IBM SPSS statistics for windows v. 27 (IBM Corp 2020). For each study site and tree species, the highest extent of bark damage on the tree trunks was determined to calculate the area of bark available to the porcupine. Thus, we determined that the bark of *V. robusta* and *V. nilotica* was available to a height of 0.2 m, and that of *S. africana* to 0.5 m (see Barthelmess 2006). We then calculated the total area of bark scars made by the porcupine on each tree and expressed it as a proportion of the total bark available for each tree. We

compared the area of bark scars and the proportional bark damage per tree among three stem diameter size classes of trees (small, medium and large) for *S. africana* using a Kruskal-Wallis test because the assumptions of analysis of variance (ANOVA) were not met and no transformation allowed the assumptions of a parametric test to be satisfied (Sokal and Rohlf 2012). For *V. robusta*, we used one-factor ANOVA. For *V. nilotica*, no comparison was necessary as there was only one size class. However, we still calculated the area of bark scars and the proportional bark damage on this species. Sample sizes of *V. karroo* and *D. rotundifolia* trees from Roodeplaat were too small for use in the size class analysis. Preference for a particular woody plant species was determined using a modification of Owen-Smith and Cooper (1987)'s food acceptability index. The index is a ratio of the use of a plant species to its availability. It ranges from 0 to 1, where 0 represents avoidance (*i.e.*, the plant species is available but not used) and 1 represents preferred (*i.e.*, all available plants of the species are utilised). We calculated the acceptability index for each woody plant species that was available and utilised. Categorical data of constituents of porcupine dung were expressed as a percentage of total weight of a dung sample. Unless otherwise specified, all values are reported as mean \pm 1 S.E.

RESULTS

Some 7% of *V. robusta* and 16% *S. africana* trees were bark damaged at Roodeplaat and Goss, respectively. Only a very small number (< 1%) of *V. nilotica* trees were targeted by porcupines for foraging, and of these, 40% were bark damaged in Bisley. The area of bark damage on *S. africana* trees differed significantly by size class (Kruskal-Wallis $\chi^2 = 9.737$, $P = 0.008$), and was greater for medium-sized trees than small trees (Table 1). The proportion of tree bark damage on *S. africana* trees was however, similar among size classes (Kruskal-Wallis $\chi^2 = 3.966$, $P = 0.138$; Table 1).

The area of bark damage on *V. robusta* was similar among size classes ($F = 1.843$, $P = 0.17$) but differed among size classes when bark damage was expressed as a proportion of total bark available for porcupine foraging (Table 1). In particular, 29% of available bark was removed on small trees, which decreased to only 7% of the bark for large trees. For *V. nilotica* trees the area of bark damage was relatively large in comparison to that of the small diameter trees of *S. africana* and *V. robusta* at the other two sites (Table 1).

Table 1. Mean (± 1 SE) area (cm^2) of bark scars and mean (± 1 SE) proportion (%) of bark damage (second row for each species) on trees caused by porcupines. In each row different lower-case letters denote significant differences among stem diameter size classes ($P < 0.05$) based on a Dunn-Bonferroni post hoc test. Calculations are based on 222 trees for *S. africana*, 90 trees for *V. nilotica* and 48 trees for *V. robusta*

Species	Diameter size class (cm^2)		
	Small	Medium	Large
<i>Spirostachys africana</i>	105.1 \pm 29.5 a 17.2 \pm 5.2% a	369.2 \pm 125.0 b 20.3 \pm 6.2% a	246.2 \pm 83.1 ab 10.2 \pm 3.7% a
<i>Vachellia nilotica</i>	111.3 \pm 83.1 10.0 \pm 5.9%	- -	- -
<i>Vachellia robusta</i>	37.0 \pm 6.5 a 29.6 \pm 6.1% a	61.4 \pm 10.8 a 18.0 \pm 3.0% ab	48.0 \pm 19.8 a 6.7 \pm 2.5% b

Overall, the proportion of tree bark damaged by porcupines was greatest for *D. rotundifolia*, *S. africana* and *V. robusta* but was lower for *V. karroo* and *V. nilotica* (Fig. 3). However, the lower proportion of bark damage for *V. nilotica* at Bisley belies the fact that many of the trees were destroyed rather than merely damaged.

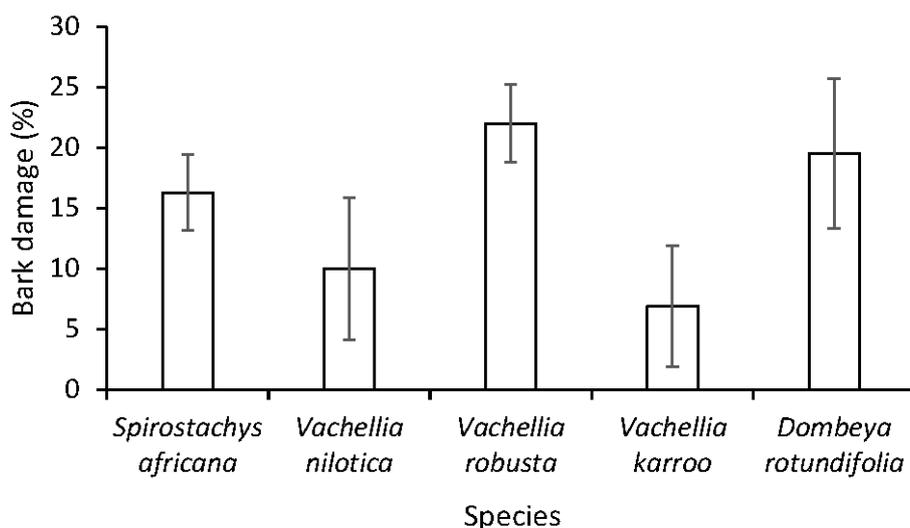


Fig. 3. Mean (\pm SE) percentage of bark damaged by the porcupine on trees at Bisley, Goss and Roodeplaat.

Porcupine foraging on *V. nilotica* at Bisley focused only on young trees so that bark damage was minimal although plants were often destroyed. Mortality of impacted trees was much greater for *V. nilotica* (57.5%, Bisley) than for *V. robusta* (2.1%, Roodeplaat). At Roodeplaat, because porcupines targeted mature plants, tree death would be a slow process, but most of the scars were located below ground. At Goss, damage on *S. africana* was mainly on the bark and porcupines ringbarked some trees thereby decreasing chances of recovery. No mortalities were recorded for *S. africana*, *D. rotundifolia* and *V. karroo*.

Porcupine foraging activities showed preference for one to three woody plant species at each site, but these were not always the most abundant species. For example, *Gymnosporia buxifolia*, *Dichrostachys cinerea* and *Ehretia rigida* were common at Roodeplaat, but were avoided while a less common species, *D. rotundifolia*, was used at a rate similar to that of the most abundant *V. robusta* (Table 2, Table S1). At Goss, *S. africana* was most abundant and utilised substantially, while three other common species (*D. cinerea*, *V. nilotica* and *V. robusta*) were avoided. Although avoided at Goss, *V. nilotica* was preferred at Bisley (Table 2).

Table 2. Acceptability of woody plants by the Cape porcupines in mesic savannas of South Africa. Acceptability = Use ÷ Availability, based on Owen-Smith and Cooper (1987). Values of availability and use represent the number of plants of each species sampled in thirty 30 m × 30 m quadrats at Roodeplaat, twenty 30 m × 30 m at Goss and ten 10 m × 10 m quadrats at Bisley

Site		Woody plant species					
		<i>S. africana</i>	<i>V. robusta</i>	<i>D. rotundifolia</i>	<i>V. nilotica</i>	<i>V. karroo</i>	<i>G. mossambicensis</i>
Roodeplaat	Availability	0	78	13	16	12	0
	Use	0	48	8	0	3	0
	Acceptability	0	0.62	0.62	0	0.25	0
Goss	Availability	338	27	0	128	0	8
	Use	222	0	0	0	0	1
	Acceptability	0.66	0	0	0	0	0.125
Bisley	Availability	0	0	0	269	0	1
	Use	0	0	0	90	0	0
	Acceptability	0	0	0	0.33	0	0

Each porcupine dung sample consisted of 8–15 pellets. Each pellet was 39.4 ± 1.2 mm in length, 14.3 ± 0.2 mm breath and 1.74 ± 0.1 g dry weight, based on 24 dung samples.

For all three sites, woody plant materials constituted > 80% of the dry weight of the dung samples during the dry season (Fig. 4). These were made up of the bark and the pith of shrubs and trees. Herbaceous plant materials such as bulbs contributed a similar amount for all the sites while seeds contributed minimally to the porcupine diet. Herbaceous plant materials were strongly represented in porcupine diet during the wet season at Roodeplaat, but was much lower at all sites during the dry season.

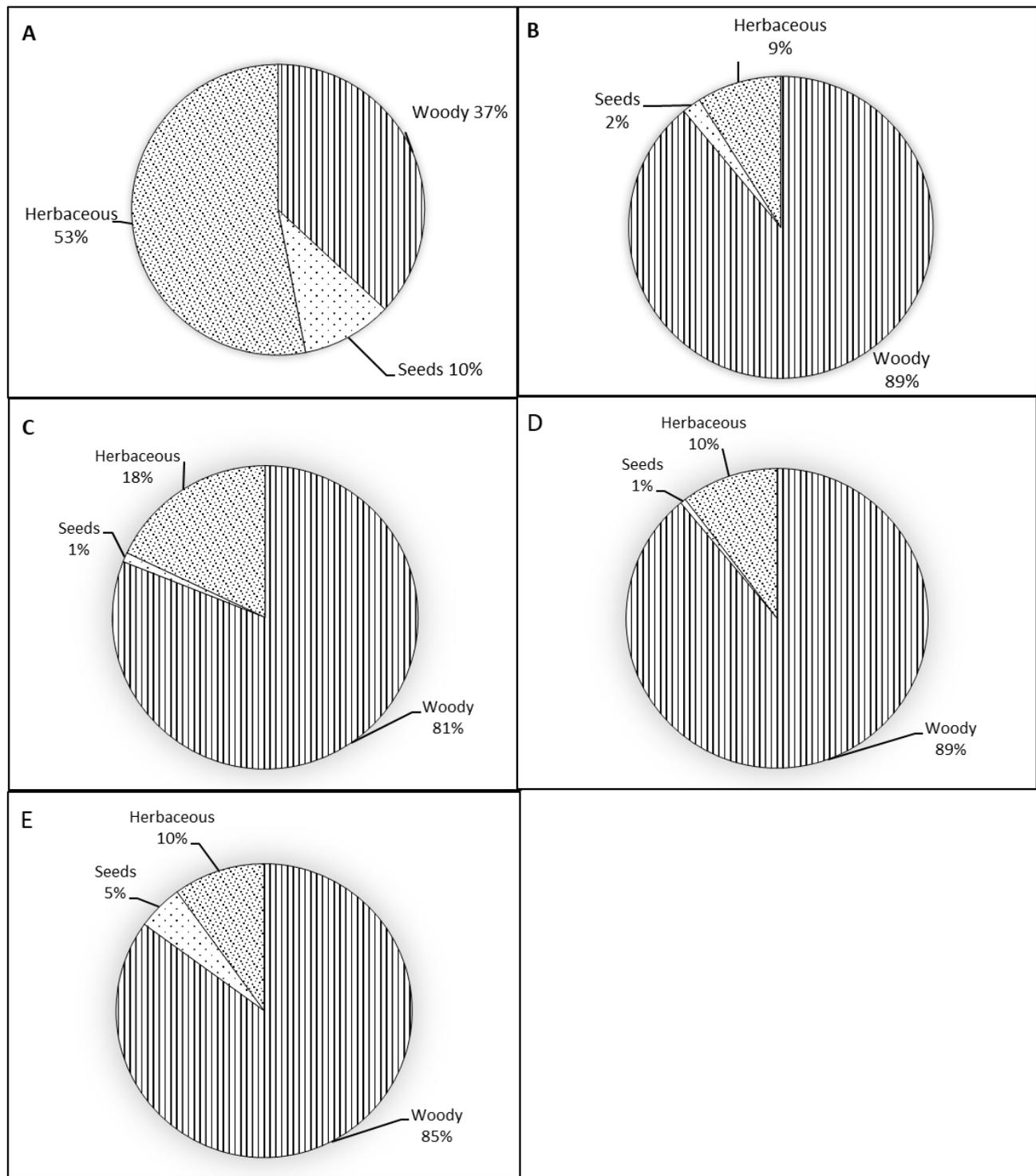


Fig. 4. Food constituents of a porcupine diet at Roodeplaat, Goss and Bisley. (a) Wet season diet at Roodeplaat, (b) dry season at Roodeplaat, (c) wet season diet at Bisley, (d) dry season diet at Bisley and (e) dry season diet at Goss.

DISCUSSION

We found that spatial and temporal variation in food availability may result in changes in food preference from one habitat to another during different times of the year. For example, Yeaton

(1988) found that porcupines showed a preference for *Burkea africana* trees over *Vachellia* spp. in the Nylsvley Nature Reserve in Limpopo Province of South Africa. In the Bokkeveld Plateau in the Northern Cape Province of South Africa, porcupines consumed the more abundant geophytes of the over hundred species available (Bragg et al. 2005). Like *Vachellia* species, there has been documented information on other herbivores such as the African elephant feeding on *S. africana* (see Shannon et al. 2008) even though the tree produces poison in the form of latex (Lennox and Bamford 2015).

In seasonal environments such as of this study, wild fruits and bulbs are mainly available in the wet season and may thus constitute part of the diet of porcupines (Bragg et al. 2005; Mori et al. 2017). We found that porcupines utilised different food resources (herbaceous plant material, fruits and bulbs, tree bark) between seasons, which is related to seasonality of availability as reported in other studies (e.g., Alkon 1999; Bragg et al. 2005; Mori et al. 2017). Different trees were targeted and utilised by porcupines in the different areas. Although *V. robusta* occurred at two sites, the species was only utilised at Roodeplaat, which partly supports the notion that porcupines target the most abundant plants. However, *V. robusta*, *V. nilotica* and *D. cinerea* were also abundant at Goss but were not utilised. From this, it can be concluded that porcupines have a significant preference for particular food, but that this preference is site specific. We are unable to speculate on what could drive this site-specific utilisation of the *Vachellia* spp.

The porcupine preference for feeding on the bark of certain trees over others has been reported in other studies (Yeaton 1988; Hafeez et al. 2011; Laurenzi et al. 2016). The current study found that there was more utilisation of woody material during the dry season at all the sites, however, it was also evident that woody material is one of the major constituents of a porcupine's diet even during the wet season (see Fig. 3). Although these findings are consistent with the suggestion that the Cape porcupine is a generalist herbivore, we noted that the utilisation of woody plants is limited to only a few species at each site. Similarly, the North American porcupine (*Erethizon dorsatum*) feeds on the phloem of *Pinus ponderosa*, an evergreen coniferous tree during the dry winter season and as such can be said to be a selective feeder (Snyder and Linhart 1997). The Cape porcupine can also be regarded as a selective feeder, at least on woody plants. The findings suggest that porcupines switch from grazing to browsing when food resources become scarce in the dry season.

Tree damage by porcupine was through debarking of the lower parts of the trees (Fig. 2), up to 60 cm height and in some cases, resulting in complete debarking. Ringbarking may sometimes lead to the death of a tree. However, in most cases scars on the tree may not kill it but negatively influence growth (Vospornik 2006; Wigley et al. 2019). Large scars may compromise the lifespan of a tree. Some trees may recover from the damage manifesting through scars by adding new layers

of growth to cover the damaged area (Cleary and Holmes 2011). Other scars are; however, permanent (Nichols et al. 2016). Bark and root damaged trees may likely be attacked by insects and fire, in some instances, the latter may result in death of the tree.

Generally, elephants are viewed as the main herbivores involved in controlling tree densities in savannas (Shannon et al. 2008). Elephant feeding behaviour is different from other large browsers because they can knock down large trees (Wigley et al. 2019; Thornley et al. 2020). The death of trees as a result of elephant herbivory creates open spaces in savannas and thus creates microhabitats that can be used by other smaller animals (Kerley et al. 2008). Ringbarking of a seedling, leading to the removal of the entire seedling by porcupines can have the same effects on the tree densities. In Pakistan, a recorded damage of 60% on *Pinus roxburghii* and 42% on *Robinia pseudoacacia* in different areas of the Tarbela Watershed Management Project was caused by porcupines (Khan et al. 2000). In addition, Khan et al. (2000) reported that seedlings of *Bombax ceiba*, *Dalbergia sissoo*, and *Eucalyptus* spp. were up-rooted by the Indian crested porcupine after transplantation.

Although the combination of savanna determinants like fire and herbivory appeared sufficient to prevent tree growth, woody plant encroachment is a major problem in many savannas (Ward 2005; O'Connor et al. 2014). The three study sites are in mesic savannas which are undergoing woody plant encroachment (O'Connor et al. 2014). In the current study, one of the study sites (Bisley) has megaherbivores (giraffes), but unlike elephants their foraging behaviour has minimum effects on vegetation density as they feed mainly on the leaves and twigs of tree branches. The foraging behaviour of elephants has been documented for reducing tree density and possible effects on ameliorating woody plant encroachment. The Cape porcupine seem to play similar roles but relative to their body size and numbers, their effects are smaller. Tree mortality brought about by porcupines foraging behaviour as observed on young individuals of *V. nilotica* at Bisley decreases structural homogeneity of the woody plant layer which is may be desired by reserve management in woody plant encroached ecosystems. Unlike elephant-induced damage on woody plants, which may lead to resprouting of damaged trees (Thornely et al. 2020), porcupine activities as observed at Bisley and Roodeplaat consists of digging and cutting out the trees below ground so that chances of resprouting are minimal. Ringbarked *S. africana* trees are unlikely to flower and produce seeds as carbohydrate reserves are used for recovery (Hölttä et al. 2006). This has implications on population dynamics of the species and vegetation structure.

CONCLUSIONS

This study demonstrated the importance of cryptic herbivores in structuring savannas. Herbivores directly influence the densities and distribution of plants through their foraging activities. For the Cape porcupine, the targeted tree species may be problem plants, such as the woody plant encroacher, *V. nilotica*, at Bisley. *Spirostachys africana* is known to form mono-specific stands while *V. robusta* dominated the low hills at Roodeplaat. Porcupines in these study sites can be said to be biological control agents in the sense that their impact on these tree species reduces the dominance of the species so that there is taxonomic and structural heterogeneity in the woody plant layer. Studies to investigate the reproductive performance of ringbarked trees and selection of tree size classes as well as species by the Cape porcupine are required. In addition, studies that consider vegetation utilisation by the Cape porcupine in contrasting precipitation regimes, such as semi-arid, mesic, and humid savannas, are also required for comparative purposes. Predictions of climate change suggest that southern Africa will experience more arid conditions, which may increase the contribution of woody plants to porcupine diets.

List of abbreviations

ANOVA, Analysis of variance.

ARC, Agricultural Research Council.

GP, Gauteng (province of South Africa).

KZN, KwaZulu-Natal (province of South Africa).

NRF, National Research Foundation.

SE, standard error of the mean.

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Supplementary materials

Table S1. Woody plant species available to the Cape porcupine in three mesic savanna sites in South Africa. (download)