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Reliability of $\delta^{13}C$ and $\delta^{15}N$ in faeces for reconstructing savanna herbivore diet

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Abstract

We tested the reliability of herbivore faecal $\delta^{13}C$ and $\delta^{15}N$ values for reconstructing diet through review of an extensive database derived from a 3-year study of ungulates in South Africa's Kruger National Park. Faeces are a useful material for stable isotope studies of diet because they record dietary turnover at very short time scales, and because sampling is non-invasive. However, the validity of faecal isotope proxies may be questioned because they represent only undigested food remains. Results from Kruger Park confirm that free-ranging browsers have faecal $\delta^{13}C$ consistent with C_3 feeding, grazer faeces are C_4, and mixed-feeder faeces intermediate. Although the respective ranges do not overlap, there is significant variation in faecal $\delta^{13}C$ of browsers and grazers (~2.0–4.0‰) across space and through time. We demonstrate that most (~70%) of this variation can be ascribed to corresponding patterns of variation in the $\delta^{13}C$ of C_3 and C_4 plants, respectively, re-enforcing the fidelity of faecal isotope proxies for diet but highlighting a need for mixing models that control for variations in plant $\delta^{13}C$ in order to achieve accurate diet reconstructions. Predictions for the effects of climate (rainfall) and ecophysiology on ^{15}N-abundance variations in mammals do not persist in faeces. Rather, faecal $\delta^{15}N$ tracks changes in plant $\delta^{15}N$, with further fractionation occurring primarily due to variations in dietary protein (reflected by %N). Controlling for these effects, we show that a dual-isotope multiple source mixing model (Isosource) can extend diet reconstructions for African savanna herbivores beyond simplified C_3/C_4 distinctions, although further understanding of variations in mammal $\delta^{15}N$ are needed for greater confidence in this approach.

Keywords: Browser; Grazer; Kruger Park; Mixed feeder; Mixing model

Introduction

Stable isotope ecology is a powerful adjunct to traditional approaches to mammal diet. The basis is that stable isotope ratios of elements such as carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in consumer tissues reflect isotopic signatures of the sources from which they are derived, with some further discrimination in consumers

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(Vogel 1978; Peterson and Fry 1987). In subtropical savannas, the bimodal distribution of $\delta^{13}C$ between plants following the C_3 (trees, shrubs, and forbs) and C_4 (grass) photosynthetic pathways is faithfully recorded in the tissues of herbivores feeding on these plants (Vogel 1978; Tieszen et al. 1979; Lee-Thorp and van der Merwe 1987; Cerling and Harris 1999). Animal $\delta^{15}N$ reflects trophic position, increasing upwards along different levels of the food chain, but is also predicted to vary with factors including rainfall, ecophysiology, protein uptake, and nutritional stress, leading to variations within trophic levels that are often greater than differences between them (Heaton et al. 1986; Sealy et al. 1987; Ambrose 1991; Sponheimer et al. 2003a).

Analyses of different materials allow researchers to study diet at different time scales. Long-lived tissues such as hair and teeth integrate an average over several months or even years, and sampled in series reveal dietary variations within individuals at this scale (Ayliffe et al. 2004; Cerling et al. 2006). Animal faeces are useful markers of dietary variation because they offer insight at high-resolution time scales, i.e. in the order of several days (Tieszen et al. 1979; Coates et al. 1991; Sponheimer et al. 2003b). Because of rapid turnover, data from faeces do not require mathematical correction for error introduced via differential growth rate and attenuation time, as in hair and teeth (e.g. Ayliffe et al. 2004). Faeces also have the benefit of being easy to collect in the field, and sampling does not require interference through manipulation or slaughter of animals.

A number of controlled-feeding studies have demonstrated consistency between $\delta^{13}C$, and less so $\delta^{15}N$, in diet and faeces, despite that faeces represent only the undigested portion of the diet and are hence only a partial reflection of food intake (Steele and Daniel 1978; Sutoh et al. 1987; Coates et al. 1991; Sponheimer et al. 2003b, c; Codron et al. 2005a). Data from field-based studies show that faecal $\delta^{13}C$ faithfully distinguishes between C_3- and C_4-based diets (Tieszen et al. 1979; Botha and Stock 2005; Codron et al. 2005a), and the readily available insights into dietary variation have provided a valuable addition to tests of contemporary models for herbivore differentiation (Codron et al. 2007a, b). However, these studies are essentially limited to differentiating between C_3 browsing and C_4 grazing from faecal $\delta^{13}C$. Additional insights that can potentially be gained through analysis of $\delta^{15}N$ are constrained because of a relative scarcity of faecal $\delta^{15}N$ data for free-ranging animals, and because of our generally poor understanding of mechanisms underlying ^{15}N-abundance variations in mammals. Further, subtle spatio-temporal changes in the $\delta^{13}C$ and $\delta^{15}N$ isotopic compositions of C_3 and C_4 vegetation have an influence on isotopic distributions amongst herbivores (Cerling and Harris 1999; Codron et al. 2005a), and are likely to be especially important for short-term materials like faeces. While researchers have begun to address this concern (Cerling and Harris 1999; Cerling et al. 2003; Codron et al. 2006, 2007a; Treydte et al. 2006), the relationship between changes in the isotope composition of faeces and available food base (plants) is not well demonstrated.

In this paper we assess the reliability of $\delta^{13}C$ and $\delta^{15}N$ in faeces of free-ranging animals for reconstructing herbivore diet, using data reported from a 3-year study of ungulate isotope ecology in the semi-arid savanna habitats of South Africa's Kruger National Park (Codron et al. 2007a, b). African savanna ungulates are well suited for this purpose because their natural diets are relatively well documented through field observations (reviewed in Gagnon and Chew 2000). First, we examine the degree of within-feeding guild and within-species variations in faecal $\delta^{13}C$ amongst free-ranging herbivores, and compare these with corresponding patterns of variation in the carbon isotope composition of local vegetation, to determine the implications of changes in plant $\delta^{13}C$ for interpreting diet. Second, we present previously unpublished faecal $\delta^{15}N$ data to test predictions for the effects of changes in plant $\delta^{15}N$, protein uptake (based on faecal %N), rainfall, and ecophysiology (adaptation to water stress, digestive physiology, and diet morpho-physiology) on variations in mammal herbivore ^{15}N abundances. Last, we employ a dual-isotope mixing model (Isosource; Phillips and Gregg 2003) for resolving dietary inputs of multiple isotopically distinguishable C_3 (leaves, fruit, and sedges) and C_4 (NADP-ME, NAD-ME, and PCK C_4 sub-pathways) food types, to determine whether this approach can provide reliable insights beyond C_3 versus C_4 feeding distinctions.

Material and methods

Details of study sites, and plant and faeces sampling protocols are described elsewhere (Codron et al. 2005b, 2007a). Specimens are from a variety of Kruger Park landscapes, collected from June 2002 to May 2005, biannually for the first 2 years and at monthly intervals thereafter. An important component of this paper is to assess the relationship between changes in faecal with plant isotope composition; hence we selected only those specimens from the faeces database for which plant data are available for the region and month of collection. Plant data represent multiple specimens of each tree, forb, and grass species present at 16 sampling transects across Kruger Park, collected during the same time period as faecal collections were made (see Codron et al. 2005b, 2007c). Hence our substantial plant data afford the opportunity for more detailed examination of the faeces–plant relationship than has previously been achieved.

$^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios, and %N, were determined by combustion of samples in an automated Elemental Analyzer (Carlo Erba, Milan), introducing resultant CO_2 and N_2 gases