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Source: Tropical Conservation Science, 13(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/1940082920958397

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Research Article

Tropical Conservation Science
Volume 13: 1–11
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Post-Release Monitoring Diet Quality and Nutritional Status of Reintroduced Burchell's Zebra and Blue Wildebeest in Maputo Special Reserve, Mozambique

Luís Jr. Comissario Mandlate[1,2] and Flávio H. G. Rodrigues[1]

Abstract

The reintroduction of wild animal species into conservations areas is widely used to restore populations of species endangered with extinction. The assessment of the quality of the diet and the nutritional status of the animals is crucial to the success of herbivore reintroduction programs, given that adequate nutrition is essential to ensure the survival and fertility of ungulates. Given this, the present study investigated the quality of the diet and nutritional status of Burchell's zebra (*Equus burchelli*, Smuts 1832) and blue wildebeest (*Connochaetes taurinus*, Burchell 1823) reintroduced into Maputo Special Reserve (MSR), in southern Mozambique. The study was conducted between July 2016 and June 2017, and the data were collected through direct observation, by driving a vehicle along the roads within the reserve that pass through the vegetation cover where zebra and wildebeest are known to occur most frequently. The composition of the diet and specific feature of the grass grazed by the two species, such as greenness (an indication of food quality) were assessed. Crude fecal protein and phosphorus were determined to evaluate the nutritional status of the two herbivore species. Both herbivores were pure grazers, consuming a diet composed entirely (100%) of grass. *Aristida barbicollis* was the principal component of the diets of both zebra and wildebeest and both species grazed almost entirely on green grass (91–100% of greenness). However, wildebeest consumed significantly more green grass (which has a better nutrient content) than zebra, which tolerated a considerably larger proportion of browner grass in both seasons. The levels of crude protein and phosphorus in the zebra and wildebeest fecal samples were not below threshold of nutritional stress recommended for large southern African herbivores, which indicates that neither the zebra nor the wildebeest populations in MSR are undernourished at the present time and that the quality of the forage found in the study area is not a factor limiting the persistence of the reintroduced populations of either species.

Keywords

nutritional status, zebra, wildebeest, Mozambique

The patterns of forage selection by herbivore are related with spacial and temporal variations in the quality and quantity of this resource (Owen-Smith, 2002; Owen-Smith & Novellie, 1982). During the rainy season, plants tend to have a low fiber content and high nutrient concentrations, with grasses providing forage of the highest quality for herbivores, whereas in the dry season, the fresh, nutrient-rich green leaves are transformed into an unpalatable strawy material, which may nevertheless be the only forage available until the vegetation sprouts again with onset of the rains

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Received 29 April 2020; Accepted 22 August 2020

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(Halsdorf, 2011). During this season, then, large herbivores face a major challenge to satisfy their nutritional needs (Ahrestani et al., 2012).

This seasonal variability forces herbivores to select alternative species or parts of the plant, which results in a shift in the composition of their diet (Owen-Smith & Cooper, 1987; Treydte et al., 2007). This response includes a spatial component, with plant communities being selected based on the proportion of more nutritious species, a strategy that can ensure the intake of plants with a greater nutrient content (Ben-Shahar & Coe, 1992; O'Reagain et al., 1995; Owen-Smith & Cooper, 1987).

The nutritional value of a forage is best assessed by determining its ability to meet the nutritional requirements of the grazing animal (Ruyle, 1993) and this assessment can be based on the amount of protein, phosphorus, and energy that the plants contain. However, large herbivores may not be selective, feeding on a variety of species or plant parts, which hinders the reconstruction of the nutritional composition of their diets (Gutbrodt, 2006; Macandza et al., 2013). In this context, the nutrient content of the feces is widely used as an indicator of the nutritional status of a herbivore's diet (Owen-Smith & Novellie, 1982), given that it provides an approximate estimate of the concentration of nutrients in the plant material consumed by the animal (Halsdorf, 2011; Kamler & Homolka, 2005; O'Shaughnessy et al., 2014).

The assessment of the nutritional status of an ungulate is important for the development of adequate management measures (Wrench et al., 1997). Fecal nitrogen and phosphorus concentrations have been widely used to assess the nutritional status of herbivores (Grant et al., 1995, 2000; Kamler & Homolka, 2005; Macandza et al., 2013; Weel et al., 2015; Wrench et al., 1997). The findings of previous studies indicate that a crude protein content of below 5–9% indicates a level of dietary deficiency, which is likely to cause nutritional stress in grazers, and may be visible in a decline in body condition (Grant et al., 2000). In the case of fecal phosphorous, concentrations of less than 2.0 g per kg over prolonged periods have also been associated with reduced reproductive success (Grant et al., 2000; Wrench et al., 1997).

The reintroduction of wild animals into conservation areas has been widely used as a strategy for the restoration of populations of endangered species that have been affected by anthropogenic impacts such as habitat loss and poaching (Mathews et al., 2006; Rantanen et al., 2010). Reintroduction has been used increasingly as a wildlife management tool for both conservation measures and economic incentives (Fischer & Lindenmayer, 2000; Mathews et al., 2006).

The Maputo Special Reserve (MSR) is one of the conservation areas in Mozambique from which the populations of some wild herbivore were almost extirpated entirely between 1977 and 1992, during the civil war (Stalmans, 2015). A multi-year reintroduction program was established in 2010 in order to restore the populations of a number of herbivores, including Burchell's zebra (Equus burchelli, Smuts 1832) and the blue wildebeest (Connochaetes taurinus, Burchell 1823) using stock obtained from parks in South Africa and Swaziland (Stalmans, 2015).

Zebra are hind-gut fermenters and have been classified as non-selective grazers, being able to tolerate larger amounts of less nutritious plant material in their diets, whereas wildebeest are ruminants, and are more selective grazers (Bell, 1971; Duncan et al., 1990; Hack et al., 2002; Sinclair & Griffiths, 1982). Both species play a fundamental role in the ecosystem, its conservation, and contribute to its potential as a tourist destination (Stalmans, 2015).

Previous studies at the MSR (Mandlate, Arsenault, et al., 2019; Mandlate, Cuamba, et al., 2019). have focused on the diet and the habitat selected by reintroduced zebra and wildebeest. However, it is important to note that a number of other factors may also determine the success of reintroduction programs, including competition, predation, disease, management practises, and even environmental education initiatives in the study area (Griffith et al., 1989; Muposhi et al., 2014; Rantanen et al., 2010). The present study focuses primarily on the quality of the diet and the nutritional status of reintroduced Burchell's zebra and blue wildebeest, given that nutrition has a direct influence on the survival and fertility of these ungulates (Wrench et al., 1997).

The present study tested four predictions: (a) the diet selected by both herbivores will be of higher quality during the rainy season in comparison with the dry season, as indicated by higher concentrations of crude protein and phosphorus in the feces during the rainy season; (b) both herbivores will experience nutritional stress during the dry season; (c) the zebra, as a non-selective feeder, will tolerate a wider range of grass species of lower nutritional quality in comparison with the more selective wildebeest, which will have a more restricted diet, feeding primarily on higher quality grasses, and (d) as a consequence, the crude protein and phosphorus concentrations in the feces will be higher in the wildebeest than in the zebra.

Methods

Study Area

The study was carried out in the Maputo Special Reserve (MSR), in southern Mozambique (26°25′ S, 32°45′ E), which has an area of 1,000 km^2 (Figure 1).

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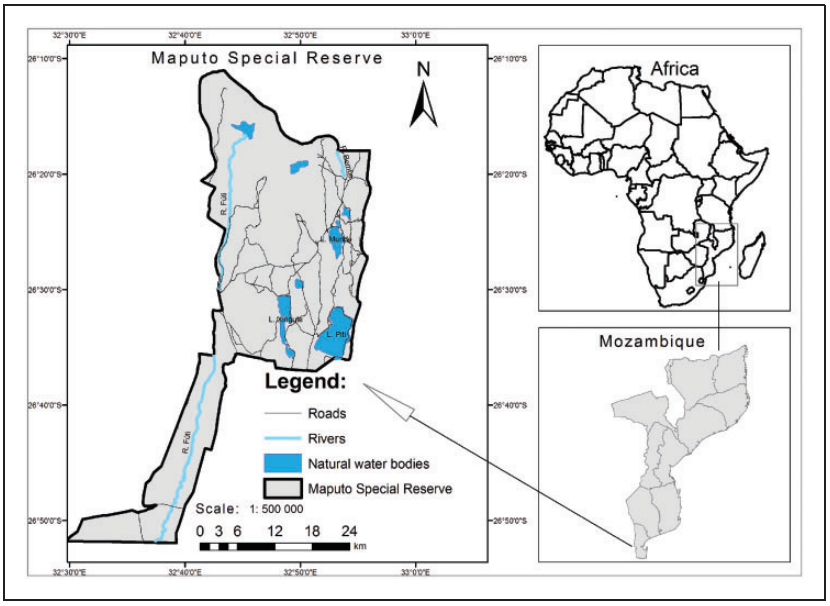


Figure 1. Location of Maputo Special Reserve, Southern Mozambique.

The current limits of the reserve are Maputo Bay to the north, the Indian Ocean in the east, the Maputo and Futi rivers, and a 2 km line east of the Salamenga–Ponta do Ouro road in the west, and the southern end of Lake Xingute and the southern limit of Lake Piti in the south. There are two distinct seasons – a hot rainy season (October-March) and a cooler dry season (April-September). The MSR receives an average of 690–1000 mm of rainfall annually (De Boer et al., 2000). The reserve is not fenced off and is encroached by human settlements and livestock in many places, with frequent wildfires during the dry season, and other illegal activities, such as hunting and fishing, occurring within its limits (Stalmans, 2015).

The predominant plant communities found in the study area (Online Appendix S1) include: (i) *Eucalyptus* plantation, (ii) dense coastal woody vegetation with species such as *Diospyros rotundifolia*, *Mimusops caffra*, and *Sideroxylon inerme*, and *Cyperus compactus* and *Monanthotaxis caffra* in the understory, (iii) semi-deciduous open forest dominated primarily by *Synzigium cordatum*, *Ziziphus mucronata*, *Phoenix reclinata*, and *Hyphaene coriaceae*, (iv) semi-deciduous forest dominated by *Terminalia sericea*, *Strichnos spinosa*, *Strychnos madagascariensis*, *Tabernamontana elegans*, and *Albizia adiantifolia*; (v) semi-evergreen forest dominated by arboreal species such as *Spirostachys africana*, *Monodora junodii*, *Balanites maughanii*, *Schotia brachypelata*, and *Afzelia quanzenzis*; (vi) shrub savanna, with species such as *P. reclinata*, *H. coriaceae* and *Vangueira infausta*, and 70% grassland cover, dominated by the grasses *Ischaemum fasciculatum*, *Digitaria eriantha* and *Setaria sphacelata*; (vii) arboreal savanna dominated mainly by grass species such as *D. eriantha*, *Panicum maximum*, *Themeda triandra*, *Schizachyrium sanguineum*, *Pogonarthria squarrosa*, *Fimbristilis* sp., *Salacia krausii*, *Eugenia capensis*, *Vigna unguiculata*, *Sporobolus africanus*, *Sporobolus nitens*, *Andropogon gayanus*, and *S. sphacelata*, while the arboreal component of this vegetation community is dominated by *Afzelia quazensis, Combretum molle*, *T. sericea*, *Strichnos madagascariensis,* and *Garcinia levingstonei*; (viii) riparian vegetation along the Futi River, with reed beds dominated by *Phragmites australis*, *Juncus kraussii*, and *C. compactus*. In places, these reed beds are fringed by patches of riparian forest dominated by *Ficus sycomorus*, *Syzygium cordatum*, and *Kigelia africana*. *Helichrysum kraussii* and *P. maximum* are found in the herbaceous layer, and (ix) mangrove forest bordering the bay and the deltas of the Maputo River and the Bembe Channel, dominated by *Avicennia marina* Vierh. and *Rhizophora mucronata* Lam. (De Boer et al., 2000; Macandza, 2011).

Since the start of the reintroduction program in 2010, the zebra population of the MSR has increased from 276 to 351 individuals, while the wildebeest population has gone from 303 to 446 (Hanekom & Cumbane, 2016). A number of other herbivore species are also found in the reserve (Hanekom & Cumbane, 2016), including African elephant (*Loxodonta africana*), with an estimated population of 400 individuals, as well as 2,611 common reedbuck (*Redunca arundinum*), 405 red duiker (*Cephalophus natalensis*), 257 gray duiker (*Sylvicapra grimmia*), 255 bushbuck (*Tragelaphus scriptus*), 200 impala (*Aepyceros melampus*), 350 kudu (*Tragelaphus*

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strepsiceros), 28 giraffe (*Giraffa camelopardalis*), 100 warthog (*Phacochoerus aethiopicus*), 255 bushbuck (*Tragelaphus scriptus*), and 230 nyala (*Tragelaphus angasii*).

Research Design and Data Collection

The present study followed Thomas and Taylor's (1990) Study Design I which was used to assess resource selection at a population level, given that individual animals were not identified. Field data were collected between July 2016 and June of 2017, and were grouped in two seasons: the dry season (which combined data from July–September 2016 and April–June 2017) and the rainy season (October 2016 through March 2017).

The study area was divided into its vegetation type (Online Appendix S1) and the data were collected by direct observation, with the vehicle being driven along the roads that traverse the vegetation types in which the zebra and wildebeest are known to be most common. Each type of vegetation was surveyed on 2–3 days, following a standard route. These routes were established based on a ground reconnaissance survey that determined the areas in the reserve where zebra and wildebeest were most likely to occur, and the areas that were inaccessible to these species. These inaccessible areas of the reserve were excluded from the analysis, given that the terrain was found to be inappropriate for either herbivore. Based on this, the data were collected in five habitat types in which the herbivore herds were encountered: eucalypt plantation (2,781.95 ha), arboreal savanna (1,27,081 ha), shrub savanna (1,31,862 ha), semi-evergreen forest (16,765.49 ha), and semideciduous open forest (661,490.88 ha).

The vehicle was driven at a mean velocity of 25 km/h, and transported two observers, who monitored the presence of ruminant herds along both sides of the road using binoculars (Zenith TEMPEST 8×30, 7.5° field). This monitoring was conducted during the peak ungulate feeding times, that is, in the early morning (6 h $30 - 10$ h 00) and late afternoon (15-h30 $-$ 18 h30). A total distance of 2,353 km was surveyed, with a mean distance of 196 km per month. An effort was made to sample as many herds as possible, although the vehicle did not return to the same area on a given day, to minimize the possibility of resampling the same herd at a given site.

Whenever a herd was detected during a survey, the vehicle was brought to a halt and a laser range finder (RZ900D Laser Distance Meter 6X) was used to determine the distance of the herd from the observer. During each encounter, an adult observed grazing was chosen as the focal animal, and it was assumed that its location represented the foraging site of its herd. Foraging sites were defined as the area where the animals were observed feeding $\geq$15 min. To reduce the likelihood that foraging by other herbivores would influence the assessment of forage selection by zebra and wildebeest, once the animals left the site, the research team immediately approached the foraging site on foot to identify freshly-grazed grass, which can be recognized by the lighter, more vivid colouration of the broken leaves and stems in comparison with older grazing (Macandza et al., 2012). The position of the site was recorded using a handheld GPS (GPS map XL, Garmin 62).

At each foraging site, a quadrat of 0.7 m^2 was established at the first identified evidence of recent grazing, with an additional eight quadrats being arranged around this central quadrat, two at each cardinal point (north, south, east, and west), spaced at least 2 m apart. If signs of fresh grazing were found in less than five of the nine quadrats sampled, an additional four quadrats were placed diagonally to the central quadrat.

Within each quadrat, the number of tufts (freshly grazed and ungrazed) of each grass species was recorded and identified, followed van Oudtshoorn (2014). For each grazed grass tuft, the greenness of the grass was recorded to provide an index of food quality. The greenness of the grass was estimated visually as the proportion of green leaves, following Walker's (1976) eight-point scale: 0%, 1–10%, 11–25%, 26–50%, 51–75%, 76–90%, 91–99% or 100% green.

Each foraging site was also surveyed visually for fresh feces, with samples of each stool being collected for analysis. The fecal samples were identified (zebra or wildebeest) based on their size and shape, following Stuart and Stuart (1993). The fecal samples of each herbivore species from the same location were aggregated into a single sample, which was placed in a paper bag and air-dried in the shade at the campsite. The minimum distance between sampling points was 200 m. A total of 244 points were sampled for the zebra and 120 for the wildebeest. The number of sampling points per road depended on the animals sightings.

Prior to the nutritional analysis, the fecal samples were oven-dried at 60°C over 48 hours and then ground to a homogeneous powder using a mortar and pestle (Codron et al., 2007, Grant et al., 1995). The Kjeldahl digestion method (Association of Official Analytical Chemists, 2001; Robbins, 1983) was used to determine the nitrogen content, and the amount obtained was converted into Crude Protein (CP) by multiplication by a factor of 6.25 (Van Soest, 1994). The phosphorus concentrations were determined using the standard spectrophotometer technique according to Association of Official Analytical Chemists (2001). The results of the fecal nitrogen and phosphorus analyses were expressed as a percentage of the dry fecal matter.

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All the nutritional analyses were conducted at the Mozambican Agricultural Research Institute (IIAM).

Data Analysis and Statistical Methods

In each season, the relative contribution of each grass species to the diet was calculated by dividing the number of species eaten in the season by the total number of species eaten during the study. The mean contribution of each grass species to the diet of the herbivores during each season was obtained by averaging the monthly values recorded during each season.

To obtain a single value of greenness, based on the categories of Walker (1976), for each grass species, the midpoints of the values recorded for each class were used to calculate a mean value for each species during the respective period. The contribution of each grass species to the diet of the herbivores was plotted against its mean greenness.

In each season, the greenness of the grasses grazed by the two herbivores was compared using Chi-square, with an $\alpha = 0.05$ significance level. For this, the classification of Walker (1976) was adapted to the characteristics of the data, with only four grass color categories being applied for analysis – (i) brown (grass 0–25% green), (ii) mainly brown (26–50%), (iii) mainly green (51–90%), and (iv) green (91–100%).

The Mean value of faecal crude protein (%) and phosphorus (g/kg) values were obtained by averaging the monthly values recorded during each season. A two-way ANOVA with an $\alpha = 0.05$ significance level was used to compare the mean protein and phosphorus levels between the two herbivore species and between seasons. In this analysis, the crude protein or phosphorus was the dependent variable, while the species and season were the factors. Prior to the analysis, the phosphorus concentrations were arcsine transformed to establish a the normal distribution.

A one-sample *t* test was applied to compare the minimum threshold of fecal phosphorus (2.0 g/kg) required to maintain grazers without suffering nutritional stress (Wrench et al., 1997) with the mean fecal phosphorus value obtained in this study (Ayres et al., 2007). The same approach was used to compare the minimum threshold of crude protein (5%) required to maintain grazers without suffering nutritional stress (Robbins, 1983) with the with the faecal crude protein value obtained in this study (Ayres et al., 2007). This was done in order to examine if the two herbivore species were or were not on nutritional stress in each season. All statistical analyses were carried out using R software (R Core Team, 2015).

Results

Grass Quality

Both herbivores were pure grazers, consuming a diet composed entirely (100%) of grass. Thirteen grass species were recorded in the zebra diet during the dry season, with 12 species being recorded during the rainy season. By contrast, the wildebeest fed on nine grasses in both seasons. *Aristida barbicollis* contributed most to the diets of both zebra and wildebeest throughout the year. *Digitaria eriantha* was the second most important grass for both herbivores in the rainy season, whereas in the dry season, *C. dactylon* was the second most important species for the zebra and *Brachiaria eruciformis* for the wildebeest (Figure 2).

Wildebeest consumed significantly more green (91–100% green) grass than zebra in both the dry ($x^2 = 136$; d.f. = 3; $p < 0.001$) and wet ($x^2 = 78.9$; d. f. = 3; $p < 0.001$) seasons (Figure 2). Wildebeest consumed more than 60% of green grass during the dry season and 70% in the wet season, while the zebra consumed 38% green grass in the dry season and 50% in the wet season. The zebra consumed considerably browner grass, in particular in the 0–25% green category, in both seasons (Figure 2).

Nutritional Status

The quantity of faecal crude protein varied significantly between zebra and wildebeest, and between dry and wet season ($F_{1;70} = 13.26$; $p = 0.0051$). The mean fecal crude protein for wildebeest was significantly higher than the mean fecal crude protein for zebra, in both seasons (Figure 3). In the dry season, the mean value recorded for the wildebeest was $5.0 \pm 0.68\%$, while that for the zebra was $4.07 \pm 0.554\%$, whereas in the wet season, it was $11.42 \pm 0.72\%$ for wildebeest and $6.03 \pm 0.32\%$ for the zebra. In both herbivores, then, fecal crude protein levels declined noticeably in the dry season, when the grass turned predominantly brown.

In the case of the fecal phosphorus levels, however, no significant variation was found among herbivore species or seasons ($F1;61 = 0.0028$; $p = 0.957$), or between the two herbivore species ($F1;61 = 3.35$; $p = 0.07$) or seasons ($F1;61 = 3.8527$; $p = 0.054$). During the dry season, the mean fecal phosphorus recorded for the zebra was 1.9 ± 0.29 g/kg, while it was 2.7 ± 0.41 g/kg for the wildebeest, whereas in the wet season, the mean was 2.72 ± 0.33 g/kg for zebra and 3.48 ± 0.60 g/kg for wildebeest (Figure 3).

The level of fecal crude protein was not significantly different from the threshold (5%) of nutritional deficiency in either the zebra ($t = -1, 66$; $df = 19$; $p = 0.11$) or the wildebeest ($t = 0.0085$; $d.f = 6$; $p = 0.99$) during the dry

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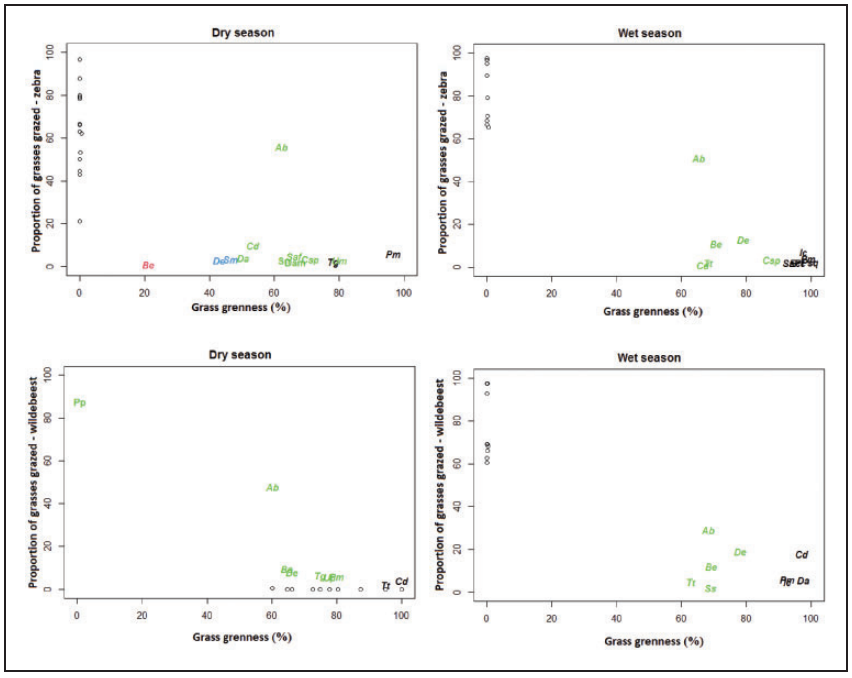


Figure 2. Percentage of Grass Grazed by Reintroduced Zebra and Wildebeest in Maputo Special Reserve, Mozambique, in Relation to its Greenness. *Ab, Aristida barbicollis*; *Be- Brachiaria eruciformis*; *Cd-Cynodon dactylon*; *Csp-Cynodon sp.*; *Da-Dactyloctenium australe*; *Dam-Díheteropogon amplectens; De-Digitaria eriantha*; *Ic-Imperata cylindrica*; *Pc-Panicum coloratum*; *Pm-Panicum maximum*; *Pp-Perotis patens*; *Psq-Pogonarthria squarrosa*; *Saf-Sporobolus africanus*; Ss-Setaria sphacelata; Sm-*Setaría megaphylla; Sn- Sporobolus nítens; Tg-Trichoneura grandiglumis*; *Tt-Themeda triandra*; *Um-Urochloa mosambicensis*; *Up-Urochloa panicoides*. Different Species Colors Represent the Classes of Their Greenness (an Indication of the Quality of the Food), Red Color: (0–25% - Brown); Blue Color (26–50% - Mainly Brown); Green Color- (51–90% - Mainly Green) and Black Color- (91–100% - Green).

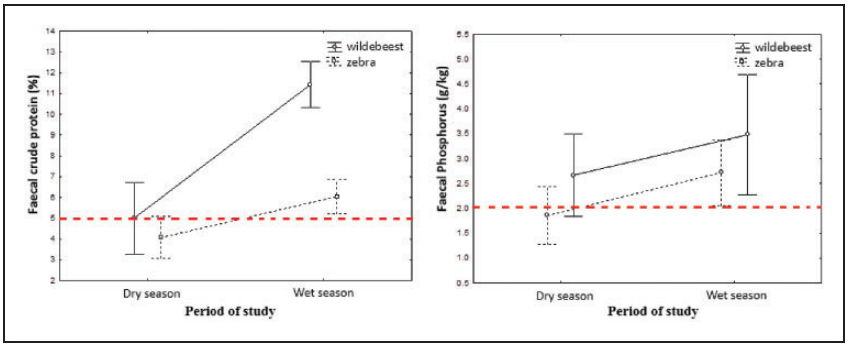


Figure 3. Mean Faecal Crude Protein and Faecal Phosphorus Levels With 95% Confidence Limits for Zebra and Wildebeest in the Maputo Special Reserve. Bars Denote 95% Binomial Confidence Intervals. The Dotted Red Line Indicates the Threshold Values of Crude Protein and Phosphorus Necessary for Grazers Maintenance.

season, while it was significantly higher than the threshold in both species during the wet season (Table 1).

Similarly, the mean fecal phosphorus levels did not differ significantly from the threshold for nutritional deficiency (2.0 g/kg) in the dry season, for either the zebra or the wildebeest. During the wet season, the mean fecal phosphorus levels were significantly higher than the threshold of nutritional stress for both zebra and wildebeest (Table 1). These results indicate that neither herbivore species was under any nutritional stress in relation to either crude protein or phosphorus, or in the dry or rainy seasons.

Discussion

The results of the present study indicate that the grass *Aristida barbicollis* contributed most to the diets of both herbivores species throughout the year. Even so, van

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Table 1. Comparisons of Faecal Crude Protein and Faecal Phosphorus Recorded for Reintroduced Zebra and Wildebeest in Maputo Special Reserve With the Thresholds Values Necessary for Grazers Maintenance.

	Values recorded in this study	One sample t-test	Nutritional status
Zebra			
Dry season			
Threshold faecal of crude protein for maintenance grazers (5%)	4.07 ± 0.554%	t = −1.6657, df. = 19, p = 0.11	+
Threshold faecal of phosphorus for maintenance grazers (2.0 g/kg)	1.9 ± 0.29 g/kg	t = −0.6284, df. = 25, p = 0.53	+
Wet season			
Threshold faecal of crude protein for maintenance grazers (5%)	6.03 ± 0.32%	t = 3.21, df. = 29, p < 0.0032*	+
Threshold faecal of phosphorus for maintenance grazers (2.0 g/kg)	3.48 ± 0.60 g/kg	t = 4.754, df = 19, p < 0.0001*	+
Wildebeest			
Dry season			
Threshold faecal of crude protein for maintenance grazers (5%)	5.0 ± 0.68 %	t = 0.0085, df. = 6, p = 0.99	+
Threshold faecal of phosphorus for maintenance grazers (2.0 g/kg)	2.7 ± 0.41 g/kg	t = 0.88, df. = 12, p = 0.22	+
Wet season			
Threshold faecal of crude protein for maintenance grazers (5%)	11.42 ± 0.72 %	t = 8.94, df. = 16, p < 0.0001*	+
Threshold faecal of phosphorus for maintenance grazers (2.0 g/kg)	3.48 ± 0.60 g/kg	t = 3.6, df. = 5, p = 0.015*	+

(*) = significant difference. (+) = not on nutritional stress, (±) = standard deviation.

Oudtshoorn (2014), classified this species as a poor-quality forage grass, due to its low leaf yield and high fiber content. The contribution of this grass is likely to be linked to its availability and greenness at the feeding sites, given that it remained mainly green (51–90%) even during the dry season.

Van Oudtshoorn (2014) classified C. dactylon, D. eriantha, and B. eruciformis as medium-quality forage grasses (Online Appendix S2). These species provided the bulk of the rest of the diets of both zebra and wildebeest, and it seems likely that their contribution is related to their relative value as forage, and their general acceptability, digestibility, and nutritional value. Previous studies have also found that the grasses selected by both zebra and wildebeest have a high nutritional value and are consumed preferentially (Ben-Shahar & Coe, 1992; Owaga, 1975; Treydte et al., 2013), although the nutrient content of these species was not analyzed in the present study. Clearly, future studies should include the analysis of nutrients to support a more conclusive interpretation of the feeding preferences of these herbivores.

In the present study, both herbivore species grazed almost exclusively on green grass, although the wildebeest consumed significantly more green grass than the zebra in both the dry and the wet seasons, while the zebra tolerated a considerably larger proportion of browner grass in both seasons. Previous studies have also reported a preference for green grass in wildebeest and the tolerance of poorer quality grass by zebra (Bell, 1971; Duncan et al., 1990; Odadi et al., 2011). This may be accounted for by the difference in the digestive systems of these two herbivores, given that, whereas wildebeest are ruminants, and require fresher grass with a high nutrient content, zebra are hindgut fermenters, which allows them to exploit forage of poorer quality, thus enabling them to be less selective (Duncan et al., 1990; Hack et al., 2002). Duncan et al. (1990) also argued that this difference in digestive capabilities may contribute to resource partitioning and facilitate the co-existence of these two herbivores. The consumption of lower quality grass by the zebra may guarantee the availability of the more digestible forage required by the foregut-fermenting wildebeest (Hack et al., 2002; Rubenstein, 2010). The greater proportion of browner grass consumed by the zebra in the MSR indicates that this may have been the case in this reserve.

In the present study, while fecal phosphorus concentrations did not vary significantly between zebra and wildebeest, the level of fecal crude protein was significantly higher in the wildebeest. Crude protein is frequently used as a predictor of both the palatability of the grass and the nutritional status of the ungulates (Ben-Shahar & Coe, 1992).

In this study, while the faecal phosphorus concentration did not differ significantly between zebra and wildebeest, the level of faecal crude protein was higher for wildebeest than for zebra. Crude protein is frequently used as a good predictor of both palatability of grass and nutritional status of ungulates (Ben-Shahar & Coe, 1992). Similar results have been obtained in other African conservation areas, such as the Timbavani Private Game Reserve, in South Africa, where Grant et al. (2000) reported higher fecal crude protein for wildebeest (7.5%) in comparison with zebra (5%), and the Mkuzi Game Reserve, also in South Africa, where Edwards (1991) recorded 8.2% fecal crude protein in wildebeest in comparison with 7% for the zebra.

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As noted above, wildebeest is a selective grazer, which is more dependent on food of higher nutritional quality, while zebra are able to tolerate larger amounts of less nutritious plant material in their diets (Bell, 1971; Duncan et al., 1990; Odadi et al., 2011).

The prediction that zebra and wildebeest will undergo nutritional stress during the dry season was not supported by the results of the present study. The levels of fecal crude protein and phosphorus did not deviate significantly from the threshold of nutritional stress (5% for crude protein or 2.0 g/kg for fecal phosphorus) in either herbivore in the dry season. This appears to reflect the more selective foraging behavior of the two herbivores during the dry season (Figure 2), when the animals searched actively for sources of greener grass, during the period when the availability of this resource declines and the nutritional value of most grasses decreases (Owen-Smith, 2002).

The greenness of the plant can be considered to be a reasonably good predictor of the nutritional quality of a grass (Groom & Harris, 2010; Owen-Smith, 1982). Given this, grazers are expected to focus their foraging activities in areas with more green grass because this would be nutritionally advantageous (O'Reagain, 1996; Le Roux, 2010). During the dry season, then, grazers should select foraging areas in which more nutritious green grasses are more dominant (O'Reagain, 1996). This was supported by the findings of the present study, given that, during the dry season, both herbivores concentrated their foraging activities in low-lying areas of clayey soil near bodies of water, where grasses tend to be evergreen (personal observation). This selective foraging for greener grass by both zebra and wildebeest is the equivalent of selecting food with a higher nutritional quality (Conneely, 2011).

The present study did not include any analysis of the nutritional content of the grasses grazed by the herbivores. Even so, as the nutrient content of the herbivore feces varies in accordance with the concentration of nutrients in the plant material these animals consume (Novellie et al., 1988), the findings of the present study indicate that the zebra and wildebeest populations of the Maputo Special Reserve are not under any significant nutritional stress at the present time, and that the quality of the forage available in the study area is not a factor limiting the long-term potential of the reserve's reintroduced zebra and wildebeest.

Implications for Conservation

In Mozambique, a range of species of wild animals are being reintroduced into a number of protected areas in order to restore the fauna lost during the recent civil war. Reliable data on the quality of the diet and the nutritional status of these populations are crucial to the success of these conservation initiatives, given that nutrition has a direct effect on ungulate survival and fertility (Wrench et al., 1997).

The findings of the present study provide valuable baseline information on the quality of the diet and the nutritional status of animals that will provide reserve managers with important guidelines for the detection of periods when the quality of the available forage declines below the critical threshold of nutritional deficit, which may impact survival and reproduction, with negative implications for conservation efforts. The results of the present study nevertheless indicated that fecal crude protein and phosphorus were above the critical threshold for large southern Africa herbivores, and that the zebra and wildebeest of the Maputo Special Reserve (MSR) are not under any significant nutritional stress, even during the dry season, which is considered to be the critical period for ungulates, when these animal face a major challenge to satisfy their nutritional needs.

The arboreal savanna habitat is the principal type of habitat used by the herbivores in the MSR, and it should be prioritized in management initiatives such as the control of illegal fires caused by the local human communities, which increase in frequency in the dry season, resulting in a disproportional decline in the availability of forage during this critical period, which is especially detrimental for the animals.

Future research in the MSR should also investigate the level of competition and resource partitioning between the two study species and other herbivores, such as the impala, kudu, nyla, warthog, and waterbuck, which are also being reintroduced into the reserve (Hanekom & Cumbane, 2016). The management of the stocking rates of these herbivores must be based on reliable estimates of the carrying capacity of the study area (Stalmans, 2015). This will be important to reduce density-related mortality, given that the principal predators of these herbivores, that is, the lion, cheetah, and hyena, that would otherwise control population growth, are absent from the MSR. are absent in the MSR.

Acknowledgments

We would like to thank the Mozambique National Administration of Conservation Areas for permission to conduct this research. A special thank you to Armando Guenha, administrator of the MSR, and to Natércio Ngovene, Eurico da Paixão, Abílio Tamele, and Rodolfo Cumbane who greatly facilitated our fieldwork. We are also grateful to Adao Ndove, Altino Cuna, Bilzia de Souza, Ivan Farinha, Sergio Ngovene, and Vilma Mafanela for their contributions to the fieldwork.

Author Contributions

L. J. C. M. conceptualized the research design, conducted field data collection, interpreted the data, and wrote the manuscript;

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F. H. G. R. assisted in the research design conceptualization and contributed to writing the manuscript.

Data Accessibility Statement

All the data used (geographic coordinates of the distributions of these herbivore species recorded, data of faecal nitrogen and phosphorus analyses) that support the results of this study I will make available from the ORCID Connecting Research and Researchers database: https://orcid.org/0000-0003-3731-0961.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) received no financial support for the research, authorship, and/or publication of this article.

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