

# Stable isotope characterization of mammalian predator–prey relationships in a South African savanna

Daryl Codron · Jacqui Codron · Julia A. Lee-Thorp ·  
Matt Sponheimer · Darryl de Ruiter · James S. Brink

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**Abstract** This paper characterizes predator–prey interactions amongst African mammals from  $C_4$  savanna environments using stable carbon and nitrogen isotope proxies for diet. Stable carbon ( $\delta^{13}C$ ) and nitrogen ( $\delta^{15}N$ ) isotope data from hair and faeces of large African mammal carnivores, and herbivores as potential prey, are presented for a diverse range of taxa. Carbon-isotope data imply that most carnivores from the “lowveld” savanna of South Africa form part of  $C_4$  grass-based food webs. Nitrogen isotope data show clear differences between trophic levels, although it appears that the magnitude of these differences varies between predators feeding on invertebrates and vertebrates,

respectively. Whilst the number of carnivore samples for which data are available is relatively few, and data for prey are restricted mainly to large ungulate herbivores, results clearly demonstrate the potential for future applications of this technique to predator–prey food webs in African savannas. In tandem with traditional approaches, stable isotopes can help elucidate patterns of predator impacts on prey populations, domestic livestock, and resolving similar food webs in palaeoenvironmental contexts.

**Keywords** Carnivore · Faeces · Hair · Herbivore · Kruger Park

D. Codron (✉) · J. S. Brink  
Florisbad Quaternary Research, National Museum,  
P.O. Box 266, Bloemfontein 9300, RSA  
e-mail: daryl@nasmus.co.za

D. Codron · J. Codron · J. A. Lee-Thorp  
Department of Archaeology, University of Cape Town,  
Private Bag,  
Rondebosch 7701, RSA

J. A. Lee-Thorp  
Department of Archaeological Sciences, University of Bradford,  
Bradford BD7 1DP, UK

M. Sponheimer  
Department of Anthropology, University of Colorado at Boulder,  
Boulder, CO 80309, USA

D. de Ruiter  
Department of Anthropology, Texas A&M University,  
College Station, TX 77843-4352, USA

J. S. Brink  
Faculty of Natural and Agricultural Science,  
Centre for Environmental Management,  
University of the Free State,  
Bloemfontein 9300, RSA

## Introduction

The African savanna biome is home to an exceptional diversity of mammal herbivores and carnivores. Interactions between predators and their prey have important ecological consequences, ranging from direct impacts on prey populations to eliciting changes in community structure by decreasing populations of certain prey species and facilitating niche availability for other taxa, and to commercial and agricultural concerns through killing of domestic livestock (Sinclair et al. 1985; Mills et al. 1995; Harrington et al. 1999; Butler 2000; Mills and Funston 2003; Grange et al. 2004; Funston and Mills 2006). The diets of mammalian carnivores are, however, extremely complex; the number and diversity of prey species killed and eaten are highly variable across space and time. As a result, documenting the diets of free-ranging carnivores by traditional methods such as field observations, fecal analysis, and summaries of known kills may be unreliable in the absence of long-term field excursions (Avenant and Nel 2002; Bothma and Coertze 2004). The nocturnal

lifestyle of many carnivores, and the large areas their home ranges may cover, further constrain traditional methods (Bothma and Coertze 2004; Avenant and Nel 2002; Avenant 2006, personal communication). There is little doubt that further resolution of predator–prey interactions is needed to understand the effects on prey populations to build frameworks for effective adaptive management and conservation of African carnivores (see Mills and Funston 2003 for a review).

A powerful tool for resolving complex ecological interactions is stable isotope ecology. This approach allows researchers to trace nutrient flow through food webs because stable isotope ratios archived in animal tissues reflect the isotopic composition of the sources from which they are derived (e.g. Post 2002). Stable carbon isotopes ( $^{13}\text{C}/^{12}\text{C}$ ) record the carbon isotopic composition of the diet; in African savannas, this approach is primarily useful for documenting variations in  $\text{C}_3$  (trees, shrubs and forbs) to  $\text{C}_4$  (grass) biomass intake (Vogel 1978; Tieszen et al. 1979; Lee-Thorp and van der Merwe 1987; Cerling and Harris 1999; Codron et al. 2005). Stable nitrogen isotopes ( $^{15}\text{N}/^{14}\text{N}$ ) reflect trophic position and environmental condition (Minagawa and Wada 1984; Peterson and Fry 1987; Sealy et al. 1987). Application of this method to carnivore studies had previously yielded important insights into predator–prey food webs in marine and freshwater systems and amongst mammals in temperate North America and Europe (Peterson and Fry 1987; Post 2002; Ben-David et al. 2004; Gorokhova et al. 2005; Urton and Hobson 2005; Voigt and Klem 2006).

To our knowledge, no isotope studies have focused on carnivores in  $\text{C}_4$  African savanna environments, except for one study that reported only  $^{15}\text{N}/^{14}\text{N}$  ratios of bone collagen from Kasungu, Malawi (Sealy et al. 1987). For southern Africa, available data are limited to leopard *Panthera pardus* from  $\text{C}_3$  western Cape habitats of South Africa (Sillen and Lee-Thorp 1994). Some attempts have also been made to characterize predator–prey interactions of fossil mammals from South African Plio–Pleistocene  $\text{C}_4$  savannas, including early hominins and archaic *Homo sapiens* (Sillen and Lee-Thorp 1994; Lee-Thorp et al. 2000; Sponheimer et al. 2005), but insights are limited due to limited understanding of isotopic predator–prey relationships in the modern context. In this study, we present stable carbon and nitrogen isotope data from hair and faeces for a variety of mammalian carnivores and herbivores to examine carnivore diets in the Kruger National Park and other “lowveld” savanna habitats of South Africa. Whilst the data presented should be considered preliminary, they demonstrate clearly the potential applications of this approach, and we discuss implications and present guidelines for refining isotope-based models of mammalian predator–prey food webs.

## Materials and methods

Kruger National Park covers a large part (~2,000,000 ha) of the lowveld semi-arid savanna in the northeast of South Africa, lying at ~300 m above sea level on average. Mean annual rainfall varies between 500 and 700 mm in the south to between 300 and 500 mm in the north (Venter et al. 2003). Rainfall is highly seasonal, falling mainly during the austral summer between October and March, whilst April to November are dry. The park is divided longitudinally into granitic substrates forming nutrient-poor soils giving rise to closed woodland savannas in the west and nutrient-rich basaltic soils supporting more open grasslands in the east (Venter et al. 2003). The northern regions (to the north of the Olifants River) are dominated by mopane *Colophospermum mopane* “shrubveld” and woodland, whilst fine-leaved *Acacia* and *Combretum* spp. trees abound in the south.

Hair samples were collected by Kruger Park veterinary staff during routine field operations. Many hair samples were also provided by local taxidermists (Gametan) in the town of White River outside the southwestern border of Kruger Park, representing animals from nearby hunting farms. Fresh, i.e. moist or wet, faeces were collected during biannual excursions to Kruger Park from June 2002 to May 2005. Faeces were identified with the assistance of local rangers, although in some cases, the samples could not be identified to species or even genus level (e.g. mongoose).

Individual hair strands were cleaned with acetone, and a section large enough for isotope analysis (~0.5 mg) was cut from the root end to ensure that the analyzed portion represented the most recent growth. Faeces were oven-dried at 60°C for 24 h and mill-ground into a homogeneous powder through a 1-mm sieve. Each hair and fecal sample was combusted in an automated Elemental Analyzer (Carlo Erba, Milan), and the resultant  $\text{CO}_2$  gas was introduced to a Finnigan MAT 252 or DELTA XP Mass Spectrometer via a continuous flow-through inlet system (Conflo).  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  ratios are expressed in the delta ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) notation in parts per mil (‰) relative to the VPDB and atmospheric  $\text{N}_2$  standards, respectively. Analytical precision, based on standard deviations of repeated measurements of laboratory plant, protein and chocolate standards, is less than 0.1‰ for  $\delta^{13}\text{C}$  and 0.3‰ for  $\delta^{15}\text{N}$ .

## Data analysis

Herbivore species were categorized into prey groups based on trophic and body-size classes that would be useful for isotopic characterization of predator diets. We identified six isotopically distinguishable prey groups based on significant differences between mean  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , or both (ANOVA  $P < 0.001$ ; Table 1). Designated prey groups are:

**Table 1** Stable carbon and nitrogen isotope data for six prey groups from the South African “lowveld” savanna based on differences in trophic ecology and body size

Prey Group	Tissue	n	Tissue data				Converted estimates for muscle			
			$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)		$\delta^{15}\text{N}_{\text{Air}}$ (‰)		$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)		$\delta^{15}\text{N}_{\text{Air}}$ (‰)	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD
Large browsers	Hair	26	-23.0	1.2	5.8	2.0	-24.6	1.2	5.8	2.0
	Faeces	108	-26.7	0.8	4.7	1.4	-24.3	0.8	6.6	1.4
Small browsers	Hair	8	-23.2	0.9	7.2	2.4	-24.8	0.9	7.2	2.4
	Faeces	47	-26.0	2.3	4.8	1.3	-23.6	2.3	6.7	1.3
Large grazers	Hair	100	-10.6	0.8	6.7	1.1	-12.2	0.8	6.7	1.1
	Faeces	321	-13.7	1.1	4.0	2.1	-11.3	1.1	5.9	2.1
Small grazers	Faeces	4	-15.6		3.6		-13.2		5.5	
<i>Aepyceros melampus</i>	Hair	42	-15.5	3.3	8.0	1.2	-17.1	3.3	8.0	1.2
	Faeces	366	-19.5	3.1	6.1	2.1	-17.1	3.1	8.0	2.1
<i>Tragelaphus angasii</i>	Hair	2	-20.2		7.7		-21.8		7.7	
	Faeces	102	-24.2	3.7	5.6	1.6	-21.8	3.7	7.5	1.6

Conversion of herbivore hair and fecal  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to estimated muscle equivalents is included in the right hand columns. Standard deviation (SD) is presented for groups with  $n \geq 5$ .

Large browsers: giraffe *Giraffa camelopardalis*, kudu *Tragelaphus strepsiceros*; small browsers: bushbuck *Tragelaphus scriptus*, steenbok *Raphicerus campestris*, grey duiker *Sylvicapra grimmia*; large grazers: Burchell's zebra *Equus burchellii*, buffalo *Syncerus caffer*, blue wildebeest *Connochaetes taurinus*, waterbuck *Kobus ellipsiprymnus*, reedbuck *Redunca arundinum*, sable antelope *Hippotragus niger*; small grazers: scrub hare *Lepus saxatilis*, cane rat *Thryonomys* sp.

large-bodied (>100 kg)  $\text{C}_3$  browsers (giraffe *Giraffa camelopardalis* and kudu *Tragelaphus strepsiceros*), small-bodied (<100 kg)  $\text{C}_3$  browsers (bushbuck *Tragelaphus scriptus*, steenbok *Raphicerus campestris*, and grey duiker *Sylvicapra grimmia*), large-bodied  $\text{C}_4$  grazers (Burchell's zebra *Equus burchellii*, African buffalo *Syncerus caffer*, blue wildebeest *Connochaetes taurinus*, waterbuck *Kobus ellipsiprymnus*, reedbuck *Redunca arundinum*, and sable antelope *Hippotragus niger*), mixed  $\text{C}_3/\text{C}_4$ -feeding impala *Aepyceros melampus*, mixed-feeding nyala *Tragelaphus angasii* and small  $\text{C}_4$ -grazing mammals (scrub hare *Lepus saxatilis* and cane rat *Thryonomys* sp.). We also include data for termites from Kruger National Park (Sponheimer et al. 2005) for comparison with data from primarily insectivorous predator species.

Animal tissues differ with respect to carbon-isotope differences between the source (diet) and consumer (Tieszen et al. 1983; Lee-Thorp et al. 1989; Ambrose and Norr 1993; Sponheimer et al. 2003a, 2006; Passey et al. 2005). This means not only that direct comparison between data from hair and faeces is misleading but also for carnivore studies that isotopic differences between various prey tissues eaten need to be accounted for. We therefore converted herbivore hair and fecal data to their ‘muscle equivalents’ based on the premise that the bulk of mammalian carnivore diets are derived from flesh. Hair and fecal  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were adjusted using discrimination factors for hair, faeces and muscle reported from controlled-feeding studies (Sutoh et al. 1987; Cerling and Harris 1999;

Sponheimer et al. 2003a, 2006; Codron et al. 2005) to estimate hair–muscle and faeces–muscle differences (summarized in Table 2). For example, herbivore hair and muscle are 3.1 and 1.5‰, respectively, enriched in  $^{13}\text{C}$  relative to diet (Cerling and Harris 1999; Sponheimer et al. 2006). Hence, the difference (1.6‰) was subtracted from herbivore hair  $\delta^{13}\text{C}$  to derive a muscle equivalent.

Similarities between adjusted hair and fecal data of large browsers ( $P=0.99$  and  $0.64$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively) and small browsers ( $P=0.96$  and  $0.99$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively) indicate some reliability of the method used for the conversions (Table 1). Even converted values for impala, a notorious mixed feeder that is expected to display widely divergent isotopic values (Vogel 1978; Codron et al. 2006), are similar ( $P=0.99$  and  $1.00$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively). In the case of grazers, converted values differed slightly between hair and faeces ( $P<0.05$  for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ). Nevertheless, these differences are too small (0.9 for  $\delta^{13}\text{C}$ , 0.8 for  $\delta^{15}\text{N}$ ) to alter overall characterization of carnivore diets in terms of  $\text{C}_3$ - and  $\text{C}_4$ -based food intake. The differences might affect qualification of different source inputs, and we thus control for this potential error in the mixing model (Isosource) discussed below. There are also patterns evinced in our data, which agree with predicted isotopic differences between tissues. For example, the data presented in Table 2 based on the findings of previous controlled-feeding studies suggest that faeces should be 1.9‰ lower in  $\delta^{15}\text{N}$  compared with both hair and muscle (see Sutoh et al.

**Table 2** Stable carbon and nitrogen isotope differences between diet, hair, muscle and faeces of herbivores and carnivores

Tissue(s)	Herbivores		Carnivores	
	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)	$\delta^{15}\text{N}_{\text{Air}}$ (‰)	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)	$\delta^{15}\text{N}_{\text{Air}}$ (‰)
$\Delta$ Diet-hair	+3.1 <sup>a</sup>	+2.9 <sup>b</sup>	+2.6 <sup>c</sup>	+3.4 <sup>c</sup>
$\Delta$ Diet-faeces	-0.9 <sup>d,e</sup>	+1.0 <sup>b</sup>	-0.9 <sup>d,e</sup>	+1.0 <sup>f</sup>
$\Delta$ Diet-muscle	+1.5 <sup>g</sup>	+2.9 <sup>b</sup>		
$\Delta$ Hair-muscle	-1.6 <sup>h</sup>	0.0 <sup>h</sup>		
$\Delta$ Faeces-muscle	+2.4 <sup>h</sup>	+1.9 <sup>h</sup>		

<sup>a</sup> Cerling and Harris (1999)<sup>b</sup> Sutoh et al. (1987)<sup>c</sup> Roth and Hobson (2000)<sup>d</sup> Sponheimer et al. (2003a)<sup>e</sup> Codron et al. (2005)<sup>f</sup> Calculated from data used in this study<sup>g</sup> Sponheimer et al. (2006)<sup>h</sup> Calculated from predicted diet-tissue differences

1987 for a review). In the current dataset, mean  $\delta^{15}\text{N}$  of herbivore faeces ( $5.1 \pm 2.1\%$ ,  $n=948$ ) is 1.8‰ lower than that of hair ( $6.9 \pm 1.5\%$ ,  $n=178$ ).

Adjusting carnivore data for diet-tissue differences is more difficult because very few studies have described discrimination factors for mammal carnivores. The only reliable data available for medium- to large-bodied mammal carnivores from controlled environments are provided by Roth and Hobson (2000) for red fox *Vulpes vulpes*. The red fox data suggest diet-hair enrichment factors of 2.6 and 3.4‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively (Table 2). No similar data could be found for carnivore faeces, hence we applied the diet-faeces differences observed for herbivores to carnivore data, i.e. -0.9 and 1.0‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively (Sutoh et al. 1987; Sponheimer et al. 2003a; Codron et al. 2005). This approach is supported by the fact that, in our data, overall mean fecal  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of carnivores (-17.5 and 8.0‰, respectively) differ from converted muscle values for herbivores (-16.6 and 6.9‰, respectively) by exactly -0.9 and 1.1‰, respectively.

### Isosource

Quantifying inputs of different food sources can be difficult because of the wide diversity of prey types carnivores may consume. Single isotope mixing models have been widely used to resolve inputs of two isotopically distinct food sources, such as proportions of  $\text{C}_3$  to  $\text{C}_4$  biomass consumed by savanna herbivores from  $\delta^{13}\text{C}$  data (Cerling et al. 2003; Sponheimer et al. 2003b; Codron et al. 2005). However, application of this method to carnivore diets is unsuitable because single isotope mixing models cannot resolve inputs of more than two sources. Isosource is an iterative mixing

model that combines evidence from two or more isotopes in considering all possible combinations between the consumer and dietary endpoints to resolve inputs of multiple sources (Phillips and Gregg 2003). The program allows the user to enter isotope data for three or more food sources and values for consumer tissues, which are adjusted for diet-tissue discriminations. It also allows the user to control for analytical error and sample variability by adjusting isotopic increment and tolerance ranges, respectively. Isosource has successfully been applied to resolve complex diets of a variety of taxa from different ecosystems, including large mammal carnivores such as bears (Ben-David et al. 2004) and the gray wolf *Canis lupus* (Urton and Hobson 2005).

Because the majority of our data for potential prey species represented large herbivores, we only tested the Isosource model for lion *Panthera leo* and spotted hyaena *Crocuta crocuta*, two carnivores known to feed primarily on medium to large body-sized ungulates (e.g. Mills and Funston 2003). In addition, data were available for hair and faeces of both species, allowing for comparisons between the information recorded in different materials. Thus, the model was repeated for hair and faeces of these carnivores. We adjusted isotope tolerance to 0.9‰ to control for potential error in combining converted "muscle" values from hair and fecal herbivore data (see Table 1). We included converted "muscle" values for four prey group categories, i.e. large browsers, small browsers, large grazers and impala. We opted for impala as the prominent, abundant mixed feeders in Kruger Park and surrounding habitats rather than the more scarce and patchily distributed nyala *Tragelaphus angasii* (Pienaar 1963). Inclusion of nyala as a fifth potential prey source in any case made no significant alterations to the results and are hence excluded from the discussion that follows. The two small graminivorous taxa (hare and cane rat) are represented by too few samples ( $n=4$ ) for statistical comparison with other potential food groups and are hence also omitted from this analysis.

### Results and discussion

Carnivore hair and fecal  $\delta^{13}\text{C}$  suggest that most taxa form part of  $\text{C}_4$  food webs in these southern African savannas (Table 3). Hair  $\delta^{13}\text{C}$  of carnivores is highest in lion (mean = -10.9‰,  $n=3$ ) and lowest in genet *Genetta* sp. (-17.1  $\pm$  2.6‰,  $n=5$ ). By contrast, mean hair  $\delta^{13}\text{C}$  of  $\text{C}_3$ -feeding (browsing) herbivores were far lower, ranging only from -22.7‰ ( $n=2$ ) in giraffe to -23.4‰ ( $n=2$ ) in bushbuck. Fecal  $\delta^{13}\text{C}$  showed similar  $^{13}\text{C}$ -enriched diets for lion (-17.0  $\pm$  1.7‰,  $n=6$ ), hyaena (-16.9  $\pm$  4.3‰,  $n=23$ ) and an unidentified small felid (-16.7‰,  $n=4$ ). Fecal  $\delta^{13}\text{C}$  for an unidentified mongoose species (-25.9‰,  $n=2$ ), and a single sample for ratel (honey badger) *Mellivora capensis*

**Table 3** Stable carbon and nitrogen isotope data for hair and faeces of carnivores from the South African lowveld savanna

Species	Common name	Hair				Faeces					
		n	$\delta^{13}\text{C}_{\text{VPDB}}$		$\delta^{15}\text{N}_{\text{Air}}$		n	$\delta^{13}\text{C}_{\text{VPDB}}$		$\delta^{15}\text{N}_{\text{Air}}$	
			(‰)	SD	(‰)	SD		(‰)	SD	(‰)	SD
<i>Mellivora capensis</i>	Ratel (honey badger)					1	-22.1		9.6		
<i>Canis mesomelas</i>	Black-backed jackal	5	-13.4	1.4	13.0	2.1					
<i>Proteles cristatus</i>	Aardwolf	2	-13.0		9.2						
<i>Crocuta crocuta</i>	Spotted hyaena	2	-13.7		10.5		23	-16.9	4.3	7.9	2.0
<i>Genetta</i> sp.	Genet	5	-17.1	2.6	12.1	0.5					
Unidentified herpestid	Mongoose						2	-25.9		7.4	
<i>Felis lybica</i>	African wildcat	1	-14.8		11.9						
<i>Caracal caracal</i>	Caracal	3	-15.3		10.1						
Unidentified felid	Small cat						4	-16.7		7.2	
<i>Panthera leo</i>	Lion	3	-10.9		9.4		6	-17.0	1.7	8.9	1.0
<i>P. pardus</i>	Leopard	1	-14.0		11.0						
Prey base											
Large browsers	Giraffe, kudu	26	-23.0	1.2	5.8	2.0	108	-26.7	0.8	4.7	1.4
Small browsers	Bushbuck, steenbok, grey duiker	8	-23.2	0.9	7.2	2.4	47	-26.0	2.3	4.8	1.3
Large grazers	Zebra, buffalo, wildebeest, waterbuck, reedbuck, sable	100	-10.6	0.8	6.7	1.1	321	-13.7	1.1	4.0	2.1
Small grazers	Hare, cane rat						4	-15.6		3.6	
<i>Aepyceros melampus</i>	Impala	42	-15.5	3.3	8.0	1.2	366	-19.5	3.1	6.1	2.1
<i>Tragelaphus angasii</i>	Nyala	2	-20.2		7.7		102	-24.2	3.7	5.6	1.6

Data for herbivores are shown for isotope control. Standard deviation (SD) is presented for groups with  $n \geq 5$

(-22.1‰), suggest much higher levels of  $\text{C}_3$ -feeding in these taxa. Predicted trophic level differences in  $\delta^{15}\text{N}$  (Peterson and Fry 1987; Sealy et al. 1987) are also strongly evident in these data. Carnivore hair  $\delta^{15}\text{N}$  is, on average, 4.3‰ higher than that of herbivores ( $P < 0.0001$ ; Table 3). Fecal  $\delta^{15}\text{N}$  values show a similar distinction, although the trophic effect appears to be slightly smaller than in hair, with carnivore faeces being 2.9‰ enriched in  $^{15}\text{N}$  compared to herbivores ( $P < 0.0001$ ).

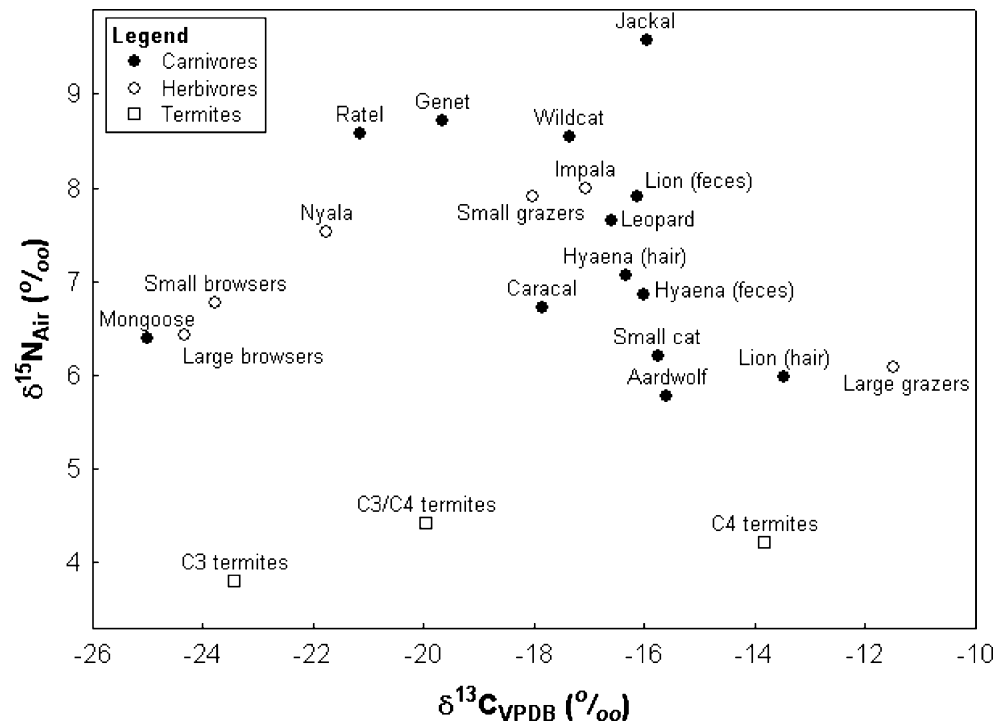
Although data presented in Table 3 demonstrate immediate evidence for trophic level differences in mammals, and differential  $\text{C}_3$  and  $\text{C}_4$  food use by carnivores, the data may be slightly misleading in terms of the isotopic relationship that exists between predators and their prey. Results of converting herbivore data to muscle equivalents, and adjusting carnivore data for expected diet–consumer discrimination effects, are displayed in Fig. 1. This analysis confirms the placement of most carnivores as members of  $\text{C}_4$  food webs. All small cat species, lion, leopard, aardwolf *Proteles cristatus*, hyaena and black-backed jackal *Canis mesomelas* cluster at the  $\text{C}_4$  end of the carbon-isotope spectrum. The implication is that although these animals may consume a variety of prey species, the majority of hunting time is spent in habitats where they encounter a predominantly  $\text{C}_4$  prey base. This finding agrees with the expectations that these carnivores are predominantly terrestrial, open savanna predators. Nonetheless, the data do

imply some utilization of  $\text{C}_3$ - or mixed  $\text{C}_3/\text{C}_4$ -based foods, with adjusted  $\delta^{13}\text{C}$  means varying from -13.5‰ in lion hair to -17.9‰ in caracal *Caracal caracal*. By contrast, mean  $\delta^{13}\text{C}$  estimated for muscle of grazing herbivores is more positive compared to the range for all carnivores (apart from data derived from lion hair), ranging from -12.0‰ in buffalo to -10.8‰ in sable antelope.

That the predominantly  $\text{C}_4$ -feeding carnivores also show evidence for utilization of at least some  $\text{C}_3$  prey items agrees with the predictions for more generalist behaviours amongst carnivores compared with most herbivore species (e.g. Vrba 1992). The data for lion are extremely interesting in this regard, in that hair and fecal  $\delta^{13}\text{C}$  seem to reflect different diets; adjusted hair  $\delta^{13}\text{C}$  indicates predominantly  $\text{C}_4$ -based prey consumption, whereas fecal data reflect food intake nearer to the middle of the  $\text{C}_3/\text{C}_4$  spectrum. These data almost certainly represent different habitats from where the samples are derived and will be discussed below.

Genet and ratel are shown by these data to incorporate a more even mix of  $\text{C}_3$ - and  $\text{C}_4$ -feeding prey species, which may include a variety of murids, insects, arachnids and other foods (Skinner and Smithers 1990). Fecal data for an unidentified mongoose species (adjusted mean  $\delta^{13}\text{C} = -25.0‰$ ) indicate almost exclusive utilization of  $\text{C}_3$ -based foods, but it is obviously not possible to explore this prediction in the absence of species-level identification of the specimens.

**Fig. 1** Stable carbon and nitrogen isotope data from hair and faeces of “lowveld” carnivores, which are adjusted for diet–tissue discriminations. Trophic positions of mammal carnivores are shown in relation to data for herbivore hair and faeces data adjusted to estimated muscle equivalents. Data for termites are from Sponheimer et al. (2005)



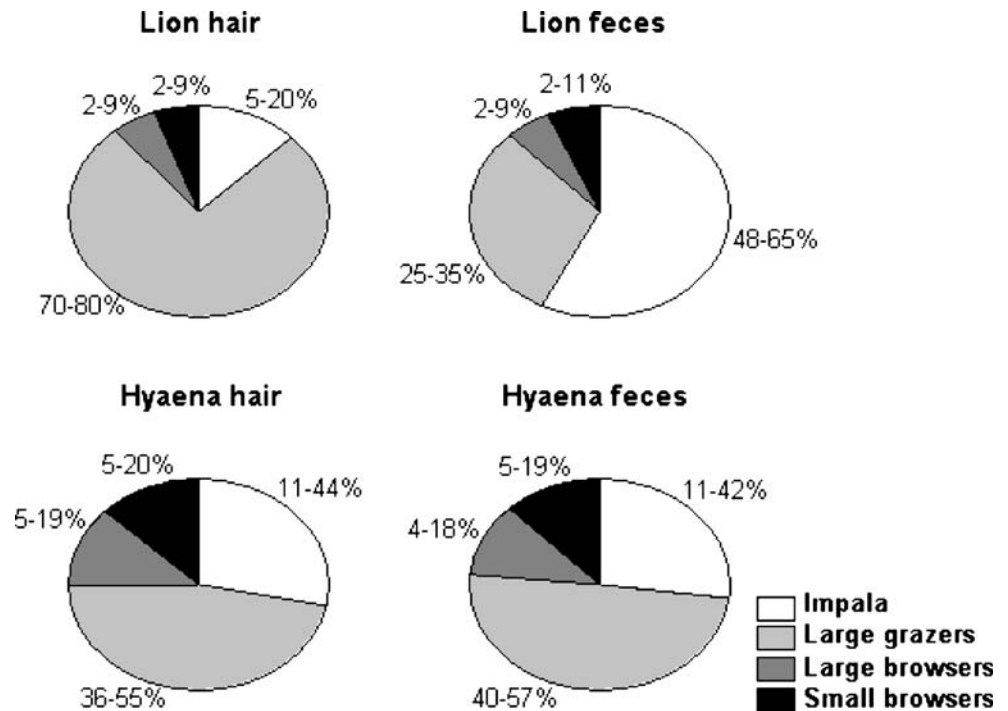
Adjustments to carnivore  $\delta^{15}N$  for trophic differences place them in an isotopic context of lower trophic levels, with most carnivores falling well within the range for ‘muscle’  $\delta^{15}N$  of herbivores (Fig. 1). Exceptions are noted, with jackal, genet and ratel all having higher  $\delta^{15}N$  values than expected if current data for herbivores represent prey species commonly eaten by these carnivores, even after adjusting data for the trophic level effect. All three (jackal, genet and ratel), however, are expected to feed predominantly on invertebrates, including many insect and arachnid species, at least in some environmental conditions (Skinner and Smithers 1990; Loveridge and Macdonald 2003). By contrast, most other carnivores included in this study feed predominantly on vertebrates, either medium- to large-sized ungulates, murids and other small mammals, or birds (Pienaar 1969; Skinner and Smithers 1990; Avenant and Nel 2002; Mills and Funston 2003). Previously, Kelly (2000) proposed that trophic level differences in  $\delta^{15}N$  differ between invertebrate and vertebrate feeders, in that the herbivore–carnivore difference is larger amongst invertebrate feeders. The higher  $\delta^{15}N$  than expected for jackal, ratel, and genet is in agreement with this prediction.

The pattern of differences in  $\delta^{15}N$  between vertebrate and invertebrate feeders is further illustrated in the data from aardwolf. Aardwolf feed almost exclusively on termites, principally members of the genus *Trinervitermes* (Richardson 1987). Available data for termites from Kruger Park suggest lower mean  $\delta^{15}N$  than that of any of the ungulate herbivores included in the current study (Fig. 1;  $C_3$  termite mean  $\delta^{15}N=3.8\pm 1.2\%$ ,  $n=14$ ;  $C_3/C_4$  mixed

termite mean= $4.4\pm 3.2\%$ ,  $n=16$ ;  $C_4$  termite mean= $4.2\pm 2.7\%$ ,  $n=6$ ). Not surprisingly, aardwolf have the lowest hair  $\delta^{15}N$  of all carnivores ( $5.8\%$ ,  $n=2$ ; Table 1). The carbon-isotope evidence for this species shows quite clearly that they feed predominantly on  $C_4$ -based items, which amongst available termite data include specimens of *Trinervitermes dispar* and also *Macrotermes ukuzii*. Yet, hair  $\delta^{15}N$  for aardwolf remains far higher ( $5.8\%$ ) than  $\delta^{15}N$  of termites even after controlling for trophic level differences using a diet–hair discrimination of  $3.4\%$  (Roth and Hobson 2000). The implication in this study is that larger trophic level  $^{15}N$ -enrichment almost certainly does occur amongst invertebrate-feeding compared with vertebrate-feeding carnivores. It is also possible that aardwolf simply feed on termites with particularly high  $\delta^{15}N$ , given that available data for termites are highly variable (range for  $C_4$  termites: from 2.3 to 10.1%). Testing differential trophic discriminations for insectivores and vertebrate-feeding carnivores will require more data for insects and arachnids from similar lowveld habitats. If this suggestion is true, however, then data for carnivores feeding on vertebrates would need to be treated differently to insectivorous taxa. Indeed, this implies that well-controlled isotope studies of predator–prey interactions may even be useful in differentiating between these two broad categories of faunivory.

Contributions of prey groups to the diets of lion and hyaena are quantified using Isosource. Results are presented in Fig. 2 based on the 25th to 75th percentiles of feasible intake ranges output by this mixing model. Results for lion hair suggest that the overwhelming majority of their

**Fig. 2** Partitioning of prey type eaten by lions and hyaena as reflected by hair and fecal  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  based on a dual-isotope, multiple-source mixing model (Isosource; Phillips and Gregg 2003). The ranges represent the 25th to 75th percentiles of feasible intake output by the model



diet (70–80%) is derived from large grazers, which may be expected from the trophic placement of adjusted lion hair isotope data displayed in Fig. 1. This finding agrees with the predictions for the composition of lion diets in Kruger Park, although impala are also an important prey item (Mills and Funston 2003; Funston and Mills 2006). Indeed, lion fecal data reflect greater utilization of mixed-feeding impala (48–65%) than large grazing ungulates (25–35%). This result is not altogether surprising because  $\delta^{13}\text{C}$  data varied by 6.1‰ on average between lion hair and faeces, a magnitude larger than can be attributed to different discrimination factors between the two tissues. Lion  $\delta^{15}\text{N}$  also reflect disparity in diet; lion hair had amongst the lowest  $\delta^{15}\text{N}$  of all carnivores, whereas fecal  $\delta^{15}\text{N}$  was relatively high, reflecting the higher  $\delta^{15}\text{N}$  of mixed feeders compared with browsing and grazing ungulates (Table 1). The most likely explanation for the apparent dietary disparity is that the data represent habitat-based variations. Our lion hair samples were collected from animals living in eastern basalt landscapes of Kruger Park where open grasslands and large grazers predominate; faeces were collected on a single occasion in a wooded granite-based habitat (24°58'36.8"S, 31°37'24"E) where grazers are less abundant (see Pienaar 1963 for a review). Indeed, the lions in Kruger are known to select foods based on availability and abundance of prey (Funston and Mills 2006).

Spotted hyaena, by contrast, show similar results for hair and faeces; results from both suggest an even consumption of large grazers and impala (Fig. 2). The hyaena results therefore imply a more opportunistic feeding style than lion, in that a wider variety of foods

are eaten constantly, rather than the animals focusing on preferred or available foods in a given region (as appears to be the case for lion; Skinner and Smithers 1990; Funston and Mills 2006).

The results of the Isosource model offer very little evidence for consumption of browsers (<10%, maximum 11%) by lion but slightly higher consumption (up to 20%) of these animals by hyaena. Indeed, browsing taxa are reported to contribute less than 10% to the diets of lion in Kruger Park (Mills and Funston 2003). For hyaena, on the other hand, it is difficult to thoroughly compare the isotopic data with predictions for diet because the number of food groups this extreme generalist is known to eat far exceeds the number of food sources used in our model (e.g. Skinner and Smithers 1990; Mills and Funston 2003). For example, hyaena in Kruger Park are expected to consume browsers such as kudu and steenbok in greater proportions than suggested by our study (Mills and Funston 2003). The case for hyaena is further addressed below.

#### Implications for future studies

Food selection by carnivores is often interpreted as a function of differences in body-size classes of prey consumed. Our results demonstrate dietary differences based on the feeding behaviour and associated habitat preferences of prey species/groups, in particular selection for open habitat,  $\text{C}_4$ -feeding herbivores, regardless of body-size class. This kind of information can directly benefit future studies of predator–prey interactions in African savannas and other environments. There are, however,

several potential limitations to isotope-based approaches and interpretations that need to be considered.

In this study, we have not attempted to control for spatio-temporal variations in the isotopic compositions of prey populations that are likely to be recorded in the tissues of carnivores. For example, impala diets may vary considerably across space and time; carbon-isotope evidence from hair and faeces of this species have already been shown to differ significantly in different landscapes of Kruger Park (Codron et al. 2006). Further spatially and seasonally constrained data for predators and their prey are needed to refine interpretations of carnivore-feeding behaviour to obtain isotopically controlled insights into shifts in prey species utilized in different regions and/or seasons.

Another limitation is that our adjustments of carnivore isotope data for diet–hair discriminations rely almost solely on data reported for red fox (Roth and Hobson 2000). However, values reported for this species may not be the same for African carnivores. It is well known, for instance, that herbivore  $\delta^{15}\text{N}$  varies not only with trophic level but also in response to ecophysiological, climatic, and nutritional mechanisms (Sealy et al. 1987; Ambrose 1991; Sponheimer et al. 2003c). Similar variations across habitats, and even between species, are likely to also occur in carnivores, although a general trend for mammals (and birds) appears to be increasing body  $^{15}\text{N}$  with increased quality of dietary protein (Robbins et al. 2005). Thus, whilst differences in diet–tissue discriminations between species may be relatively small (except perhaps between vertebrate-feeding and invertebrate-feeding taxa), further data are needed. Controlled-feeding studies and combination of isotope evidence with traditional approaches to carnivore diets would confirm and improve methods and interpretations followed in this study.

Our approach also assumes that muscle is the only material eaten by carnivores, in particular species feeding on vertebrates. However, many carnivores will ingest hair, feathers, bone and other components of their prey, each of these materials having different isotopic signatures. A clear example of this problem can be drawn from the spotted hyaena. One previous study of hyaena in Kruger Park found impala to be the most commonly eaten prey species due to their extreme abundance (Pienaar 1969). However, our data suggest that large grazers form an equally substantial or even greater component of the diets of lowveld hyaena (36–57%). Mills and Funston (2003) also report relatively higher consumption of browsing kudu and steenbok by hyaena in Kruger Park than appears evident in our data. Hyaena are well-known bone crushers ingesting considerable quantities of this tissue alongside with animal flesh. Carbon in both the organic (collagen) and inorganic (apatite) phases of bone is enriched in  $^{13}\text{C}$  relative to muscle (Tieszen et al. 1983; Lee-Thorp et al. 1989;

Ambrose and Norr 1993). This means that the  $^{13}\text{C}$ -enriched portion of their diets may include not only tissues of  $\text{C}_4$  feeders but also skeletal material of browsers and/or mixed feeders, leading to an under-representation of more  $\text{C}_3$ -reliant prey in isotope mixing models when we assume ingestion of only muscle.

Despite the caveats outlined above, our study demonstrates clearly the potentials of stable isotope-derived characterizations of mammalian predator–prey interactions. A number of applications of direct consequence to wildlife management and carnivore ecology can be identified over and above the immediately obvious use of this method for resolving complex diets of a variety of species whose feeding habits may otherwise be difficult to document because of large home ranges, nocturnal hunting, etc. (e.g. Avenant and Nel 2002; Bothma and Coertze 2004).

Predators may play an important role in limiting prey populations, especially within confined, fenced areas characteristic of many wildlife preserves across southern Africa. Increased predation pressure has been proposed as the ultimate factor responsible for roan antelope *Hippotragus equinus* population crashes in the northern Kruger Park during the 1980s (Harrington et al. 1999; Grant et al. 2002). Today, Kruger Park's roan population remains at risk of local extinction. Mills et al. (1995) tested the effects of predation on several of Kruger's large ungulate species based on analysis of available data for changes in population sizes over recent decades. They suggested that buffalo suffered most from predator pressure, whereas wildebeest and zebra were less affected by changes in lion population fluxes. Isotope data from suitable archived tissues would be especially useful for providing direct insight into the changes in predator–prey interactions in the past and would assist in confirming these hypotheses. Indeed, bone collagen, tooth enamel, hair and fecal data for hippotragines including sable antelope (this study) and roan (unpublished data) suggest that these species have significantly lower  $\delta^{15}\text{N}$  values than sympatric large grazing ungulates. Hence, changes in consumption of hippotragine taxa compared with other grazers should be readily discernible from historical isotope trajectories in predators such as lion.

Another concern for wildlife management planning is that carnivores are often implicated in the killing of domestic livestock, but it has been difficult to quantify the magnitude of this problem (Butler 2000). Stable isotope studies may assist in future assessments of carnivore impacts on agricultural systems. For example, one recent carbon isotopic study showed that the diet of the common vampire bat *Desmodus rotundus* living in Costa Rican primary and secondary rainforests is primarily composed of blood of domestic livestock rather than that of native mammals (Voigt and Klem 2006). In addition, artificial feeds and fertilizers tend to be substantially  $^{15}\text{N}$ -enriched

compared with naturally occurring nitrogen pools (e.g. Yoo et al. 1999). Thus, domestic livestock are likely to offer an isotopically distinguishable food source from free-ranging herbivores, in terms of  $\delta^{15}\text{N}$  and perhaps  $\delta^{13}\text{C}$  if their diets differ significantly from wild animals, which in turn may be readily detected from stable isotope data for ‘problem’ carnivores.

Finally, because stable isotope studies are applicable to palaeoenvironmental contexts, they can provide information about the role of predation in the evolutionary history of mammal community assemblages. For example, predation has been implicated as a fundamental constraint to competition and co-existence of hindgut-fermenting equids and foregut-fermenting bovids (Duncan et al. 1990) and likely had important outcomes for early hominin differentiation (Brain 1981). In response to the latter, Lee-Thorp et al. (2000) used stable carbon-isotope data in an attempt to identify likely predators of early hominins and indeed the carnivore specie(s) largely responsible for bone accumulations in South African Plio–Pleistocene cave deposits. Their data suggest isotopic similarity between mixed  $\text{C}_3/\text{C}_4$  hominins and other primates with the saber-toothed cat *Megantereon* and hyaena *Crocuta*, whereas leopards likely formed part of early  $\text{C}_4$  food webs proper. Results of the current study suggest that further insight into past predator–prey relationships can be gleaned from dual-isotope approaches. Stable nitrogen isotopes in bone do not, however, normally preserve in deep time due to postmortem denaturation of biological proteins. In these instances, trace elements (principally Sr/Ca ratios) can replace  $\delta^{15}\text{N}$  as a trophic level indicator (Sillen and Lee-Thorp 1994; Sponheimer et al. 2005). Further studies in modern African systems should improve models for isotopic reconstructions of predator–prey relationships in the past and may culminate in particularly revealing insights into the behavioural ecology of early hominins and other extinct mammals.

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