

Resource use and the nutritional status of sable antelope in the Okavango Delta region of northern Botswana

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Abstract

The resource-use patterns and nutritional status of sable antelope herds were investigated in the Okavango Delta region of northern Botswana for comparison with those documented for declining sable antelope populations elsewhere in southern Africa. GPS collars recorded the relative use of floodplain, upland and wooded grassland habitats by the sable herds while VHF beacons facilitated locating the herds for direct observations on feeding. Surprisingly, the sable herds made greatest use of upland grasslands, rather than the floodplain grasslands exposed after floodwater had receded, during the dry season months. In the upland grasslands, they exploited tall, fibrous grass species that retained quite high levels of greenness through the dry season. This ability, together with partial use of the floodplain and some browsing on new leaves and flowers, helped maintain dietary nitrogen and phosphorus levels, as indicated by faecal nutrient levels, above maintenance thresholds through the dry season. Hence, the sable herds in the study region did not seem to be limited nutritionally under the rainfall and flooding conditions prevailing during the study.

Key words: Botswana, *Hippotragus niger*, nutritional status, Okavango Delta, resource use

Résumé

Les schémas d'utilisation des ressources et le statut nutritionnel de hardes d'antilopes sable ont été étudiés dans la région du delta de l'Okavango, dans le nord du Botswana, pour les comparer à ceux qui sont documentés pour d'autres populations de ces antilopes qui sont en déclin ailleurs en Afrique australe. Des colliers GPS ont

enregistré la fréquentation relative des habitats de plaines inondables, des terres surélevées et de prairies arborées par les antilopes sable tandis que des balises VHF facilitaient la localisation des hardes pour observer leur alimentation en direct. Étonnamment, pendant la saison sèche, les hardes de sable fréquentaient surtout les prairies élevées, plutôt que celles des plaines inondables exposées après la décrue. Dans les prairies surélevées, elles consommaient des espèces d'herbes hautes et fibreuses qui restaient assez vertes pendant toute la saison sèche. Cette capacité, tout comme la fréquentation partielle de la plaine inondable et la consommation d'une certaine quantité de jeunes feuilles et de fleurs, a permis de maintenir le taux d'azote et de phosphore du régime alimentaire, comme l'indique le taux fécal de ces nutriments, au-dessus du seuil requis, pendant toute la saison sèche. Donc, les antilopes sable de la région étudiée n'ont pas semblé être limitées, au point de vue nutritionnel, par les conditions dues aux chutes de pluie et aux inondations observées pendant l'étude.

Introduction

Sable antelope (*Hippotragus niger*) have recently declined substantially in abundance in South Africa's Kruger National Park (Ogutu & Owen-Smith, 2005; Owen-Smith *et al.*, 2012a), raising questions about possible causes. Particularly in contention is whether this decline was (1) an outcome of habitat desiccation following several years of consistently low rainfall, or (2) a consequence of heightened predation or competition, due to the augmentation of water points which spread the presence of water-dependent grazers such as zebra (*Equus quagga*) and buffalo (*Syncerus caffer*) into the sable range. Our study was aimed

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at investigating the resource dependency of sable antelope in a part of their distribution range where the species had remained generally abundant. Periodic aerial counts showed little overall change in sable numbers in northern Botswana since 1990 (Department of Wildlife and National Parks, unpublished data), apart from a local decline in the Okavango Delta region. Changing surface-water availability would not be a factor in this region, nor had the abundance of predators or competing grazers changed. Accordingly, our study was focused on the procurement of food resources in terms of the grass species consumed and the retention of green foliage by these grasses through the dry season. Uplands soils derived from Kalahari sand are infertile and support predominantly unpalatable grass species. Grazing ungulates are restricted to the upland regions during peak flooding through the early dry season, but later in the dry season, the receding floodwaters expose regenerating green foliage in the temporarily inundated grasslands. The availability of this green foliage should alleviate the nutritional stress that is normally most intense for grazers towards the end of the dry season.

In the Kruger National Park, sable antelope consume a wide range of grass species, but select strongly for greener grass during dry season months (Macandza, Owen-Smith & Cain, 2012a; Owen-Smith, le Roux & Macandza, 2013). Elsewhere, sable depends on grassy valleys termed 'dambos' to provide green forage through the dry season, especially following burning (Estes & Estes, 1974; Grobler, 1981; Magome *et al.*, 2008; Parrini & Owen-Smith, 2010). Although dependent on access to surface water during the dry season, sable drink at intervals of 3–4 days and can travel several kilometres to and from water points (Cain, Owen-Smith & Macandza, 2012). Other grazers favouring relatively tall grass may compete with sable for food (Macandza, Owen-Smith & Cain, 2012b). The overall distribution of sable antelope within the Kruger Park appeared negatively related to the abundance of ungulates serving as principal prey species for lions (*Panthera leo*), emphasizing the importance of predation as a limiting factor (Chirima *et al.*, 2013).

Accordingly, we expected that:

1 Sable would concentrate on floodplain grasses during the late dry season months when the receding flood waters promoted green grass regrowth, and utilize both upland and floodplain grasslands during the wet season when green grass was widely available.

2 Sable would feed on a wide range of grass species during the wet season months, but restrict their diet to those grass species that remained greenest during the dry season.

3 Through accessing the green grass on the floodplain during the dry season, sable would maintain faecal nitrogen and phosphorus levels in their dung above maintenance levels throughout the year.

Methods

Study area

The study was situated in the Kwedi, Duba Plains and Mapula concessions, located in the north-east of the Okavango Delta in northern Botswana. Specific details of the region and vegetation types are provided elsewhere (Hensman, 2012). Annual rainfall recorded at Vumbura Camp amounted to 500 mm in 2009 and 436 mm in 2010, compared with the long-term mean of 513 mm recorded nearby at Shakawe and Maun (1964–1994, McCarthy, Bloem & Larkin, 1998). The first rainfall ending the dry season occurred at the end of October in 2009 and during mid-November in 2010. In both 2009 and 2010, the Okavango Delta experienced exceptionally high floods due to high rainfall in the catchment in Angola. The floodwater reached its peak in the Kwedi concession in mid-May 2010, after which water levels remained high until the beginning of July. Thereafter, flooding subsided until the floodplain was completely exposed in mid-September 2010. This pattern was similar in 2009, although not documented specifically.

Vegetation types were mapped using Google Earth (CNES/SPOT image dated 31/05/2008). For the purposes of this study, the eight vegetation types distinguished by Hensman (2012) were grouped into three habitat types differing in the composition of the grass layer: upland grassland, upland woodland and floodplain grassland (Fig. 1). Digitizing errors were fixed using standard topology generation procedures implemented in ArcMap 10.0. Temporal changes in greenness within these habitat types were obtained using 16-day composites of MODIS Normalized Difference Vegetation Index (NDVI) images (MODISv5), representing December 2009, January 2010 and August 2010 to November 2010. Comparisons of greenness were restricted to the upland and floodplain grassland habitats because of the potentially confounding influence of greenness in the tree layer on greenness in the upland woodland.

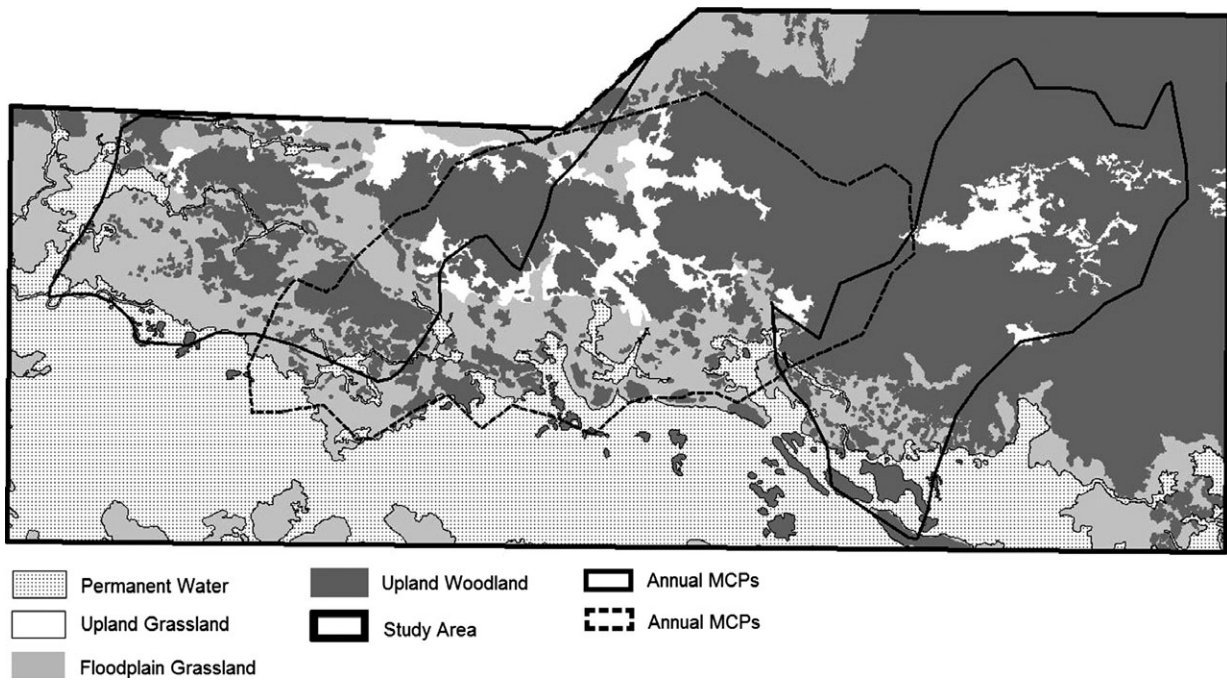


Fig 1 Mapped distribution of the three habitat types in the study area, with the outlines of the home ranges of the three sable antelope herds imposed

Data collection

One adult female from each of the three sable herds present in the study area was fitted with a GPS collar allowing remote download of stored data, provided by Africa Wildlife Tracking (<http://www.awt.co.za>). These three herds occupied adjacent home ranges that overlapped only marginally. Collars were scheduled to record GPS locations hourly. The first two GPS collars were fitted in August 2009 on the Eastern and Western herds, and the third one in October 2009 on the Central herd. GPS devices in the collars placed on the Eastern and Western herds stopped delivering data around the beginning of December 2009 and were replaced in March 2010. The collar placed on the Central herd failed to deliver data after March 2010 and could not be replaced. Collars were removed in November 2010. Hence, habitat occupation by the sable under wet season (December–March) conditions was represented thoroughly for one herd and fragmentarily for the other two herds. Habitat occupation by the Central herd was recorded for only the terminal part of the 2009 dry season and not at all for the dry season of 2010.

Occupation of habitat types by sable was based on daily GPS locations recorded at 08:00, representing the time of

day when foraging activity predominates (Owen-Smith, Goodall & Fatti, 2012b). To simplify the analysis, GPS records from those herds with functioning collars at the time were combined during the months when direct foraging observations were also recorded. In total, 322 GPS locations were recorded at 08:00 and formed the basis for the analysis of habitat use (49 in December, 31 in January, 62 in August, 59 in September, 62 in October and 59 in November).

For observations on food selection, herds were located during either the morning or afternoon foraging sessions, using the VHF beacons included in the collars. All three herds were habituated to tourist vehicles and could be approached to within 20 m, even on foot. While animals in the herd under observation were foraging, we defined the foraging site as the area where the majority of the herd had been feeding on the 15th min of the hour. Once the herd had moved off, the location of a feeding site was confirmed using fresh hoof prints and signs of fresh grazing. The habitat type and predominant grass species present were noted. We recorded the grass species present within up to ten 1×1 m quadrats placed every 3 m along the foraging path. If there were no bite marks within a quadrat, an additional quadrat was placed a

metre further along the path until fresh bite marks were enclosed. In each quadrat, we noted those grass species that had been grazed and counted the number of bites taken from each tuft. A grass species scored as grazed if at least one fresh bite was found on any of the tufts within any of the quadrats. A bite was defined as an area of cropped grass that could be covered by a closed fist. All sedges were grouped as 'sedges' (including *Cyperus denudatus*, *C. haspan*, *C. longus*, *Fimbristylis longiculmus* and *Schoenoplectus corymbosus*). Tuft greenness was estimated as the proportion of leaves in the tuft that were green, classified into eight categories (0%; 1–10%, 11–25%, 26–50%, 51–75%, 76–90%, 91–99%, 100%). Direct observations of foraging made during morning or afternoon sessions were assumed to be independent samples of food choices. Foraging observations were switched to a different herd at least every third day of data collection. In total, 158 independent samples were collected: 83 during December 2009–January 2010 and 75 during August 2010–November 2010. Palatability ratings for grass species were taken from van Oudtshoorn (1999). For assessing nutritional status from faecal samples, dung pellets deposited during foraging observations were collected later from the top of the piles to avoid soil contamination. Samples were air-dried in brown paper bags and submitted to BemLab (<http://www.bemlab.co.za>) for analysis for nitrogen (N) and phosphorus (P). A Leco instrument and Bray II extraction were used, respectively, followed by analysis on an inductively coupled plasma spectrometer. Results were expressed as percentage of dry matter. Six samples per month (two from each herd) were collected from December 2009 to January 2010 and from September 2010 to November 2010. Only four samples were collected during August 2010 as the Central herd could not be located then.

Data analysis

Use of upland grassland, upland woodland and floodplain was determined by counting the number of GPS locations at 08:00 in each habitat type each month as a proportion of the total number of GPS locations at this time recorded in all habitat types each month. The availability of each grass species in each habitat type was estimated as the number morning or afternoon foraging sites where the species was present divided by the total number of samples in these habitats. Following Owen-Smith and Cooper

(1987), the seasonal acceptability of each grass species was estimated as the number of samples where a grass species was eaten divided by the number of samples where the grass species was present in each season. Forage species that did not occur in ten or more foraging sites in at least one of the habitats or seasons were excluded from the analyses. The seasonal dietary contribution of each grass species was assessed as the number of bites recorded from each species divided by the total number of bites recorded across all species in each season. Chi-squared tests were used to compare these estimates between seasons, but derived *P*-values must be evaluated conservatively because bites are not independent. A greenness value for each species was obtained by averaging the mid-point greenness values for each species across all quadrats containing that species in each foraging site within each season. A one-way ANOVA with season as a factor was used to compare faecal N and P content between seasons. The sample size was too low to establish differences between herds in these nutritional measures. All statistical analyses were carried out in R (R Development Core Team 2008), version 2.13.1.

Results

The upland and floodplain grasslands exhibited closely similar levels of greenness, as represented by NDVI, from November 2009 through January 2010 in the wet season. The floodplain grasslands remained partially inundated during August into the beginning of September. From later July through mid-November 2010, the floodplain remained consistently much greener than the upland grassland (Fig. 2). The sable herds occupied mainly the upland woodland and floodplain during the wet season but shifted their foraging time to the upland grassland, at the expense of both of the former habitats, through the dry season months (Fig. 3).

Of the 46 different grass species encountered in foraging sites, 17 grass species occurred in more than ten foraging sites in at least one of the two seasons (Table 1). *Urochloa mosambicensis*, *Paspalum scrobiculatum*, *Panicum repens* and sedges were available mostly on the floodplain, and *Brachiaria brizantha* plus *Schmidtia pappophoroides* mostly in the upland grassland (Table 1). *Panicum maximum* had greatest availability in upland woodland, while *Aristida meridionalis*, *Eragrostis rigidior* and *Hyperthelia dissoluta* were commonly available in all three habitat types (Table 1).

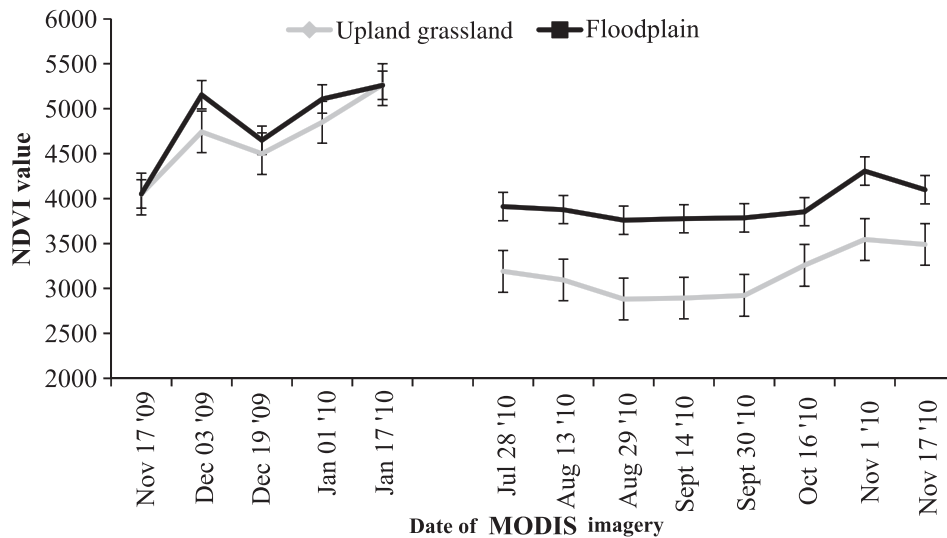


Fig 2 Trends in green vegetation biomass as indexed by Difference Vegetation Index (NDVI) from MODIS satellite imagery over the study period, comparing the floodplain and the upland grassland regions

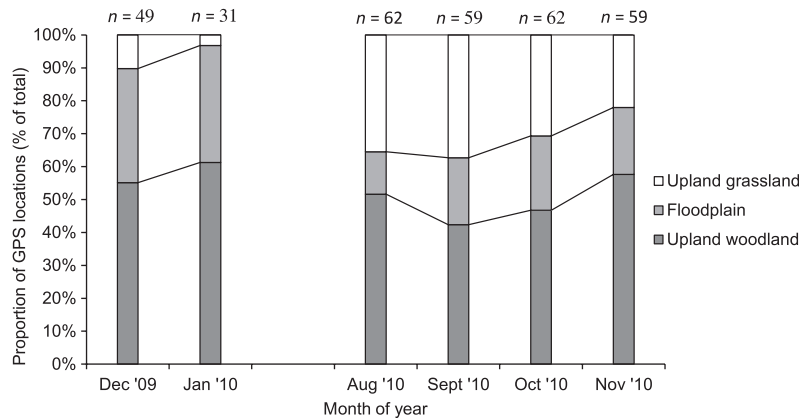


Fig 3 Change in the proportion of daily GPS locations in floodplain, upland grassland and upland woodland habitats for three sable herds combined through December 2009–January 2010 in the wet season and from August to November 2010 in the dry season

During December and January when grasses were mostly green, most grasses of high forage value, for example both *Panicum spp.*, and *Digitaria eriantha*, were highly acceptable to sable (Fig. 4a). Through August–November, some grasses of low-to-moderate forage value also became frequently accepted by sable. All of the species that were commonly encountered in foraging sites still had 10% or more of their leaves green even during the dry season months (Fig. 4b). Sedges remained greenest and were highly accepted representing 10% of the diet of sable during August–November although the floodplain was

used least then (Table 1). The greenest grass species in this period, *H. dissoluta*, was almost always eaten when present and made the greatest dietary contribution year-round (Table 1). *Aristida meridionalis* was equally important in the diet during the dry season months, but mostly ignored in the wet season. Frequently encountered but seldom eaten grasses included *A. junciformis*, *A. canescens*, *Pogonarthria squarrosa* and *E. lehmanniana*. Grass species restricted mostly to the floodplain contributed 24% of the diet of sable between December and January, but comparatively little during the dry season (Table 1).

Table 1 Habitat-specific availability, seasonal availability and seasonal dietary contribution of forage species encountered by three sable herds in more than ten foraging sites during at least one of the two seasons in the Okavango Delta, expressed as proportions

Forage species	Habitat-specific availability			Seasonal dietary contribution		Seasonal dietary contribution	
	Floodplain grassland	Upland grassland	Upland woodland	December-January	August-November	December-January	August-November
<i>Eragrostis rigidior</i>	0.95	0.54	0.46	0.58	0.67	0.05	0.05
Sedges	0.75	0.02	0.06	0.30	0.12	0.02	0.10
<i>Cynodon dactylon</i>	0.45	0.17	0.44	0.47	0.31	0.08	0.12
<i>Aristida junciformis</i>	0.43	0.07	0.02	0.22	0.09	0.00	0.00
<i>Aristida meridionalis</i>	0.40	0.63	0.39	0.40	0.55	0.01	0.17
<i>Panicum repens</i>	0.35	0.02	0.07	0.20	0.05	0.10	0.00
<i>Hyperthelia dissoluta</i>	0.33	0.39	0.18	0.41	0.16	0.25	0.15
<i>Pogonarthria squarrosa</i>	0.28	0.15	0.10	0.18	0.17	0.00	0.00
<i>Aristida canescens</i>	0.25	0.00	0.07	0.12	0.11	0.00	0.01
<i>Stipagrostis uniplumis</i>	0.25	0.20	0.23	0.17	0.25	0.01	0.01
<i>Schmidtia pappophoroides</i>	0.23	0.46	0.29	0.04	0.35	0.09	0.04
<i>Paspalum scrobiculatum</i>	0.23	0.00	0.01	0.12	0.03	0.08	0.00
<i>Urochloa mosambicensis</i>	0.23	0.00	0.00	0.14	0.00	0.06	0.00
<i>Aristida stipitata</i>	0.20	0.48	0.41	0.13	0.51	0.01	0.06
<i>Panicum maximum</i>	0.15	0.17	0.27	0.13	0.19	0.03	0.03
<i>Digitaria eriantha</i>	0.13	0.33	0.20	0.17	0.37	0.09	0.08
<i>Eragrostis lehmanniana</i>	0.10	0.17	0.11	0.06	0.13	0.00	0.00
<i>Brachiaria brizantha</i>	0.08	0.22	0.07	0.02	0.17	0.00	0.05

Chi-squared tests were used to compare differences in dietary contribution and availability between seasons. Bold numbers indicate comparisons that were significant at $P < 0.05$. Availability = the number of samples (grouped morning and afternoon foraging sites) where a species was present divided by the total number of samples for all vegetation types. Dietary contribution = the number of bites recorded from each species divided by the total number of bites recorded across all species in each season.

Diet quality as indicated by faecal N and P levels was substantially higher in December and January than during August–November (Fig. 5; N: ANOVA, $F_{1,37} = 4.24$, $P < 0.001$; P: ANOVA, $F_{1,37} = 8.71$, $P < 0.001$).

Discussion

Rather than concentrating in the floodplain grasslands as floodwater subsided during the late dry season, the sable herds shifted their grazing more towards the upland grasslands at this time of the year, contrary to expectations. All three herds also shifted their home ranges further from the floodplain in the dry season and made greater use of the upland vegetation types at this time of the year possibly due to displacement by competing grazers (Hensman, 2012). Nevertheless, faecal nitrogen levels for these sable herds remained above the maintenance threshold (10–12 g kg⁻¹ as dry matter; Grant *et al.*, 2000) through this period, except August before the floodwater had retreated. They were also above those recorded for a sable

herd in the Punda Maria region of Kruger Park during the dry seasons of both 2006 (~11 g kg⁻¹) and 2007 (~12 g kg⁻¹; Macandza, 2009). Even lower faecal nitrogen levels (under 9 g kg⁻¹) had been recorded for sable herds in Kruger Park in 2002 when drought conditions prevailed (Henley, 2005). In Pilanesberg Game Reserve where sable was thriving, faecal nitrogen levels remained between 11 and 13 g kg⁻¹ throughout the dry season months (Magome *et al.*, 2008). In the nearby Kgaswane Mountain Reserve, faecal nitrogen levels of sable dropped as low as 12 g kg⁻¹ in the late dry season of a year when no burning occurred, but were elevated as high as 16.5 g kg⁻¹ in the preceding year when green flush became available in newly burnt grassland (Parrini & Owen-Smith, 2010). Phosphorus levels of around 2.4 g kg⁻¹ retained by the Okavango sable herds through the late dry season were similar to those exhibited by Kruger Park sable during the dry season in 2006, but higher than those shown in Kruger Park in the following year (Macandza, 2009). At Kgaswane, faecal phosphorus levels amounted to 2.4 g kg⁻¹ in the dry season

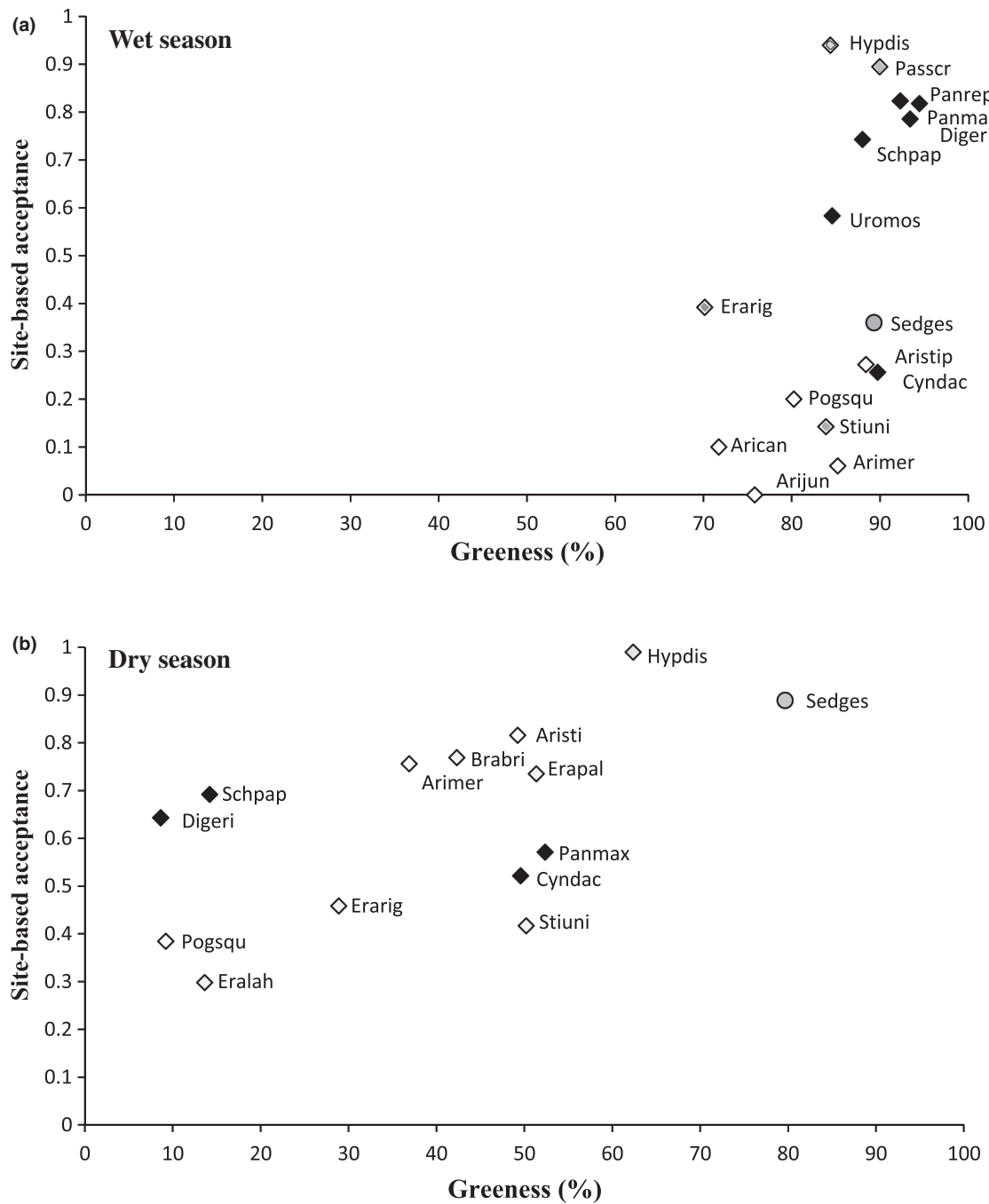


Fig 4 Acceptance frequencies of grass species encountered in more than ten foraging sites in relation to their averaged seasonal greenness. ♦ = high value forage; ◇ = poor value forage; ◐ = medium value forage; and ● = unlisted value forage (from van Oudtshoorn, 1999). Arican – *Aristida canescens*; Arijun – *Aristida junciformis*; Arimer – *Aristida meridionalis*; Aristip – *Aristida stipitata*; Brabri – *Brachiaria brizantha*; Cyndac – *Cynodon dactylon*; Digeri – *Digitaria eriantha*; Eralah – *Eragrostis lehmanniana*; Erarig – *Eragrostis pallens*; Erapal – *Eragrostis rigidior*; Hdis – *Hyperthelia dissoluta*; Panmax – *Panicum maximum*; Panrep – *Panicum repens*; Passcr – *Paspalum scrobiculatum*; Pogsqu – *Pogonarthria squarrosa*; Stiuni – *Stipagrostis uniplumis*; Schpap – *Schmidia pappophoroides*; and Uromos – *Urochloa mossambicense*. (a) Wet season months (December–January); (b) Dry season months (August–November)

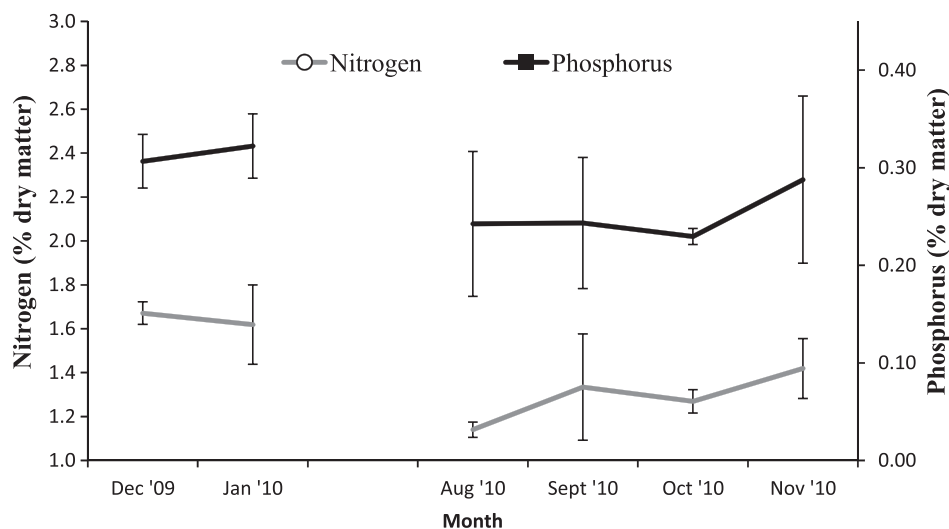


Fig 5 Trends in faecal nitrogen and phosphorus contents in sable antelope dung samples (mean values plus 95% confidence limits)

of the year when no burning occurred and 2.9 g kg^{-1} in the year when burning was followed by new regrowth (Parrini & Owen-Smith, 2010). Overall, these comparisons indicate that the three sable herds observed in the Okavango region were not nutritionally limited during the study period. This does not exclude the possibility that nutritional limitations could arise under drier conditions than those prevailing during the study period.

The sable herds in the Okavango region were apparently able to maintain their nitrogen, and hence protein, intake by concentrating their grazing on grass species and sedges in the upland grasslands that retained a substantial amount of green leaf through the late dry season months, most notably *H. dissoluta*. *Hyperthelia dissoluta*, commonly known as yellow thatching grass, is a tall and hence fibrous bunch grass regarded as of low forage value for cattle (van Oudtshoorn, 1999). A substantial dietary contribution at this time of the year was also made by *A. meridionalis* (giant three-awn grass), likewise a tall, fibrous grass rated of low forage value. Nevertheless, the sable also commonly consumed some of the more palatable grass species that presented mostly brown material during this time of the year, such as *D. eriantha* (common finger grass) and *S. pappophoroides* (sand quick grass). *Cynodon dactylon* (couch grass) was also commonly grazed where it grew in thick mats on termite mounds. Furthermore, the sable spent around 20% of their foraging time in the floodplain grasslands in the late dry season, with this green supplement probably contributing to the nutritional level maintained. A further contribu-

tion probably came from browsing on flowers and new leaves recorded for the Okavango sable during October–November (Hensman *et al.*, 2012). The concentration of the sable herds in the floodplain during the wet season months may have been related to their elevated nutritional requirements through this period, which spans late gestation and early lactation (sable calves are typically born through February–March in southern Africa; Skinner & Chimimba, 2005).

Hyperthelia dissoluta, along with other grass species rated of low nutritional value to cattle, was also highly utilized by sable herds in the Pretorius Kop region of Kruger National Park (Owen-Smith, le Roux & Macandza, 2013). Other studies have documented the high contribution by tall, stemmy grass species to the diet of sable (Wilson & Hirst, 1977; Grobler, 1981; Parrini, 2006). Sable antelope have relatively narrow muzzles, potentially facilitating their ability to extract green leaves from among stems in tall grass, although we observed that they commonly ingested stems along with leaves.

Overall, our findings indicate that the sable herds that we observed in the Okavango Delta region were not limited nutritionally; at least, not under the rainfall and flooding conditions prevailing at the time of our study. This was partly dependent on their capacity to exploit the tall and hence fibrous grass species prevalent on sandy, nutrient-deficient soils in the upland grassland region at times when they were inhibited from exploiting the floodplains grasslands due to the concentration of other grazers there. Although these sandy soils appear deficient in nitrogen and mineral nutri-

ents, the water infiltration that they allow seems to promote a greater retention of green foliage through the dry season than is typical of the more palatable grasses prevalent on clayey soils. The ability of sable antelope to exploit these conditions, less attractive to other grazers, contributes to the distinct grazing niche that they occupy.

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