Assessing diet in savanna herbivores using stable carbon isotope ratios of faeces

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In African savannas, browse-based resources (C_3 plants) are isotopically distinct from grasses (C_4 plants). The carbon isotopic composition of the basic plant diet is recorded in animal tissues. Mammal faeces are a readily accessible, non-invasive, sample material for temporally resolved dietary reconstructions. Faeces, however, include both undigested plant matter and waste, hence accuracy of dietary calculations could potentially be compromised by shifts in plant isotopic values related to seasonal or spatial differences, or by variability in the isotopic differences between faeces and diet. A controlled feeding study of four ungulate species showed a small, consistent difference between diet and faeces of -0.9 ‰, irrespective of whether the diet was C_3 or C_4-based. Results from faeces of taxa known to be pure grazers, pure browsers, and mixed-feeders from the Kruger National Park were entirely consistent with their diets, but the accuracy of dietary reconstructions is enhanced with data from local plant communities.

Key words: herbivores, diet, plants, faeces, isotopic variability

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Introduction

In African savannas, stable carbon isotope ($^{13}C/^{12}C$) ratios measured from animal tissues, are commonly used to infer aspects of feeding behaviour and habitat utilisation by animals (Vogel 1978; Tieszen *et al.* 1979; Van der Merwe *et al.* 1988; Cerling *et al.* 2003; Sponheimer *et al.* 2003a). The basis of this application lies in anatomical and physiological differences in plants at the base of the food chain. Plants that follow the C_3-photosynthetic pathway are consistently depleted in ^{13}C (mean $\delta^{13}C$ value ~ -27.0 ‰) compared to plants with a characteristic Kranz leaf anatomy that follow the C_4-pathway (mean $\delta^{13}C$ value ~ -12.5 ‰) (Smith & Epstein 1971; Vogel 1978). In subtropical African savanna environments, almost all trees, forbs, and shrubs are C_3, while grasses are almost exclusively C_4 (Vogel *et al.* 1978). Animal tissues record the carbon isotopic composition of the basic plant diet, and thus reflect proportions of C_3 (browse) to C_4 (grass) intake (Vogel 1978; Tieszen *et al.* 1989; Cerling & Harris 1999).

Most carbon isotopic studies of diet have made use of hard tissues, such as tooth enamel or bone collagen (e.g. Vogel 1978; Ambrose & DeNiro 1986; Lee-Thorp *et al.* 1989; Cormie & Schwarcz 1996; Cerling *et al.* 2003; Sponheimer *et al.* 2003a), while fewer have used faeces (Tieszen *et al.* 1979, 1989; Van der Merwe *et al.* 1988; Vogel *et al.* 1990; Sponheimer *et al.* 2003b). Isotopic analysis of faeces is potentially a useful tool for studying short-term dietary trends in free-ranging herbivores. Mammal faeces repre-

sent diet for the few days prior to deposition, while other tissues such as hair and skeletal material aggregate dietary information over several months or years (Ambrose & Norr 1993; Sponheimer *et al.* 2003c). In addition, sampling of faeces is non-invasive, and no manipulation or slaughter of animals is necessary.

Faeces, however, are composed largely of undigested materials, and are therefore a partial reflection of dietary intake. Relatively little is known about the relationship between dietary and faecal carbon isotopic compositions (but see Sponheimer *et al.* 2003c). Here we assess the viability of using carbon isotopic data from faeces as a dietary proxy in two ways. Firstly, we present the results of a controlled feeding study in which four ungulate herbivores were fed diets of known isotopic values, to determine the relationship between dietary and faecal isotopic composition under both C_3 and C_4 dietary

Methods

Controlled Feeding Study

Llamas *Lama glama*, alpacas *Lama pacos*, horses *Equus caballus*, and goats *Capra hircus* at the Brigham Young University Department of Animal Science were housed in pens and fed a variety of diets with different photosynthetic adaptations and isotopic compositions. These were a C_3 browse plant (alfalfa, *Medicago sativa*), a C_4 grass (coastal Bermuda grass, *Cynodon dactylon*), and a C_3 grass (tall fescue, *Festuca arundinacea*), respectively. Only one feed was on offer in each pen. Animals were fed each diet for a minimum of three weeks before isotopic analysis of faeces were carried out, although in most cases each individual was kept on a specific diet for several months.

Sample Collections in Kruger National Park

Faecal samples were collected from eight sampling sites during June 2002, January 2003, and June 2003

Table 1
Summary of collection sites in Kruger Park for faecal and plant collections

Site #	Region	Geology	Visual Description	Latitude	Longitude
1	South	Basalt	Grassland	25° 14' 12.0"	31° 59' 08.4"
2	South	Basalt	Riverine	25° 20' 30.4"	31° 56' 25.7"
3	South	Granite	Shrubveld	25° 04' 19 1"	31° 36' 37.9"
4	South	Granite	Dense woodland	25° 01' 02.3"	31° 46' 55.8"
5	North	Basalt	Grassland	23° 06' 58.6"	31° 22' 24.7"
6	North	Alluvial	Riverbed	23° 12' 27.8"	31° 14' 17.6"
7	North	Granite	Woodland	23° 13' 15.3"	31° 13' 55.8"
8	North	Basalt	Sodic	23° 09' 54.7"	31° 18' 00.4"

regimes. Second, we report results of stable carbon isotopic analysis of animals with known diets from the Kruger National Park, to test whether our data can correctly classify different types of diets. Finally, we aimed to show that accurate reconstructions of diet based on faecal isotopic analysis requires extensive analysis of local vegetation, as the isotopic composition of plants may shift in small but significant ways over space and time.

(Table 1). Each site was a circle ~10 m in diameter. These sites were selected to represent the nutrient-rich basaltic, and nutrient-poorer granitic soils of the southern KNP, as well as the arid 'bushveld' of the north (Venter *et al.*, 2003). The vegetational structure of these sites varied to include open grassland, woodland savanna, and riparian zones.

Faeces of the grazing Burchell's zebra *Equus burchelli* and blue wildebeest *Connochaetes taurinus*, browsing giraffe *Giraffa camelopardalis* and greater kudu *Tragelaphus strepsiceros*, and mixed-feeding impala *Aepyceros melampus* were collected

for analysis. Only recently deposited, i.e. fresh or damp specimens were collected so as to ensure that samples represented the appropriate season, and were not contaminated by fungi, soil, and insects (Wrench *et al.* 1996). Each dung pile encountered was taken to represent a different individual of the relevant species. We collected not only faeces, but also plant samples, to provide baseline isotopic data for KNP vegetation. Plant specimens represented the local diversity of trees, forbs, and grasses at each site. At each site, between three and five (and in some cases more than five) specimens of each plant species present was collected during each month of sampling.

Analytical Techniques

Plant and faeces samples were oven-dried at 60 °C for 24 hours and thereafter mill-ground through a 1 mm sieve into a homogenous powder. Each individual sample was combusted in an automated Carlo-Erba device (Carlo Erba, Milan), and the resultant CO_2 gas was analysed for $^{13}C/^{12}C$ ratios, using a continuous flow-through (CONFLO) inlet

system attached to a Finnigan MAT 252 Mass Spectrometer (Finnigan, Bremen). By convention $^{13}C/^{12}C$ ratios are expressed in the delta (δ) notation in parts per mil (‰) relative to the PDB standard. Standard deviations for repeated measurements of laboratory protein, plant, and chocolate standards were less than 0.1 ‰.

Results and Discussion

Controlled Diet Study

Faeces of alpacas, llamas, horses, and goats, fed diets of known isotopic compositions, had $\delta^{13}C$ values very similar to those of their diets (Table 2). On a C_3 grass diet (tall fescue, $\delta^{13}C$ = -26.4 ‰), faecal $\delta^{13}C$ values were slightly lower compared to the diet (mean $\delta^{13}C_{faeces}$ = -27.1 ± 0.2 ‰, n = 9; mean $\Delta_{diet-faeces}$ = -0.7 ‰). On a C_4 diet, coastal

Table 2

Faecal $\delta^{13}C$ data for four ungulate herbivores fed diets of different carbon isotopic compositions, showing the consistency between dietary and faecal $\delta^{13}C$ values, and the isotopic discrimination (-0 9 ‰) between diet and mammal faeces

Diet	Species	n	$\delta^{13}C_{faeces}$ (‰) Mean	SD	^{13}C diet	Δ_{d-f} (‰) Mean	SD
Alfalfa	Horse	8	-27.6	0 4	-26.8	-0 8	0.4
	Alpaca	4	-27.4	0.3	-26.8	-0.6	0 3
	Llama	7	-27.6	0.4	-26.8	-0.9	0.5
	Goat	5	-27.9	0.1	-26.8	-1.1	0.1
	Average	24	-27.6		-26.8	-0.9	
	SD		0.2			0.2	
CBG	Horse	4	-15.4	0.8	-13.6	-1.9	0.8
	Alpaca	3	-14.2	0.2	-13.6	-0.6	0.2
	Llama	5	-14.6	0.3	-13.6	-1.0	0.3
	Goat	7	-14.4	0.3	-13.6	-0.8	0.3
	Average	19	-14.7		-13.6	-1.1	
	SD		0.5			0.6	
Tall Festue							
	Horse	5	-26.9	0.2	-26 4	-0 5	0.2
	Llama	2	-27.1	0.2	-26.4	-0.7	0.3
	Goat	4	-27.2	0.1	-26.4	-0.8	0.1
	Average	9	-27.1		-26.4	-0.7	
	SD		0.2			0.2	
All Diets		54	-0.9			0.4	

n = number of samples; SD = standard deviation; Δ_{d-f} = diet-faeces difference for $\delta^{13}C$.

Bermuda grass ($\delta^{13}C$ = -13.6 ‰), faecal $\delta^{13}C$ values were again slightly lower than the diet ($\delta^{13}C_{faeces}$ = -14.7 ± 0.5 ‰, n = 19; mean $\Delta_{diet-faeces}$ = -1.1 ‰). Faecal $\delta^{13}C$ of animals fed C_3 browse (alfalfa, $\delta^{13}C$ = -26.8 ‰) were also similar to, though slightly depleted from, the dietary value (mean $\delta^{13}C_{faeces}$ = -27.6 ± 0.2 ‰, n = 24; mean $\Delta_{diet-faeces}$ = -0.9 ‰). Hence, these data show that herbivore faecal $\delta^{13}C$ values consistently record the isotopic composition of the basic plant diet, with some discrimination leading to slightly lower $\delta^{13}C$ values in faeces.

Overall, the isotopic discrimination between diet and faeces was -0.9 ‰, with very small deviations (SD = 0.4) from this value being observed for different species on different diets (Table 2). A comparable result (-0.8 ‰) has previously been reported from a similar controlled feeding study (Sponheimer et al. 2003c). It might be argued that faecal $\delta^{13}C$ values reflect a bias towards less digestible items, such as grasses. While this is no doubt true, the effect should be very small. Indeed, some authors have suggested that grass and browse-based foods do not differ in overall digestibility (Robbins et al. 1995; Gordon & Illius 1996). Notably, we observed no difference in the isotopic offset between diet and faeces for herbivores fed browse-based food (alfalfa) compared to grasses. Thus, we can expect that free-ranging herbivores display a similar diet-faeces isotopic difference, regardless of whether C_3 or C_4 plants are eaten, or whether browse-based foods (such as alfalfa in this study) or grasses are consumed. The data show that the isotopic value of an herbivore's diet can be consistently and accurately predicted from the $\delta^{13}C$ value of its faeces, simply by adding 0.9 ‰ to the faecal value.

Faecal $\delta^{13}C$ of Kruger National Park herbivores

To test for accuracy of faecal data in wildlife situations, we chose to analyse faeces of species with known diets to determine whether analysis of faecal $\delta^{13}C$ could be used to correctly reconstruct their diets. Wilde-

beest and zebra are known to be pure or near-pure grazers, while giraffe and kudu feed almost exclusively on browse-based items (Hall-Martin 1974; Owen-Smith 1993; Skinner & Smithers 1990; Bodenstein et al. 2000). $\delta^{13}C$ values of wildebeest and zebra faeces from Kruger Park (mean = -13.5 ± 1.4 ‰, n = 21; and -14.0 ± 1.4 ‰, n = 29, respectively) are consistent with a C_4 grass diet (Table 3). Browsing giraffe and kudu had significantly lower (ANOVA, p <0.00001) faecal $\delta^{13}C$ values (mean = -26.7 ± 0.9 ‰, n = 44; and -26.6 ± 0.7 ‰, n = 28, respectively), indicating pure C_3 diets. The respective ranges of faecal $\delta^{13}C$ values representing grazing and browsing groups did not overlap. Thus, faecal $\delta^{13}C$ values of herbivores from Kruger National Park clearly distinguished known grazers from browsers.

Impala are mixed-feeders that incorporate different proportions of browse/grass into their diets depending on sex, age, season, habitat, and other environmental variables (Dunham 1982; Skinner & Smithers 1990; Meissner et al. 1996). Faeces of mixed-feeding impala had $\delta^{13}C$ values (mean = -20.7 ± 2.8 ‰, n = 129) intermediate between those of pure grazers and browsers, and are significantly different compared to both groups (ANOVA, p <0.00001, Table 3).

$\delta^{13}C$ values for the majority (25–75 % of the range) of specimens from grazing zebra and wildebeest were between -14.7 and -13.5 ‰, and similarly for browsing giraffe and kudu were -27.2 to -26.2 ‰. Variability within faecal $\delta^{13}C$ of Kruger National Park grazing and browsing taxa was hence very small. The 25–75 % range for impala faeces was larger, between -23.0 and -19.0 ‰, distinguishing them from pure grazing and pure browsing taxa. Hence our data show that the carbon isotopic composition of herbivore faeces are consistent with that of the diet, in that C_3, C_4, and mixed C_3/C_4-feeding groups can be distinctly and consistently separated.

The utility of faecal $\delta^{13}C$ as a dietary proxy could be further enhanced if reconstructions are used not only to qualify diet, but to quantify proportions of C_3/C_4 intake amongst dif-

Table 3

Carbon isotopic data for herbivore faeces from Kruger National Park, collected during June 2002, January 2003, and June 2003 Browsing giraffe (Giraffa camelopardalis) and greater kudu (Tragelaphus strepsiceros) are clearly distinct from the grazing Burchell's zebra (Equus burchellii) and blue wildebeest (Connochaetes taurinus). Mixed-feeding impala (Aepyceros melampus) have faecal $\delta^{13}C$ values intermediate between that of grazers and browsers Estimated %C$_4$ intake was calculated using previously published data for C$_3$ and C$_4$ plants (see Vogel et al 1978) as dietary endpoints

| Species | Diet | n | $\delta^{13}C_{PDB}$ (‰) | | Estimated %C$_4$-intake |
			Mean	SD	
Giraffa camelopardalis	C$_3$ browser	44	-26.7	0.9	10*
Tragelaphus strepsiceros	C$_3$ browser	28	-26.6	0.7	10*
Connochaetes taurinus	C$_4$ grazer	21	-13.5	1.4	95
Equus burchellii	C$_4$ grazer	29	-14.0	1.4	95
Aepyceros melampus	Mixed C$_3$/C$_4$ feeder	129	-20.7	2.8	50

n - number of samples,   SD – standard deviation $\delta^{13}C_{PDB}$ (‰) = ^{13}C ^{12}C ratio of sample relative to the PDB standard

* ~10 % C$_4$ intake by browsers, especially giraffe, is unlikely, and although this value probably reflects insignificant levels of grass consumption, the value is corrected when local plant data are incorporated into calculations.

ferent species and across various spatio-temporal scales. Previously published plant data for South Africa revealed average $\delta^{13}C$ values of -27.0 ‰ for C$_3$ plants and -12.5 ‰ for C$_4$ grasses (Vogel et al. 1978). Using these values as C$_3$ and C$_4$ isotopic endpoints, and correcting for the diet-faeces isotopic discrimination of -0.9 ‰, faecal $\delta^{13}C$ values were converted to percentage C$_4$ intake. For example, faeces with a value of -27.9 ‰ were taken to represent a 100 % C$_3$-based diet, and those with a value of -13.4 ‰ a 100 % C$_4$ grass diet.

Calculations of %C$_4$ intake suggested that grazing zebra and wildebeest consume an average 95 % grass, browsing giraffe and kudu have 90 % C$_3$ diets, and mixed-feeding impala eat a mix of 50 % grass and 50 % browse on average (Table 3). Both zebra and wildebeest are known to supplement their diets, on occasion, with some C$_3$ foods such as shrubs and forbs, which would account for the ~5 % C$_3$ composition of their diets (Skinner & Smithers 1990). However, ~10 % utilisation of grasses by browsing taxa are less likely. While percentage C$_4$ intake of giraffe are expected to be near to zero, kudu are known to eat small amounts of grass, but this resource seldom makes up

as much as 10 % of the diet. Owen-Smith & Cooper (1989), for instance, found that grass intake by kudu in the Nylsvley Nature Reserve peaked during the early wet season (September), and even then grasses made up only 7.5 % of total food intake. Thus, results for browsers suggest that while faecal $\delta^{13}C$ values reliably distinguish between, and qualify the diets of, grazers, browsers, and mixed-feeders, further assessment of just how accurate reconstructions of percentage C$_3$/C$_4$ consumption is required.

The isotopic composition of C$_4$ and C$_3$ plants may vary over space and time, creating uncertainty regarding isotopic endpoints and estimates of %C$_4$ intake (Cerling et al. 2004). Very small $\delta^{13}C$ differences (1 ‰ or less) in C$_4$ plant $\delta^{13}C$ values have been reported for different photosynthetic subpathways. Xeric adapted NAD-ME and PCK grasses appear to be slightly depleted in ^{13}C compared to mesic NADP-ME grasses, but the range of $\delta^{13}C$ values for each group overlap considerably (Hattersley 1982; Cerling & Harris 1999). C$_3$ plants are more variable as isotopic discriminations are influenced by environmental conditions. Plants growing in well-watered or cooler conditions, and those exposed to low levels of light intensity may
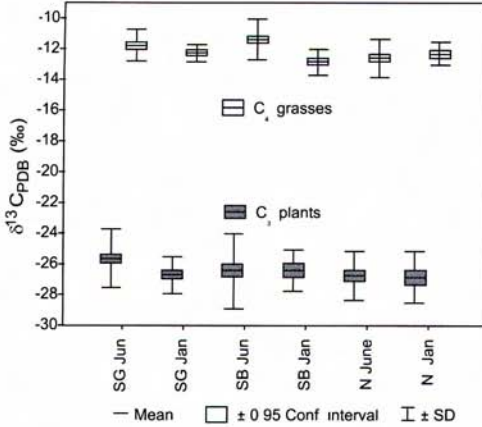
Fig. 1. Boxplot with means, 95 % confidence interval, and standard deviation (SD) of regional and seasonal carbon isotopic data for C_3 trees and forbs and C_4 grasses from Kruger National Park, collected during June 2002, January 2003, and June 2003. (SG = southern granites, SB = southern basalts; N = northern KNP).

be ^{13}C-depleted compared to plants in more open habitats, arid areas, and upper canopy level plants and plant parts (Farquhar *et al.* 1982; Tieszen 1991; Van der Merwe & Medina 1991; Stewart *et al.* 1995). Animal δ^{13}C values vary with variations in the isotopic composition of the plants they utilise. For example, animals that feed in forests have lower δ^{13}C values than those utilising more open habitats (Ambrose & DeNiro 1986; Van der Merwe *et al.* 1988; Van der Merwe & Medina 1991).

In Kruger National Park, isotopic variations within C_3 and C_4 plant groups were generally small, but in some cases significant differences were observed (Fig. 1). C_3 tree-leaves and forbs collected from southern granites during June were slightly ^{13}C-enriched (mean = -25.6 ± 1.9 ‰, n = 139) compared to plants from southern basalts (mean = -26.4 ± 2.4 ‰, n = 144) and from the northern KNP (mean = -26.7 ± 1.6 ‰, n = 94) (Tukey's HSD, p <0.001). Southern granite C_3 plants were also enriched in June compared to January (mean = -26.6

± 1.2 ‰, n = 49) (p <0.01). Northern grasses from June were depleted in ^{13}C (mean = -12.6 ± 1.2 ‰, n = 126) compared to grasses from southern granites and basalts (mean = -11.8 ± 1.0 ‰, n = 84; and mean = -11.3 ± 1.3 ‰, n = 97, respectively) (p <0.01). A significant seasonal difference was observed for grasses from the southern basalts, with June specimens being ^{13}C-enriched (mean = -11.3 ± 1.3 ‰, n = 97) compared to those from January (mean = -12.8 ± 0.8 ‰, n = 38) (p <0.0001).

Given the small, but in several cases significant, spatial and temporal variations in plant isotopic composition, we redressed analysis of percentage C_3/C_4 intake. Plants were divided into samples representing southern granites, and southern basalts, and the northern KNP, and groups collected during the dry (June) and wet (January) season, respectively (Table 4). These groupings provided regionally and seasonally specific C_3 and C_4 dietary endpoints for the Kruger Park. To account for variation in plants within specific regions or seasons, a range of δ^{13}C values were used as dietary endpoints, defined as the mean plant value ± the standard deviation. Correcting for a -0.9 ‰ average isotopic difference between diet and faeces, these endpoints were then used to determine several broader classes of $\%C_4$-intake, at intervals of 10 %, for faeces from Kruger National Park (Table 4). Because of variations in the carbon isotopic composition of C_3 plants, faecal values denoting <10 % C_4 intake were treated as reflecting pure C_3 diets. For example, faeces collected from northern sites during June with a δ^{13}C value between -29.4 ‰ and -25.3 ‰ were taken to reflect a diet comprised of no grass, while a value between -14.8 ‰ and -12.5 ‰ denoted a diet comprised of more than 90 % C_4 grass. We expected that small overlaps between the dietary groups classified in Table 4 would have a negligible influence on dietary reconstructions, because of our large plant sample sizes and the wide range of δ^{13}C values used to define dietary endpoints.

Figure 2 shows the diets of Kruger National Park herbivores according to reconstructions

Table 4

Dietary classifications for faeces from Kruger Park, derived from regional and seasonal mean plant $\delta^{13}C$ values +/- the standard deviation to define dietary endpoints, and assuming a diet-faeces isotopic discrimination of -0 9‰

Region	Month	%C_4-intake	$\delta^{13}C$ faeces (‰) Min	$\delta^{13}C$ faeces (‰) Max	Month	%C_4-intake	$\delta^{13}C$ faeces (‰) Min	$\delta^{13}C$ faeces (‰) Max
South granites	Jan	0	-28 7	-26.1	June	0	-28.4	-25.0
		<20	-26 0	-24.6		<20	-24.9	-23.7
		20-30	-24.5	-23.2		20-30	-23.6	-22.3
		30`40	-23.1	-21.7		30`40	-22 2	-20.9
		40-50	-21.6	-20.3		40-50	-20.8	-19.6
		50-60	-20.2	-18.9		50-60	-19.5	-18.2
		60-70	-18.8	-17 4		60-70	-18 1	-16.8
		70-80	-17.3	-16.0		70-80	-16.7	-15.4
		80-90	-15.9	-14.8		80-90	-15.3	-14.2
		>90	-14.7	-13.7		>90	-14.1	-11.6
South basalts	Jan	0	-28.6	-25.7	June	0	-29.7	-25.8
		<20	-25.6	-24.6		<20	-25 7	-24.3
		20-30	-24.5	-23.3		20-30	-24 2	-22.8
		30`40	-23.2	-22.0		30`40	-22.7	-21.3
		40-50	-21.9	-20.6		40-50	-21.2	-19.8
		50-60	-20.5	-19.2		50-60	-19.7	-18.2
		60-70	-19.1	-17.9		60-70	-18.1	-16.7
		70-80	-17.8	-16.5		70-80	-16.6	-15.2
		80-90	-16.4	-15.3		80-90	-15 1	-13.8
		>90	-15.2	-12.9		>90	-13.7	-11.0
North	Jan	0	-29.4	-25.3	June	0	-29.1	-25.2
		<20	-25.2	-24.8		<20	-25.1	-24.8
		20-30	-24.7	-23.5		20-30	-24.8	-23.4
		30`40	-23.4	-22.0		30`40	-23.3	-22.0
		40-50	-21.9	-20.6		40-50	-21.9	-20.6
		50-60	-20.5	-19.1		50-60	-20.5	-19.1
		60-70	-19.0	-17.7		60-70	-19.0	-17.8
		70-80	-17.6	-16.2		70-80	-17.7	-16.3
		80-90	-16.1	-14.9		80-90	-16.2	-15.0
		>90	-14.8	-12.5		>90	-14 9	-12.3

based on Kruger Park faecal and plant $\delta^{13}C$ data. The majority of grazer (zebra and wildebeest) faeces advocate diets comprised of 90–100 % grass, although several (34 %) specimens from these species suggest some utilisation of browse-based foods. Browser faecal $\delta^{13}C$ values, however, all indicate that these species rely entirely on C_3 foods, with grasses making no contribution to their diets. These results are more consistent with dietary predictions for browsers than estimates of %C_4 intake derived from calculations based on previously published data for

plants in South Africa, which denoted an unlikely ~10 % C_4 diet in browsing giraffe and kudu (Table 3). Thus, these data show that the accuracy of dietary reconstructions based on faecal $\delta^{13}C$ is increased if data from local vegetation, and variations in the isotopic composition of plants, are considered.

Indices of browse/grass consumption by impala indicate a wide range of diets (Fig. 2). As with faecal $\delta^{13}C$ values, dietary categorisations of mixed-feeding impala are clearly distinguishable from browsers and grazers. This observation is a clear indication
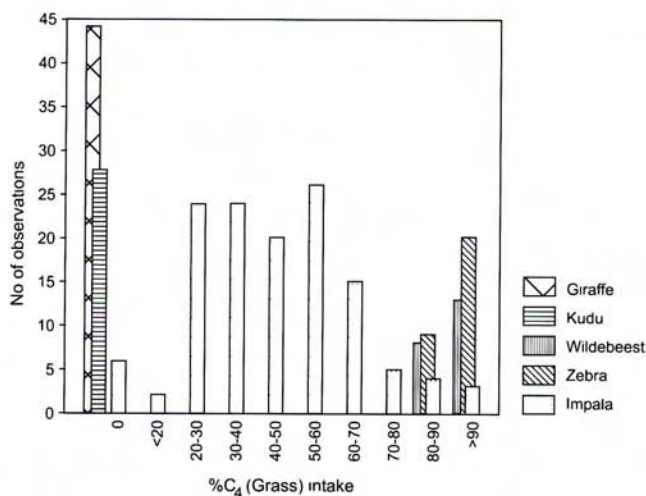
Fig. 2. Histogram combining specimens collected throughout Kruger National Park during June 2002, January 2003, and June 2003, showing reconstruction of $\%C_4$ consumed, derived from herbivore faecal $\delta^{13}C$ values using local vegetational data to define variance in isotopic endpoints.

that a diet constituting a mix of C_3 and C_4 food items is readily identifiable using faecal $\delta^{13}C$, and as such, any isotopic differences between mixed-feeder specimens would indicate true dietary differences. Thus, with local vegetational data providing baseline information about dietary endpoints, reliable dietary differences (such as spatial and seasonal shifts) can be derived from $\delta^{13}C$ values in faeces of herbivores that consume varying proportions of C_3 and C_4-based resources.

Conclusions

We conclude that stable carbon isotopic analysis of faeces is a reliable tool for reconstructing proportions of browse/grass consumption in herbivores. Faeces have a short turnover time (several days) compared to hard tissues such as hair and skeletal material that grow over several months or years. Hence, use of faeces as short-term dietary indicators allows for tracing herbivore diets at very high temporal resolutions. In combination with longer-term indicators like hair,

teeth, and bone, $\delta^{13}C$ values of herbivores can provide dietary information for a multitude of species across a wide spatial and temporal spectrum (months, years, or even decades). Isotopic studies of diet can, in turn, be used to provide quantifiable information regarding wildlife conservation issues such as differential resource utilisation, habitat manipulation through diet, and even inferring habitat change, over short- and long-term intervals.

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