

# Stable isotope composition of faeces as an indicator of seasonal diet selection in wild herbivores in southern Africa

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**We used stable carbon isotopes and nitrogen contents of faeces to investigate diet selection differences among wild grazers, browsers and mixed-feeders at seasonal intervals across a year in the Hluhluwe–Umfolozo Park, South Africa. Faecal  $\delta^{13}\text{C}$  values showed that wildebeest and warthog selected predominantly  $\text{C}_4$  plant material throughout the year. Impala ingested significantly more  $\text{C}_3$  plant material during the winter months than in all other months. Nyala also ingested more browse during winter. The nitrogen content of wildebeest faeces was significantly lower in winter than in summer, suggesting a possible decline in diet quality during the dry winter months. No significant seasonal trend in faecal nitrogen content was evident for nyala or warthog. Nitrogen contents of impala faeces were significantly higher in spring than in other seasons. Faecal isotopic and nutrient content analyses appear to be useful indicators of short-term diet selection and nutritional status of free-ranging herbivores. Analyses show resource partitioning among the different herbivores at finer time resolutions than can be obtained from bone collagen or isotopic analysis of tooth enamel.**

## Introduction

Numerous methods exist to delineate dietary patterns of wild animal populations, all with certain strengths and limitations. Both oesophageal fistulae experiments and visually observing animals while they are feeding offer a direct indicator of the food consumed. However, oesophageal studies are mostly restricted to caged animals fed controlled diets whereas visual observation of wild animals feeding is time-consuming and it is often difficult to see what and how much food shy or nocturnal mammals eat. Rumen samples can be obtained from free-ranging animals, though it is often impractical to gain sufficient samples, especially when working on rare or endangered species. Micro-histological faecal analysis gives good quantitative indications of the diet for a whole population over a long period provided that problems of plant species identification from minute fragments and the time-consuming nature of the method can be overcome.

Stable isotopic markers of animal tissues,<sup>1–4</sup> of the rumen<sup>5</sup> and faeces<sup>6</sup> have been used to indicate whether animals are grazers, browsers or mixed-feeders. The advantage of this method is that it requires no disturbance of the animals and can indicate dietary intake over different time scales, from a few days to a few years. This method is based on the differential fractionation of  $^{13}\text{C}$  by plants during photosynthesis.  $\text{C}_3$  plants (that illustrate the Calvin photosynthetic cycle) discriminate more against the

heavier isotope ( $^{13}\text{C}$ ) than  $\text{C}_4$  plants, with  $\text{C}_3$  foliage averaging  $-26.5\text{‰}$  (relative to the Vienna Pee Dee Belemnite (VPDB) standard) and  $\text{C}_4$  foliage (Hatch-Slack cycle) averaging  $-12.5\text{‰}$  VPDB. In South Africa, 90% of the grass cover along the east coast and interior is of  $\text{C}_4$  type,<sup>4</sup> while most trees and shrubs are  $\text{C}_3$ . Savannas thus provide a unique environment with a distinct isotopic signature difference between the  $\text{C}_3$  trees, shrubs and some dicotyledonous forbs, and the  $\text{C}_4$  grasses. Vogel<sup>4</sup> used this difference between plant types to show that the  $^{13}\text{C}$  content of animal tissue reflects the proportion of browse and graze ingested by animals. Van der Merwe *et al.*<sup>2</sup> were also able to distinguish the proportions of  $\text{C}_3$  and  $\text{C}_4$  plants consumed by elephants from bone collagen carbon isotopic ( $\delta^{13}\text{C}$ ) values. Turnover rates of  $\delta^{13}\text{C}$  in bone collagen are slow and represent a long-term average of the food consumed, whereas isotopic values of faeces indicate resource use over a few days. Controlled feeding experiments conducted on captive animals<sup>7,8</sup> showed that faecal isotopic composition is related to the feed ingested and has been employed to indicate short-term diet selection in herbivores. In a field study, van der Merwe *et al.*<sup>8</sup> showed that  $\delta^{13}\text{C}$  values of elephant dung changed seasonally to indicate higher proportions of browse during low rainfall months.

The chemical composition of faeces has been used to determine the quality of the herbage ingested. For example, protein content of faeces has been correlated with the nitrogen content of the feed<sup>9,10</sup> and this approach has been used to indicate trends in the nutritive quality of certain ruminants' diets, particularly when relative differences, as opposed to absolute values, are of primary concern.<sup>9,11,12</sup> Gates and Hudson<sup>11</sup> showed that the crude protein in faeces of wapiti reflected the seasonal trend of herbage quality decline in winter, while Grant *et al.*<sup>12</sup> reported that faecal N values distinguished between feeding guilds (grazers, mixed-feeders and browsers). This relationship between protein content of the feed and the faeces is influenced by the ingestion of plants, in particular browse, that contains high amounts of tannin or have low digestibility.<sup>13–15</sup> Soluble phenolics that are more common in browse inhibit protein digestion and can cause excess protein to reach the faeces.<sup>16</sup> Although it has been shown that predicting dietary from faecal N is hampered when caged animals are fed low-quality browse,<sup>13,14</sup> it is unlikely that animals continuously consume such large quantities of low-quality browse in the wild. Field studies have shown that unpalatable woody species become acceptable only during extended dry times when little else is available.<sup>17,18</sup> Cooper and Owen-Smith<sup>19</sup> observed that plant species with high levels of condensed tannins (>5%) tended to be rejected as food by free-ranging impala, kudu and goats in a 213-ha enclosure containing natural wooded savanna at animal densities comparable to their typical home ranges.

Protein content of faeces could thus prove a useful means of indicating whether opportunistic feeders that are able to switch to eating browse in the drier months fare better at maintaining nutritional condition than pure grazers. The aim of the study reported here was to examine whether diet choices on a seasonal time-scale allow different feeding guilds to maintain nutritional condition during the dry season. Four species were chosen to cover a spectrum of possible feeding guilds: wildebeest (*Connochaetes taurinus*) (grazer), warthog (*Phacochoerus aethiopicus*) (grazer, but also known to eat forbs and underground parts of plants), nyala (*Tragelaphus angasii*) (browser) and impala (*Aepyceros melampus*) (mixed-feeder). We used isotopic analysis of carbon in faeces as an indicator of the proportion of browse to graze ingested, and faecal nitrogen contents (%) were used to infer seasonal changes in forage quality.

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## Materials and methods

### Study area

Hluhluwe–Umfolozi Park (28°00′–28°26′S, 31°43′–32°09′ E) is situated in the foothills of the escarpment to the west of the coastal plain in central KwaZulu-Natal, South Africa. Hot, wet summers and cold, dry winters characterize the reserve. Mean annual rainfall is 990 mm for Hluhluwe in the north and 720 mm for Umfolozi in the south. Rainfall peaks between October and March. The park is located in Natal lowveld bushveld<sup>20</sup> (Vegetation type 26), which is characterized as mixed scrub and savanna. The park includes patches of forest and riverine forest, thicket and various more widespread savanna woodland types.<sup>21</sup> Small, intensively grazed patches dominated by short, stoloniferous grazer-tolerant grass species, known as ‘lawn’ grasses, are interspersed between tall, fire-prone ‘bunch’ grasses, the latter constituting the dominant grassland type across much of the park. Nearly all the grasses are C<sub>4</sub> and the shrubs and trees are C<sub>3</sub>. Fresh, clean dung samples were collected and identified from 10 sites, 5 in Hluhluwe and 5 in Umfolozi, on a monthly basis from March 2000 to March 2001.

Faeces were oven-dried at 60°C and ground in a Wiley mill to pass through a 40-mm mesh screen. Faecal samples were combusted in an automated Carlo-Erba CHN analyser (Carlo-Erba, Milan, Italy) and stable carbon isotopes were analysed using a Finnigan-MAT 252 (Bremen, Germany) mass spectrometer. Results are expressed as δ<sup>13</sup>C relative to the VPDB standard.

Mean δ<sup>13</sup>C values of lawn ( $n = 51$ ) and bunch ( $n = 48$ ) grass samples for the sites were obtained from another study (C. Coetsee, University of Cape Town, unpublished data). Mean δ<sup>13</sup>C values for woody species were extracted from a study undertaken (T. Mgidi, University of Cape Town, unpublished data) across a range of nitrogen-fixing *Acacia* species as well as several non-fixing tree species in the Hluhluwe–Umfolozi Park. These isotope values of vegetation were used to determine the relevant C<sub>3</sub> and C<sub>4</sub> endpoints.

Diet-to-faeces fractionation was assumed to occur and we adjusted our faecal-to-diet results by adding –0.8‰ to all our δ<sup>13</sup>C faecal values. This adjustment is based on the findings of a recent study by Sponheimer *et al.*,<sup>8</sup> who reported that faecal δ<sup>13</sup>C values were depleted by a mean of 0.8‰ for a range of mammals fed either a C<sub>3</sub> or C<sub>4</sub> diet for six months or more. Other studies that investigated fractionation that occurs between dietary δ<sup>13</sup>C values and those of faeces<sup>7,8,22</sup> have indicated higher values. For instance, Jones *et al.*<sup>7</sup> showed that steers fed C<sub>3</sub> material for 120 days and then switched to a C<sub>4</sub> diet for 100 days had faecal δ<sup>13</sup>C values depleted (more negative) by 2‰. Although Jones *et al.*<sup>7</sup> suggest that a C<sub>3</sub> to C<sub>4</sub> diet shift is reflected in the faeces within six days, it possibly takes longer for the animal tissues or secretions to manifest a δ<sup>13</sup>C label congruent with the current feeding regime. Since there is no information on what fractionation occurs in the field, we used the conservative value derived by Sponheimer *et al.*<sup>8</sup>

### Statistical analysis

The number of dung samples collected per species varied widely between months. To increase the power of a one-way ANOVA, monthly samples were pooled into four seasons: summer (December, January and February), autumn (March, April and May), winter (June, July and August) and spring (September, October and November), and analysed for statistical differences. Where the assumption of a one-way ANOVA was violated, a non-parametric Kruskal-Wallis ANOVA test was used. Significant seasonal differences were identified using a Tukey honestly significant difference (HSD) for unequal  $n$  test.

## Results

Mean δ<sup>13</sup>C values for the lawn (–12.8‰ VPDB) and bunch (–12.6‰ VPDB) grass samples (C. Coetsee, unpubl. data) were combined to give a mean value of –12.7‰ VPDB to reflect a 100% C<sub>4</sub> diet. A value of –28.5‰ VPDB (T. Mgidi, unpublished data) was estimated to correspond to a 100% C<sub>3</sub> diet, whereas δ<sup>13</sup>C values between these endpoints represent a mixture of C<sub>3</sub> and C<sub>4</sub> herbage.

### Faecal isotopes

The diet of warthogs (Kruskal-Wallis;  $\chi^2 = 6$ ,  $P = 0.11$ ) was dominated by C<sub>4</sub> grass throughout the year, with the C<sub>3</sub> component reaching a maximum of 10% during the drier winter months (Fig. 1). Similarly, wildebeest ( $F_{(3,54)} = 0.05$ ,  $P = 0.68$ ) had a predominantly grass diet with the highest C<sub>3</sub> fraction (20%) selected during autumn and winter (Fig. 1). Impala consumed significantly more C<sub>3</sub> material during winter than in all other seasons ( $F_{(3,106)} = 15.63$ ,  $P = 0.00$ ) (Fig. 1). Nyala ( $F_{(3,40)} = 1.54$ ,  $P = 0.22$ ) also showed the same pattern of increased C<sub>3</sub> (approximately 40%) consumption during the winter months (Fig. 1).

### Forage quality

Impala and nyala faecal nitrogen concentrations fluctuated around 1.8% throughout the year, whereas yearly fluctuations in nitrogen concentrations for wildebeest and warthog were slightly lower, at about 1.4% (Table 1). The nitrogen concentrations of impala dung were significantly higher in spring ( $F_{(3,106)} = 8$ ,  $P = 0.00$ ) than in all other seasons (Table 1). Wildebeest dung, on the other hand, had significantly higher nitrogen values in summer than in winter ( $F_{(3,54)} = 3.55$ ,  $P = 0.02$ ) (Table 1). There was no significant seasonal variation in nitrogen concentrations for warthog ( $F_{(3,10)} = 2.91$ ,  $P = 0.2$ ) or nyala ( $F_{(3,40)} = 0.78$ ,  $P = 0.93$ ) faeces (Table 1).

## Discussion

Controlled feeding trials where animals were fed either 100% C<sub>3</sub> or C<sub>4</sub> diets showed that the carbon isotope values of faeces and the herbage ingested were closely related.<sup>5,8</sup> However, this relationship could be skewed if animals consume a mixture of C<sub>3</sub> and C<sub>4</sub> foods that vary in digestibility, since the least digestible fraction of the diet will be over-represented in the faeces. For example, 20% C<sub>3</sub> material ingested might be represented as 80% in the faeces if the C<sub>4</sub> grass component is more completely assimilated. This is especially true for premixed lab diets that contain ingredients with varying degrees of digestibility, but is unlikely to bias faecal δ<sup>13</sup>C values in the field (see discussion in ref. 8), since studies have shown that tree and shrub leaves are generally not less digestible than grasses.<sup>23,24</sup>

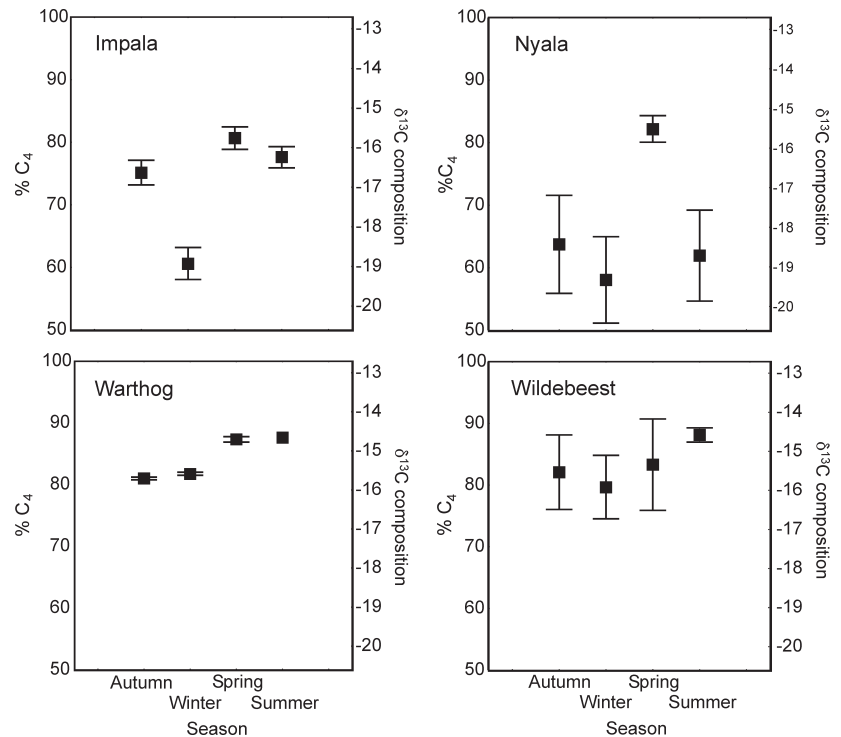
Our results show that both nyala and impala consume mainly grass throughout the year. The proportion of dietary C<sub>4</sub> material ingested by impala and nyala varied seasonally and declined from approximately 80% in the summer to just below 60% in winter. Impala, in particular, consumed significantly more C<sub>3</sub> vegetation during winter when rainfall was low, than in all other seasons. Impala have been classed as intermediate or mixed feeders that prefer to graze;<sup>25</sup> previous studies reported that shifts to browse during low-rainfall months coincided with periods when grass quality and availability declined.<sup>25–29</sup> Less is known about nyala diets, although they are generally perceived to be browsers because of their preference for wooded habitat. High grass selection by nyala has been found previously in two rumen studies conducted in reserves with similar vegetation and in close proximity to Hluhluwe–Umfolozi Park.<sup>26,30</sup> Anderson<sup>30</sup> showed that the percentage of monocotyledonous material

(stem and leaf) from 374 nyala rumen samples collected over a two-year period was generally around 75%, declining sharply to a low of 25% in August, the mid-point of the dry winter season.

Seasonal dietary shifts as recorded for impala and nyala possibly help them maintain nutritional status by selecting for shrub or tree species in the winter when this forage has higher crude protein levels than grasses. In our study, faecal nitrogen concentrations of impala and nyala were not significantly lower in winter as would have been expected had they continued to ingest low-quality grass during the dry months. The results agree with those of Anderson,<sup>30</sup> suggesting an almost complete overlap in resources utilized by impala and nyala. Such overlap could enhance competition between the two species, particularly when shared resources become limited. Population crashes of nyala, such as that experienced in the Ndumu Game Reserve<sup>31</sup> during a particularly dry year, could be exacerbated by the presence of competitors such as impala. This is reason for concern because impala are not thought to occur naturally in the Hluhluwe–Umfolozi region and therefore could have a significant effect on the nyala populations through their similar feeding requirements.

In contrast to the seasonally mixed feeding of impala and nyala, wildebeest and warthog ingested predominantly C<sub>4</sub> material throughout the year. This agrees with other studies showing wildebeest to be pure grazers<sup>4–6</sup> and that of Mason's,<sup>32</sup> which showed that dicotyledonous material is low in the stomach content of warthogs from Hluhluwe–Umfolozi Park. The overwhelming dependence of wildebeest and warthog on grasses suggests that these species could suffer nutritional declines during winter or droughts when crude protein levels of grass are low. This was found for wildebeest, whose faecal nitrogen concentration was significantly lower in winter than in summer, whereas warthogs showed no dry season decline in faecal nitrogen. This could arise because warthogs change their feeding habits during winter, spending more time digging up roots of grasses, which are more nutritious than the shoots.<sup>32</sup> Visual examination of warthog stomach contents showed that grass leaf blades and sheaths were the dominant constituent in the wet season, with a shift to stolons, stems bases and rhizomes in the dry months.<sup>32</sup>

In seasonally stochastic environments where availability of nutrient-rich food varies widely, wild herbivores need to use resources in such a way as to maintain condition. Knowing the critical faecal nitrogen contents below which weight loss occurs is a useful indicator of an animal's nutritional status,<sup>11,13,14</sup> yet few studies have used this approach for different herbivore species. Based on reported weight losses in wapiti at faecal N levels below 1.6%,<sup>11</sup> Wrench *et al.*<sup>13</sup> calculated that a concentration of less than 14 g N/kg (2.24%) could indicate a nitrogen shortage in grazers like wildebeest. However, it is not appropriate to predict critical nitrogen values for wildebeest from nitrogen levels at which wapiti showed weight loss, since the two have very different digestive systems. The average faecal nitrogen values of wildebeest and warthog in our study were well below this value and fluctuated around 1.4%. This is also considerably lower than the means of 1.8% and 1.9% found for impala and nyala, respectively. These faecal N values for the mixed-feeders



**Fig. 1.** Average seasonal contribution of C<sub>4</sub> plants to diet as calculated from isotopic analysis of the faeces of four ruminant species: impala, nyala, wildebeest and warthog, from March 2000 to March 2001. The ratio of C<sub>3</sub> to C<sub>4</sub> vegetation in the faeces is expressed as a percentage, with a δ<sup>13</sup>C value of -12.7 ‰ representing a 100% C<sub>4</sub> diet and -28.5 ‰ a 100% C<sub>3</sub> diet (0% C<sub>4</sub>). The months were divided into four seasons: summer (December, January, February), autumn (March, April, May), winter (June, July, August), and spring (September, October, November). Lines indicate ± 0.95 × standard error.

in the Hluhluwe–Umfolozi Park are lower than the 2.6% reported for impala in poor condition in the Kruger National Park<sup>12</sup> and less than the 2.1% found for impala across the KNP during the dry season.<sup>32</sup> They are, however, higher than the yearly average of 1.5% found for free-roaming impala in the Timbavati area.<sup>28</sup> Determining critical faecal N levels for comparisons of the nutritional performance of mixed-feeders and browsers is complicated by the presence of tannins in browse. It

**Table 1.** Average seasonal % nitrogen concentration in the faeces of four ruminant species: impala, nyala, wildebeest and warthog from March 2000 to March 2001. The months were divided into four seasons: summer (December, January, February), autumn (March, April, May), winter (June, July, August), and spring (September, October, November).

Season	n	% N	s.e.*
<b>Impala</b>			
Autumn	10	1.59 <sup>b</sup>	0.07
Winter	25	1.74 <sup>b</sup>	0.06
Spring	28	2.08 <sup>a</sup>	0.05
Summer	47	1.75 <sup>b</sup>	0.06
<b>Nyala</b>			
Autumn	4	1.82	0.11
Winter	15	1.92	0.15
Spring	9	2.22	0.23
Summer	16	1.89	0.14
<b>Wildebeest</b>			
Autumn	12	1.26	0.08
Winter	24	1.17 <sup>b</sup>	0.07
Spring	8	1.4	0.11
Summer	14	1.48 <sup>a</sup>	0.08
<b>Warthog</b>			
Autumn	3	1.26	0.18
Winter	8	1.25	0.09
Spring	2	1.77	0.09
Summer	1	1.67	

\*Standard error.

is thus unclear whether the higher faecal N levels of the mixed-feeders in our study were due to the incorporation of woody species with relatively high nitrogen contents in winter or whether it was merely a consequence of higher tannin levels that resulted in undigested protein reaching the faeces.

It is evident from this study that faecal isotope and simultaneous nutrient analysis offers a quick and effective way of determining seasonal diet selectivity and nutritional status of free-ranging animals. The method has several advantages over traditional methods employed in dietary research on mammals. It is non-intrusive as it does not involve the culling or manipulation of animals and it is less time intensive than direct observation of animal feeding or micro-histological analysis. Faecal isotopic analysis also allows us the opportunity to examine diet selectivity over short timescales. Coupled with nitrogen analysis, it should prove a valuable tool to managers requiring information on numerous aspects of mammalian dietary ecology.

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