

ELEPHANT (*LOXODONTA AFRICANA*) DIETS IN KRUGER NATIONAL PARK, SOUTH AFRICA: SPATIAL AND LANDSCAPE DIFFERENCES

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African elephants (*Loxodonta africana*) are mixed feeders, incorporating varying proportions of grass and browse into their diets. Disagreement persists as to whether elephants preferentially graze or browse, and the degree to which the consumption of these foods is a reflection of their local availability. We used stable carbon isotope analysis of feces to investigate seasonal and spatial variation in the diets of elephants from Kruger National Park (KNP), South Africa. Elephant diets (overall average ~35% grass) are shown to be distinct from those of grazers (>90% grass), browsers (<5% grass), and another mixed-feeder, the impala (*Aepyceros melampus*; ~50% grass). Fecal $\delta^{13}\text{C}$ values suggest that elephant populations from northern KNP eat more grass (~40%) during the dry season than do their southern counterparts (~10%). The wet-season diets of elephants from northern and southern KNP include similar amounts of grass (~50%), because elephants in the south, but not in the north, ate significantly more grass during this time. Although habitat differences in KNP appear to account partially for variations in elephant diets, the specific influence of each habitat type on diet selectivity is not clear. The homogeneity of woody vegetation in the north (dominated by *Colophospermum mopane* “shrubveld”) may deter browsing and force elephants in this area to opt for alternative food sources (grass) throughout the seasonal cycle.

Key words: carbon isotopes, elephants, feces, nitrogen

The African elephant (*Loxodonta africana*) is regarded as a high-impact megaherbivore species of the savanna. African elephants are believed to have a significant effect on local habitat conditions because they can consume large amounts of woody vegetation (Ben-Shahar 1998; Bowland and Yeaton 1997; Cumming et al. 1997; Jachmann and Bell 1985; Owen-Smith 1988). In spite of these assumptions, however, contention persists with regard to their dietary preferences, including whether elephants are primarily browsers or grazers (see Cerling et al. 1999).

In the past, there have been both browsing and grazing members of the elephant phylogenetic lineage (e.g., Cerling

et al. 1999; Owen-Smith 1988). Cerling et al. (1999) analyzed stable carbon isotopic ratios in tooth enamel carbonate from extinct proboscideans believed to be ancestral to both extant genera, *Loxodonta* and *Elephas* (Asian elephants). Their results reveal a diet shift from predominantly grazing in the late Miocene through the Pliocene and Pleistocene, to primarily browsing some time after 1 million years ago. However, modern elephant molar teeth have retained a high-crowned form, which has long been interpreted as a dental modification for an abrasive grazing diet (Cerling et al. 1999).

Among modern African elephants, it has been suggested that members of the forest subspecies of elephants (*L. africana cyclotis*) are browsers, whereas savanna elephants (*L. a. africana*) feed mostly on grass (Tangley 1997). The former is generally accepted, but the diet of savanna elephants remains unresolved. Different populations are thought to consume varying proportions of browse and grass depending on region, vegetation cover, water availability, soil nutrient composition,

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rainfall, and season (Cerling et al. 2004; Field and Ross 1976; Koch et al. 1995; Owen-Smith 1988; Short 1981; Williamson 1975). For example, elephant diets in Hwange National Park, Zimbabwe, appeared to consist almost entirely of woody plants (Williamson 1975). Conversely, Wing and Buss (1970) reported that elephants in Uganda relied primarily on grasses (approximately 90% of bulk). Such geographical variations in diet have prompted some authors to classify elephants as browsers (e.g., Dublin 1995; Jachmann and Bell 1985), whereas others maintain they are primarily grazers (e.g., Norton-Griffiths 1979; Tangle 1997).

Stable carbon isotope ecology provides a means for quantifying consumption of browse or grass by herbivorous mammals in African savannas. Stable carbon isotope ratios are distinct between plants using the C_3 photosynthetic pathway and those that use the C_4 photosynthetic pathway (Smith and Epstein 1971). In subtropical savannas, trees, shrubs, and forbs are C_3 , whereas almost all grasses use C_4 photosynthesis (Vogel et al. 1978). Because the carbon from food consumed is incorporated into animal body tissues, herbivore $^{13}C/^{12}C$ ratios reflect the proportions of grass to browse consumed (Cerling and Harris 1999; Vogel 1978). The carbon isotopic composition of feces also has been shown to be consistent with dietary values (even though these represent the excreted, undigested portion of the diet), during both experimental (Codron et al. 2005a; Sponheimer et al. 2003b) and field studies (Tieszen et al. 1979, 1989; van der Merwe et al. 1988).

In this study, we use stable carbon isotopic data from feces in Kruger National Park (KNP), South Africa, to investigate elephant diets. We also look for seasonal and geographic variability in diets throughout KNP. We have opted to use feces because these reflect the diet of an animal over the last 2 or 3 days before deposition, which allows investigation of seasonal change, whereas materials such as bones and teeth integrate the dietary signal over a longer period of time (Sponheimer et al. 2003b). Furthermore, fecal samples are easily collected without invasion or slaughter of animals. Our data are augmented by analysis of fecal nitrogen (N) content, which is a rough measure of diet quality (Holecheck et al. 1982; Leslie and Starkey 1985). The carbon isotopic ratios and associated percentage N (%N) results for local vegetation and selected sympatric browsers, grazers and mixed-feeding impalas (*Aepyceros melampus*) are included as a comparative ecological framework.

MATERIALS AND METHODS

Study area.—Kruger National Park is situated in northeastern South Africa, between 22°20' and 25°32'S and 30°53' and 32°02'E. In total it covers an area of 18,992 km², forming part of the “lowveld” savanna (approximately 300 m above sea level) between the Drakensberg escarpment to the west and the Mozambique coastal plain in the east. Climate and geological substrate vary throughout KNP, and the resulting vegetational differences allow mixed-feeding species such as elephants and impalas to use a variety of plant foods and to adjust their diets according to season and food availability. The various ecotypes of KNP are well documented, providing the opportunity to assess spatiotemporal dietary shifts based on differing

environmental conditions including plant composition, geology, and climate (Gertenbach 1980; Venter and Gertenbach 1986; revised in Venter et al. 2003).

Kruger National Park lies within 2 climatic zones. The south and central portions, that is, the area south of the centrally located Olifants River (hereafter referred to as southern KNP), lie in the “lowveld bushveld” zone with an average annual rainfall of 500–700 mm (Venter et al. 2003). The region north of the Olifants River (northern KNP) is in the arid “bushveld,” where mean annual rainfall is 300–500 mm. Rainfall occurs in the austral summer between November and March (i.e., the wet season), with a peak in January and February.

The geological succession of KNP changes from west to east, subdividing KNP in roughly north–south bands of different geology, with granitic rocks in the west and basaltic rocks in the east. Granites tend to form nutrient-poor substrates, whereas basaltic soils are nutrient rich. In southern KNP, the vegetation on granitic soils is dominated by broad-leaved species such as *Combretum*, whereas fine-leaved species such as *Acacia* dominate on the basalts. The arid bushveld of northern KNP is dominated by *Colophospermum mopane* (mopane) shrubveld, a tree species that is completely absent in the south (Venter et al. 2003).

Methods.—Elephant fecal samples were collected from the northern and southern granites and basalts, respectively, for 2 dry (winter of June 2002 and 2003), and 2 wet (summer of January 2003 and February 2004) seasons. To better interpret the carbon isotopic results from elephant feces, we also collected local vegetation as well as feces from browsing herbivores (giraffe [*Giraffa camelopardalis*] and greater kudu [*Tragelaphus strepsiceros*]), grazing herbivores (African buffalo [*Syncerus caffer*], blue wildebeest [*Connochaetes taurinus*], and Burchell's zebra [*Equus burchellii*]), and mixed-feeding herbivores (impala). Only recently deposited, that is, fresh or damp, feces were collected to ensure that samples represented the appropriate season, and were not contaminated by fungi, soil, and insects (see Wrench et al. 1996). Vegetation samples were taken from various tree, forb, and grass species from within circular transects (approximately 10-m diameter) established in different habitats (riverine, open savanna, closed woodland, and thorn thickets) throughout KNP (described in detail by Codron et al. [2005b]). Fecal and plant sampling was concentrated around the Shingwedzi restcamp area in the north, around the Skukuza camp on southern granites, and around the Lower Sabie and Crocodile Bridge restcamps on southern basalts.

Fecal and plant samples were oven-dried at 60°C for 24 h, homogenized, and ground. Carbon isotope ratios and percent nitrogen were obtained by combusting the samples in an automated elemental analyzer (Carlo-Erba, Milan, Italy) and introduced via a continuous flow-through system (CONFLO) to a Finnigan Mat 252 mass spectrometer (Finnigan, Bremen, Germany). $^{13}C/^{12}C$ ratios are presented in the standard delta (δ) notation in parts per thousand (‰), relative to the Pee Dee belemnite standard. Sample $\delta^{13}C$ values were calibrated against several working laboratory standards of known isotopic composition. Standard deviations for repeated measurements of these standards were less than 0.1‰.

We estimated the percentage of C_4 grass in each sample. To do so, we assumed a diet-feces fractionation of -0.9% (Codron et al. 2005a; Sponheimer et al. 2003b), and we used isotopic endpoint values for C_3 and C_4 vegetation that were specific to the region and season when the feces were collected. For example, feces collected from northern KNP during the dry season were assumed to denote a 100% C_4 grass diet if the $\delta^{13}C$ value was -13.3% ($-12.4 - 0.9\%$) or above, whereas feces from the wet season in southern KNP with a $\delta^{13}C$ value of -27.5% ($-26.6 - 0.9\%$) were taken as representative of a 100% C_3 diet. Thus, our calculations of percentage C_4 (% C_4) intake do not rely on published

TABLE 1.—Plants in C₃ photosynthesis (PS) group (trees and forbs) and C₄ photosynthesis group (grasses) sampled in northern and southern regions of Kruger National Park (KNP), showing $\delta^{13}\text{C}$ values and percentage N. Plants were sampled during the dry season (June 2002 and 2003) and the wet season (January 2003 and February 2004). Seasonal and regional mean $\delta^{13}\text{C}$ values for C₃ and C₄ plants, respectively, provided the isotopic endpoints for calculations of percentage C₄ intake from fecal $\delta^{13}\text{C}$ values.

Plant PS group	Region	Season	n	$\delta^{13}\text{C}$ (‰)		N (%)	
				\bar{X}	SD	\bar{X}	SD
C ₃ trees and forbs	Northern KNP	Dry	94	-26.7	1.6	1.8	0.7
		Wet	131	-26.8	1.5	2.8	1.3
	Southern KNP	Dry	233	-26.4	1.9	1.6	0.7
		Wet	198	-26.6	1.2	2.6	1.3
C ₄ grasses	Northern KNP	Dry	94	-12.4	1.1	0.8	0.4
		Wet	117	-12.3	0.9	1.7	0.8
	Southern KNP	Dry	136	-11.5	1.1	0.7	0.5
		Wet	143	-12.6	0.7	1.6	0.6

global data for C₃ and C₄ plants, but are based rather on a robust set of vegetation data specific to the study area and sampling period. Nevertheless, these calculations must be treated as approximations, rather than absolute values, because we cannot determine exactly which of the plants in the given range were actually eaten by the animals. However, employing KNP-specific regional and seasonal plant data as a baseline for determining %C₄ consumption from feces enhances the accuracy of these calculations (Codron et al. 2005a).

RESULTS

Overall plant and fecal $\delta^{13}\text{C}$.—Plants in KNP had $\delta^{13}\text{C}$ values entirely consistent with expectations for C₃ and C₄ vegetation, within rather narrow ranges (Table 1). These data are reported and discussed in detail by Codron et al. (2005b). All trees and forbs were C₃ (combined mean $\delta^{13}\text{C} = -26.6 \pm 1.6\text{‰}$; $n = 656$) and significantly depleted in ^{13}C compared to grasses, which were all C₄ (mean $\delta^{13}\text{C} = -12.2 \pm 1.1\text{‰}$; $n = 490$; analysis of variance, $P < 0.0001$; Table 1). Similarly, fecal $\delta^{13}\text{C}$ of browsing taxa conformed to a C₃-based diet (combined mean = $-26.6 \pm 0.9\text{‰}$; $n = 81$), and known-grazer $\delta^{13}\text{C}$ was consistent with a C₄ diet (combined mean = $-14.1 \pm 1.3\text{‰}$; $n = 120$; Table 2). Fecal $\delta^{13}\text{C}$ values of mixed-feeders were distinct from those of browsers and grazers ($P < 0.0001$; Table 2). Elephants (mean $\delta^{13}\text{C} = -22.8 \pm 3.0\text{‰}$; $n = 192$) and impalas ($-19.9 \pm 3.1\text{‰}$; $n = 164$) also differed significantly from each other ($P < 0.0001$), with elephants consuming approximately 35% and impalas about 50% C₄ grass (Table 2).

Geographical and seasonal variation in plant $\delta^{13}\text{C}$.—No significant north–south differences were found between mean $\delta^{13}\text{C}$ values of different plant groups (Tukey's honestly significant difference, $P = 0.0623$ for trees and forbs, $P = 0.0708$ for grasses; Table 1). Differences between the dry and wet seasons in C₃ plant $\delta^{13}\text{C}$ values were not significant for either region ($P = 0.6907$ in the south, $P = 0.9754$ in the north; Table 1). Grasses from the south were approximately 1‰ lower in $\delta^{13}\text{C}$ during the wet season than the dry ($P < 0.0001$), but mean $\delta^{13}\text{C}$ of grasses from the north did not change seasonally ($P = 0.9582$; Table 1).

TABLE 2.—Comparison of geographical and seasonal variations in mean $\delta^{13}\text{C}$, percentage C₄-grass intake, and percentage N of elephants (*Loxodonta africana*) with sympatric herbivores in Kruger National Park (KNP). Comparative browsers are represented by giraffe (*Giraffa camelopardalis*) and greater kudu (*Tragelaphus strepsiceros*); grazers by African buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes taurinus*), and Burchell's zebra (*Equus burchellii*); and mixed-feeders by impala (*Aepyceros melampus*).

Diet group	Region	Season	n	$\delta^{13}\text{C}$ (‰)		%C ₄ in diet	%N	
				\bar{X}	SD		\bar{X}	SD
Browsers	Northern KNP	Dry	19	-26.5	0.6	10	2.5	0.4
		Wet	21	-26.4	0.8	10	2.3	0.4
	Southern KNP	Dry	28	-26.6	1.0	5	2.7	0.8
		Wet	13	-27.1	0.8	5	2.5	0.6
Grazers	Northern KNP	Dry	9	-13.6	1.2	95	1.2	0.3
		Wet	25	-13.7	0.9	95	1.3	0.3
	Southern KNP	Dry	59	-13.8	1.3	90	1.2	0.3
		Wet	27	-15.2	1.1	90	1.8	0.8
<i>Aepyceros melampus</i>	Northern KNP	Dry	31	-22.5	2.3	35	2.2	0.6
		Wet	33	-18.4	3.6	65	1.7	0.5
	Southern KNP	Dry	61	-20.1	2.6	50	1.8	0.4
		Wet	39	-18.9	2.8	60	2.2	0.5
<i>Loxodonta africana</i>	Northern KNP	Dry	56	-22.2	1.9	40	1.2	0.4
		Wet	39	-20.5	3.1	50	1.4	0.5
	Southern KNP	Dry	61	-25.9	1.3	10	1.2	0.3
		Wet	36	-20.7	1.8	50	2.0	0.6

Overall, the small differences (generally $< 1\text{‰}$) between plants from different regions of KNP and from different seasons indicate that spatiotemporal differences of more than 1‰ between KNP herbivore fecal $\delta^{13}\text{C}$ values (Table 2) reflect true dietary differences rather than merely recording shifts in plant $\delta^{13}\text{C}$.

Geographical and seasonal variation in fecal $\delta^{13}\text{C}$.—Browser and grazer species did not show any significant spatial or seasonal shifts in fecal $\delta^{13}\text{C}$ ($P = 0.9996$ for browsers, $P = 0.9576$ for grazers; Table 2). By contrast, feces of mixed-feeding impalas and elephants differed between northern and southern populations (Table 2). Fecal $\delta^{13}\text{C}$ of impalas from the north were lower than those from the south during the dry season, indicating that northern populations ate a significantly lower proportion of grass during this period (approximately 35% in the north and approximately 50% in the south; $P < 0.0001$). However, fecal $\delta^{13}\text{C}$ suggests that, during the wet periods, northern and southern impala populations consumed similar proportions of grass (approximately 65% and approximately 60%, respectively; $P = 0.9998$; Table 2).

Examination of dry-season fecal $\delta^{13}\text{C}$ data for elephants show that northern populations consumed significantly more grass than in the south (approximately 40% in the north and approximately 10% in the south; $P < 0.0001$; Table 2). In the wet season, elephant fecal $\delta^{13}\text{C}$ showed that they increased their grass consumption to approximately 50% in both regions ($P < 0.01$ for the north; $P < 0.0001$ for the south; Table 2). Hence, southern elephants displayed much greater seasonal variation, switching from a chiefly browsing diet in the dry season to a more mixed diet in the wet season. The comparatively higher grass intake by northern elephants during the

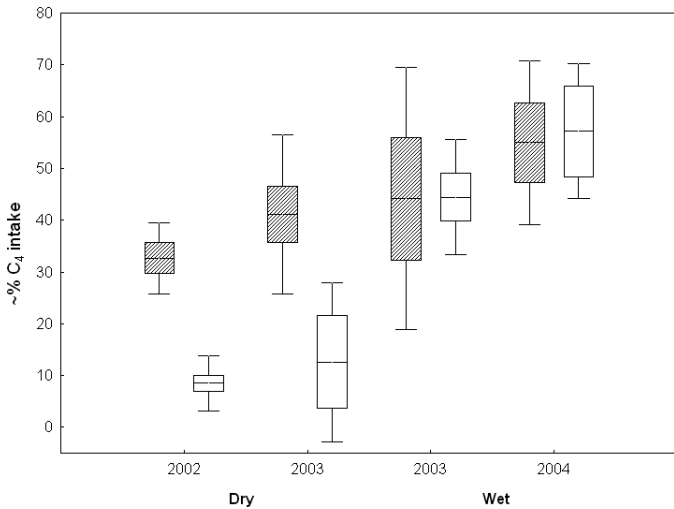


FIG. 1.—Boxplot showing seasonal and geographical changes, over 2 years, in the carbon isotopic composition of elephant (*Loxodonta africana*) feces from the northern (patterned) and southern (white) parts of Kruger National Park during dry and wet seasons. Plots show mean (horizontal line), 95% confidence interval (box), and 1 SD above and below the mean.

dry season, and the gross dry- to wet-season shift in grass consumption in the south, was recurrent for both years (Table 2; Fig. 1).

Percentage nitrogen of plants.—Percentage nitrogen (representing crude protein content) of browse foods (trees and forbs) was consistently higher (combined $\bar{X} = 2.2\% \pm 1.1\%$ SD, $n = 656$) than that of available grasses ($1.2\% \pm 0.7\%$, $n = 490$; $P < 0.0001$; Table 1). Predictably, all plant groups increased in crude protein content from the dry to the wet season ($P < 0.0001$; Table 1). Plant %N was generally higher in the north than in the south, although geographical differences in %N were only significant for C₃ vegetation ($P < 0.001$ for trees and forbs combined, $P = 0.2255$ for grasses; Table 1).

Percentage nitrogen of feces.—As expected, browsers had the highest fecal %N (combined $\bar{X} = 2.5\% \pm 0.6\%$, $n = 81$), whereas grazers had the lowest ($1.3\% \pm 0.5\%$, $n = 120$; Table 2). Mixed-feeding impalas had fecal %N ($\bar{X} = 1.9\% \pm 0.5\%$; $n = 164$) intermediate between the browser and grazer species ($P < 0.0001$; Table 2). Elephants, although a mixed-feeding species, had fecal N levels ($\bar{X} = 1.4\% \pm 0.5\%$, $n = 192$) as low as those of the grazer species ($P = 0.9176$; Table 2). Seasonally, herbivore feces from southern KNP paralleled the trend observed in plants, generally increasing in %N from the dry to the wet season ($P < 0.0001$; Tables 1 and 2). In particular, elephant feces from southern KNP showed a dramatic increase in %N from the dry to the wet season, coinciding with a sharp seasonal increase in grass consumption (from approximately 10% to approximately 50%) by these elephants ($P < 0.0001$). In contrast, fecal N content of browsers, grazers, and elephants from northern KNP was similar during both seasons ($P = 0.3277$) and northern impala fecal N decreased from the dry to the wet season ($P < 0.05$; Table 2). Geographical differences in fecal %N were only significant for grazers, impalas, and elephants, and only during

the dry season, that is, grazer and elephant fecal %N was higher in the north ($P < 0.01$), whereas impala fecal %N was higher in the south ($P < 0.01$; Table 2).

DISCUSSION

Examination of carbon isotopic data for feces from KNP reveals that the mixed-feeding species elephant and impala have variable diets, shifting toward greater or less grass consumption depending on region and season (with more grass usually being consumed in the wet season—Owen-Smith 1988; Skinner and Smithers 1990). However, different patterns emerge from dry season data in terms of north–south differences in use of grass and browse. In the case of impalas, southern populations consumed more grass (approximately 50%) than did northern populations (approximately 35%—Sponheimer et al. 2003a). Among elephants, the northern populations consistently eat higher proportions of grass (approximately 40%) than their southern counterparts (approximately 10%; Fig. 2). This finding is supported by data from Vogel et al. (1990), examination of which showed higher $\delta^{13}\text{C}$ values in elephant feces from northern KNP (combined $n = 14$ for feces from Punda Maria and Shingwedzi) compared with those from the south ($n = 11$ for Satara, Skukuza, and Malelane combined).

Colophospermum mopane is reportedly a staple food item for many elephant populations living in southern Africa (e.g., Skinner and Smithers 1990; Smallie and O'Connor 2000). Given the dominance of this tree species among northern vegetation, one might expect elephants in northern KNP to use more browse than their southern counterparts. Furthermore, the vegetation of northern KNP is generally regarded to be more woody and to have a higher ratio of tree to grass leaves than that of the southern areas (e.g., Gertenbach 1983; Scholes et al. 2003). Scholes et al. (2003) put forward a scenario for impact of elephants on woody vegetation in KNP, asserting that the woody plant fraction of elephant diets increases in areas with a high ratio of tree to grass leaves, such as mopane-dominated vegetation. By contrast, our results show that elephants do not consume food in proportion to its local abundance, an interpretation consistent with several other studies (e.g., Seydack et al. 2000; Short 1981; Skinner and Smithers 1990; Styles and Skinner 2000; Tieszen et al. 1989; Williamson 1975). For instance, Tieszen et al. (1989) found that in Tsavo National Park, Kenya, habitat changes from woodland to grassland over about a 50-year period had little effect on the proportions of browse and grass consumed by elephants. Elephants in Kasungu National Park, Malawi, an area where tree density is high, used a relatively high percentage of grass at certain times of the year, possibly because of the presence of seasonally flooded grassy areas (“dambos”—van der Merwe et al. 1988). In addition, the low palatability of *Brachystegia* trees likely contributed to the high degree of grass consumption by elephants in Kasungu during the wet season (Jachmann and Bell 1985).

The question that needs to be addressed, based on current evidence, is why do elephants in northern KNP consume higher

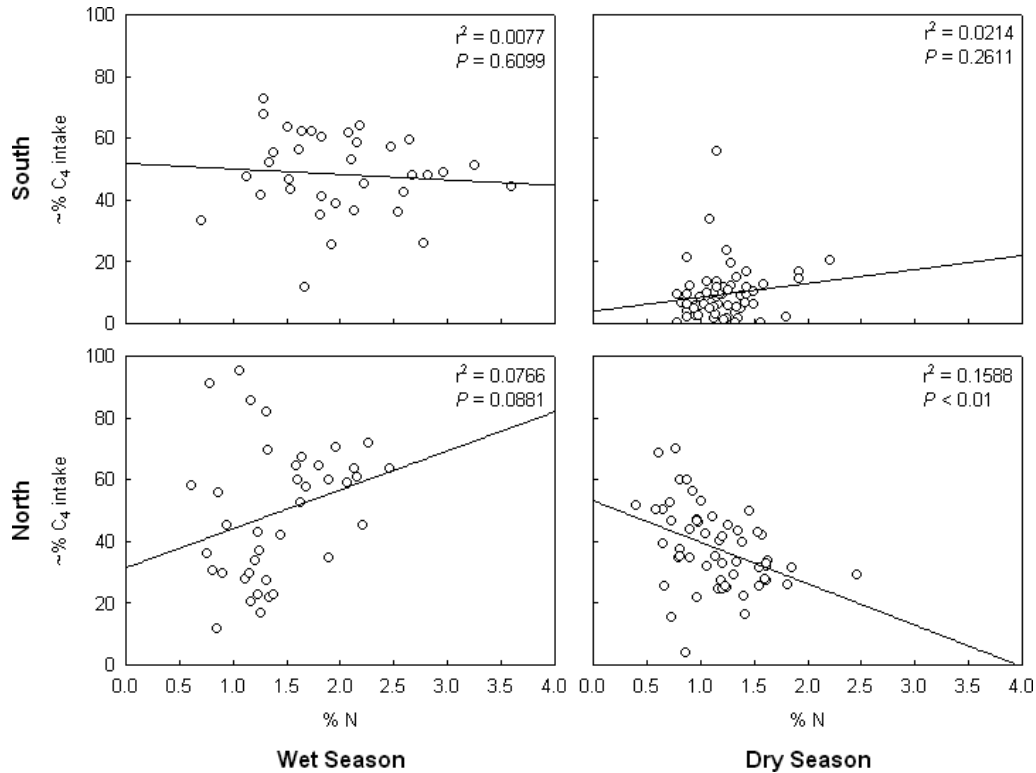


FIG. 2.—Scatterplots showing correlation between percentage C₄ intake and fecal percentage N for elephants from northern and southern Kruger National Park during the wet (January and February) and dry (June) seasons, respectively.

proportions of grass than those in the south? Cooper and Owen-Smith (1985) suggested that grasses are normally preferred to browse because of greater palatability and overall lower tannin concentrations. Thus, elephants in northern KNP possibly select grasses based on higher nutritional value. In southern African savannas, the nutritional content of local vegetation is conventionally attributed to differences between sweetveld and sourveld grassland habitats. Plants (and soils) from more arid regions (as is northern KNP) are often nutrient rich (especially during the dry season) compared to those in high-rainfall, sandy habitats, where nutrients leach from the soil (Acocks 1988; Tainton 1999). However, examination of our data revealed no north–south differences in the %N of grasses from KNP during both wet and dry seasons. Ellery et al. (1995) showed that the slower growth rates of grasses in dry areas often result in lower lignin and higher protein concentrations. Thus, although crude protein content of grasses did not differ between northern and southern KNP, it is possible that the overall nutritive value of grasses is higher in the north than in the south because of lower concentrations of lignin in the cell walls of the former.

Browse foods are consistently higher in N than is grass (Table 1), and thus one might predict that elephant fecal %N is a direct function of the proportions of browse to grass consumed (e.g., Greyling 2004). Because fecal N content is widely considered an indicator of diet quality, the relationship between %C₄ intake and fecal %N should provide insight into the mechanisms underlying browse or grass selection. Multiple linear regression analysis of fecal data for elephants revealed that %C₄ intake and

fecal N content are not significantly correlated (Fig. 2). Even though a significant correlation ($P < 0.01$) was observed between %C₄ intake and fecal %N of northern KNP elephants during the dry season, the relationship remains weak ($r^2 = 0.1588$). The lack of any strongly significant relationship between these 2 variables persisted when data were both log- and arcsine-transformed. Hence, the relative proportions of browse and grass consumed by elephants cannot be considered an important predictor of fecal N content.

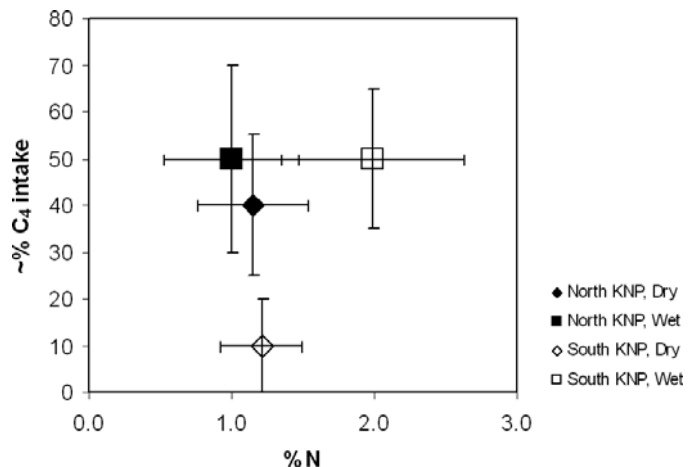


FIG. 3.—Bivariate plot of percentage C₄ intake and fecal percentage N of Kruger National Park elephants from different regions and seasons. Symbols denote mean values, and bars represent ± 1 SD.

The fact that no relationship exists between grass intake and fecal N content in elephants does not necessarily rule out selection for grasses based on nutritional value. Despite being more proteinaceous than grasses, woody plants contain larger quantities of indigestible compounds (such as condensed tannins and lignin), rendering browse foods no more, or even less, digestible than grass (Gordon and Illius 1996; Robbins et al. 1995). Indeed, elephant feces from southern KNP showed a dramatic increase in N content from the dry to the wet season, coinciding with a sharp seasonal increase in grass consumption by elephants in this area from approximately 10% to approximately 50% (Fig. 3). Nevertheless, attributing geographical differences in grass intake to a preference for more nutritional grasses can, at best, only partially explain their diets in KNP.

One of the most striking features of KNP vegetation is the abundance, and almost complete dominance, of mopane among the woody vegetation of the northern regions, and the complete absence of this tree species from the areas south of the centrally located Olifants River (Venter et al. 2003). Mopane has often been listed as a favored food source for African elephants, with the young leaves being preferred for their high protein content (e.g., Ben-Shahar 1998; Guy 1976; Skinner and Smithers 1990; Smallie and O'Connor 2000; Styles and Skinner 2000; Viljoen 1989; Williamson 1975). However, the leaves are rich in digestion-inhibiting secondary compounds (Styles and Skinner 2000) and the plant has a sinewy, fibrous physical composition (Kennedy 2000). These factors seem to render mopane trees less palatable at certain times of the year (Cooper and Owen-Smith 1985; Styles and Skinner 2000). For example, Styles and Skinner (2000) have shown that mopane bark appears to be most palatable during the winter months, largely because of its lower tannin content and total phenols. During the summer months, bark would be most nutritious but accompanied by high tannins and increased total phenols.

Barnes (1982) reported that elephants in Ruaha National Park, Tanzania, moved great distances in search of different food species in *Brachystegia* woodlands during the dry season. They did this, he believed, to avoid ingesting lethal doses of toxins from the few browse species available to them. A similar finding was reported by Jachmann and Bell (1985) for elephants in Kasungu, Malawi. Styles and Skinner (2000) found that elephants in Northern Tuli Game Reserve, Botswana, very rarely occupied the mopane scrub areas before the onset of spring rains. These observations suggest that elephants inhabiting mopane-dominated habitats might seek alternative resources (e.g., grasses) during the dry season, or for most part of the year.

Browse foods comprise higher concentrations of protein-precipitating phenolic compounds than do grasses, thus a browse-rich diet is expected to lead to raised fecal N levels (Robbins et al. 1987). The absence of a significant correlation between %C₄ intake and fecal %N of elephant feces from southern KNP during the dry season ($P = 0.2611$, $r^2 = 0.0214$; Fig. 2), where mean browse intake was at a maximum (approximately 90%), strengthens the argument that elephants diversify their diets to avoid ingesting high doses of digestion-inhibiting compounds. Thus, it seems likely that southern KNP

elephants eat a variety of poor-quality browse foods during the dry season, hence fecal %N remained low despite the browse-dominated diet (see also Freeland et al. 1985). Indeed, large herbivores are expected to avoid competition with smaller, more concentrate selectors through bulk intake of poor-quality, low-N foods (e.g., woody material—Gordon and Illius 1996; Owen-Smith 1988). By contrast, %C₄ intake and fecal %N for dry-season feces from northern KNP did show a significant (albeit weak) correlation ($P < 0.01$, $r^2 = 0.1588$), which is perhaps attributable to the browse portion of the diet being largely confined to a single species, that is, the phenol-rich *C. mopane*.

It is also interesting to note the differences between mixed-feeding elephants and impalas (see Table 1). The wet-season diets of impalas in the south and elephants in the north, respectively, did not differ much from diets in the dry season (approximately 10% increase in grass consumption for both species), but their respective fecal %N increased from the dry to wet season, as would be expected. However, impalas in the north and elephants in the south experienced a dietary shift of similar proportions in that both species ate significantly more grass during the wet season. Despite the similarity in magnitude of the dietary shift for northern impalas (approximately 30% more grass) and southern elephants (approximately 40% more grass) from the dry to the wet season, changes in fecal %N were different between these 2 species. Although fecal N levels for elephants in the south increased from the dry to the wet season the opposite was found for impalas in northern KNP. Thus, it would seem that impalas in the north are not able to avoid the effects of ingesting woody vegetation with high tannin content, hence the elevated fecal %N in the dry season compared to the wet. However, elephants in the south may be able to do so by feeding on a wider diversity of woody species, which would alleviate the toxic effects of any 1 species (Freeland et al. 1985). Impalas and elephants in northern KNP consumed similar proportions of browse during the dry season (approximately 60–65%). Nevertheless, elephants in northern KNP, like impalas, are also faced with little diversity in the woody component of the vegetation, and yet they seem able to deal with the effects of ingesting secondary compounds; they retained relatively low fecal N levels, regardless of season and the amount of browse foods consumed.

In summary, it would seem that elephants in northern KNP use a relatively high proportion of grass as an alternative resource in an otherwise homogeneous, mopane-dominated, landscape. In turn, the variable, and questionable, nutritive value of mopane may further deter elephant use of this resource. The wider diversity of woody plant species in southern KNP allows elephants to exploit this resource more efficiently, especially during the dry season when grass production is low.

CONCLUSION

This study has demonstrated that carbon isotopic analysis can be used to examine browse and grass consumption by mixed-feeding savanna herbivores. Data from feces proved to be a very useful material for documenting spatial and temporal shifts. The

relative ease with which this kind of analysis can be carried out means that large numbers of samples can be analyzed in a matter of days and the data can be subjected to rigorous statistical testing. In turn, samples from many different places or time periods can be compared, whereas more traditional approaches to diet are much more time-consuming. Here, we showed that elephants in KNP consume varying proportions of browse to grass in different regions and seasons, and we were able to relate these to landscape variations within KNP.

This technique is potentially useful not only for understanding or exploring the biological function of diet, but in the case of high-impact megaherbivore species such as elephants, carbon isotopic analysis can become an important management tool. For example, elephants are widely accepted to impact more heavily on local vegetation in areas where they consume higher proportions of woody plants. In a reserve such as KNP, in which proposed elephant management plans are based on differentiation of zones of high and low impact by elephants (Whyte 2001), examination of carbon isotopic data offers quick insight into the degree of manipulation of woody vegetation in different regions.

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