Journal of Arid Environments 134 (2016) 33–48

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Stable isotope analyses of rock hyrax faecal pellets, hyraceum and associated vegetation in southern Africa: Implications for dietary ecology and palaeoenvironmental reconstructions

Andrew S. Carr [a, *], Brian M. Chase [b], Arnoud Boom [a], Javier Medina-Sanchez [a]

[a] Department of Geography, University of Leicester, Leicester, LE1 7RH, UK
[b] Centre National de Recherche Scientifique, UMR 5554, Institut des Sciences de l'Evolution – Montpellier, Département Paléoenvironnements, Université Montpellier, Bat.22, CC061, Place Eugène Bataillon, 34095, Montpellier, Cedex 5, France

A R T I C L E I N F O

Article history:
Received 16 March 2016
Received in revised form
10 June 2016
Accepted 27 June 2016

Keywords:
Dassie
Urine
C_3/C_4 plants
Herbivore
^{13}C
^{15}N
Faeces

A B S T R A C T

Rock hyrax middens are important palaeoenvironmental archives in southern Africa. Carbon and nitrogen isotope measurements on middens (hyraceum) are key components of climate reconstructions, but their interpretations require refinement. Although $\delta^{15}N$ in hyraceum often correlates with independent proxies for palaeo-aridity, the impacts of dietary and physiological controls on hyraceum $\delta^{15}N$ remain to be resolved. We analyse $\delta^{13}C$ and $\delta^{15}N$ in plant foliage, hyrax faecal pellets and hyraceum from 21 sites across southern Africa. Faeces are generally depleted in ^{13}C ($\delta^{13}C$ typically < −20‰), suggesting significant browsing. Grazing is rarely dominant and probably occurs only when palatable grass is available. Variability in faecal and foliar $\delta^{15}N$ is large, but foliar $\delta^{15}N$ is positively correlated with faecal $\delta^{15}N$. The diet-faeces $\delta^{15}N$ offset is uncorrelated with climate (aridity), but is correlated with %N in faeces. Faecal $\delta^{15}N$ is positively correlated with modern hyraceum $\delta^{15}N$, and the relationships with aridity index for foliar and faecal (body tissue) $\delta^{15}N$ are comparable. These observations implicate diet as a significant control on hyraceum $\delta^{15}N$ and we observe no strong evidence for metabolic controls on hyraceum $\delta^{15}N$. More data are required to refine these relationships, but these observations are consistent with current palaeoenvironmental interpretations of midden $\delta^{15}N$ and $\delta^{13}C$.

1. Introduction

The communal latrines (middens) of the rock hyrax (*Procavia capensis*) have emerged as a key palaeoenvironmental archive for desert regions in southern Africa (Scott and Bousman, 1990; Gil-Romera et al., 2006; Chase et al., 2012). Several studies have developed palaeoclimatic records using sequential analysis of stable carbon and nitrogen isotopes through stratified hyraceum, the crystallised urinary material (cf. faecal pellets) that forms many hyrax middens (Scott and Vogel, 2000; Chase et al., 2009, 2010; 2011, 2012; 2013, 2015a; 2015b). Changes in hyraceum isotopic signals have been inferred to largely relate to the stable isotope composition of the animal's diet and thus, to environmental controls on plant isotopic composition in the midden environs (Chase et al., 2012). It has been argued that this interpretation is supported by facets of the midden geochemistry (Carr et al., 2010) and by: 1) the close correlations in temporal isotopic trends between discrete midden (colony) records (Chase et al., 2010); 2) correlations of such trends with independent palaeoenvironmental archives, which furthermore show the isotopically opposite responses to those predicted by dominantly metabolic controls on urine (hyraceum) stable isotope composition (Chase et al., 2009, 2011, 2013, 2015b); and 3) good correlations between isotope and pollen data from the same midden (Chase et al., 2015a, 2015b).

Notwithstanding, the fundamental isotope systematics of the diet-herbivore system within rock hyrax habitats remain to be fully elucidated. Observational data pertaining to feeding behaviour exist for several hyrax species (*Procavia johnstoni and Heterohyrax brucei;* Hoeck, 1975), including *Procavia capensis* (Lensing, 1983; Fourie, 1983), but isotopic data from materials other than hyraceum are limited (e.g. DeNiro and Epstein, 1978). The aim of the present work is to significantly expand our understanding of the dietary variability and the isotope ecology of the rock hyrax (*Procavia capensis*) via an extensive study of stable carbon and nitrogen

* Corresponding author.
E-mail address: asc18@leicester.ac.uk (A.S. Carr).

http://dx.doi.org/10.1016/j.jaridenv.2016.06.013
0140-1963/

isotopes relating to the animal's diet (derived from faecal pellets) and to their potential diet (derived from plants around hyrax colonies) across a range of climatic conditions. The latter data are also of wider value as systematically-derived $\delta^{13}C$ and $\delta^{15}N$ data from contemporary soils and plants in southern Africa are still relatively limited (cf. Heaton et al., 1986; Aranibar et al., 2008). Such data provide important benchmarking and calibration information for various aspects of palaeoenvironmental research in this region (e.g. Codron et al., 2013).

1.1. Carbon and nitrogen isotopes in faeces

The stable carbon and nitrogen isotope compositions of animal tissues (e.g. hair and bone) and faecal matter provide insights into herbivore diet (Ambrose and DeNiro, 1986a; Codron et al., 2005; Codron and Codron, 2009; Botha and Stock, 2005; Sponheimer et al., 2003a). An assessment of dietary preferences using faeces is particularly useful as information is obtained without disturbing the animal and, unlike hard tissue it allows insights into feeding behaviour and dietary variability (Sponheimer et al., 2003a; Codron et al., 2005). In much of southern Africa, warm growing season, aridity-adapted C_4 grasses are preferentially consumed by grazers and exhibit leaf tissue $\delta^{13}C$ in the range −10 to −14‰. C_3 plant tissue $\delta^{13}C$ typically measures −28 to −25‰ (Vogel, 1978; Codron et al., 2005, 2013). Given such a separation, analysis of herbivore faecal $\delta^{13}C$ allows grazing, browsing and mixed feeding behaviours to be differentiated (Sponheimer et al., 2003a; Codron and Codron, 2009).

The nitrogen isotope signature of herbivore faeces is more complex to interpret. Body tissue $\delta^{15}N$ may be affected by several factors, including trophic level (Schoeninger and DeNiro, 1984), diet (plant isotopic composition, food quality, protein content (Sponheimer et al., 2003b/2003c)) and physiology (e.g. water stress (Ambrose and DeNiro, 1986b; Ambrose, 1991) or hind/foregut fermentation (Sealy et al., 1987; Codron and Codron, 2009)). A tendency for higher herbivore body tissue $\delta^{15}N$ under arid conditions has been associated with physiological processes related to water conservation. Specifically, it has been proposed that drought-tolerant herbivores excrete more ^{14}N-enriched urea and thus have higher body tissue $\delta^{15}N$ under conditions of drought stress (Ambrose and DeNiro, 1986a, 1986b, 1987; Sealy et al., 1987). Such physiological explanations were originally motivated by the combined observations of a negative correlation between rainfall and $\delta^{15}N$ in bones and the apparent absence of any relationship between plant (i.e. diet) $\delta^{15}N$ and rainfall (Ambrose and DeNiro, 1987; Heaton et al., 1986). Subsequently, multiple studies have demonstrated significant, albeit scattered, relationships between foliar $\delta^{15}N$ and aridity (e.g. Craine et al., 2009; Hartman and Danin, 2010; Murphy and Bowman, 2006; Szpak et al., 2013), and others have specifically considered the relationship between plant and herbivore $\delta^{15}N$, finding that both increase with aridity, with a 2–3‰ offset attributable to trophic level enrichment, but no progressive increase in herbivore $\delta^{15}N$ relative to plant $\delta^{15}N$ (Schwarcz et al., 1999; Hartman, 2011; Murphy and Bowman, 2006). While the precise mechanisms for such enrichment in plants (i.e. dietary source) are still debated (Craine et al., 2015) these findings imply that body tissue $\delta^{15}N$ in herbivores is potentially influenced by diet.

Rock hyraxes are generally independent of water (i.e. drought-tolerant), but when available, they will drink freely (Skinner and Chimimba, 2005). In South Africa hyrax bone collagen $\delta^{15}N$ has been reported to be relatively high compared to other herbivores (up to 17‰; Sealy et al., 1987). In hyraceum from rock hyrax middens $\delta^{15}N$ ranges from −2‰, (at the De Rif midden in the Cederberg Mountains north of Cape Town; Chase et al., 2011) to +20‰ (at Austerlitz in the arid northern Namib Desert; Chase et al., 2010) and can vary by up to 5‰ within stratified hyraceum during the Holocene (e.g. Chase et al., 2009, 2015a). As $\delta^{15}N$ analysis of hyrax middens has become an important component of recent palaeoenvironmental studies, there is an impetus to refine our understanding of $\delta^{15}N$ dynamics in rock hyraxes and their ecosystems. More generally, control(s) on herbivore tissue $\delta^{15}N$ remain to be fully elucidated (e.g. Hartman, 2011). As a first step to addressing this we assess: 1) the natural variability in hyrax faecal $\delta^{15}N$ within and between hyrax colonies, 2) the relationship between faecal $\delta^{15}N$ and dietary $\delta^{15}N$ (i.e. foliar $\delta^{15}N$ from plants surrounding colonies), and 3) the relationship between faecal $\delta^{15}N$ and hyraceum $\delta^{15}N$. These are considered across a variety of biomes and climatic zones in southern Africa. Although a total understanding of ^{15}N dynamics in any animal may require laboratory experimentation (e.g. Sponheimer et al., 2003a, 2003b), we can hypothesise that if $\delta^{15}N$ variability within hyrax middens is largely an environmental signal derived from the animal's diet, modern faecal and hyraceum $\delta^{15}N$ should correlate with dietary (local vegetation) $\delta^{15}N$ (with some as yet undetermined trophic level offset).

2. Methods and materials

2.1. Study sites and sampling

Rock hyrax faecal pellets were collected from 21 sites across southern Africa. These sites span both the summer and winter rainfall zones (Table 1 and Fig. 1) and include sites in the Fynbos, Savanna, Succulent Karoo, Grassland and Nama Karoo biomes. Sites in the Fynbos biome are all located in the montane fynbos of the Cape Fold Belt Mountains. Sites in the west of the biome (De Rif [DR], Pakhuis Pass [PP], and Kliprandfontein [KRF]; Figs. 1 and 2f) lie in the Cederberg Mountains and are characterised by >75% winter rainfall and shrubby C_3 vegetation containing largely asteraceous, restioid and proteoid elements. Fynbos sites in the southern Cape Fold Belt Mountains (Seweweekspoort [SWP] Meiringspoort [MP], Baviaanskloof [BK], Papkuilsfontein [PKF]) experience more summer rainfall, with a greater presence of succulents and some C_4 grasses on nearby finer grained substrates (Mucina and Rutherford, 2006). Several middens (SWP1-3) are present at Seweweekspoort, each with different aspects and altitudes within the rock faces of the Seweweekspoort valley (Chase et al., 2013). Here, three separate sets of faecal pellet samples were collected in association with the middens SWP-1, SWP-2 and SWP-3 (Fig. 3a). 1) SWP-1 is surrounded by a mosaic of environments, ranging from exposed north-facing rocky slabs to a more sheltered and densely vegetated drainage line, 2) SWP-2 occupies an exposed cliff with shallow soils and low water retention potential, 3) SWP-3 is located at the valley bottom, in an area of relatively high water availability and limited potential evapotranspiration. Similarly, the two middens at Baviaanskloof (BK1 and BK2) are located either side of the NW/SE orientated Baviaanskloof valley, with BK2 the more shaded. An additional site, Jaakvlakte (JV), lies near to the Doring River within the Succulent Karoo Biome, albeit close to the Fynbos Biome (Figs. 1 and 2e).

None of the Nama Karoo sites were associated with midden accumulations, but they hosted extant hyrax colonies and their inclusion provided an opportunity to expand the range of environmental conditions considered within the study. These sites, which are located at the western margins of the summer rainfall zone, include a significant proportion of C_4 grasses (particularly *Stipagrostis* sp.). Nama Karoo vegetation in general displays a diversity of plant growth forms, and includes a range of annuals, geophytes and succulents (Mucina and Rutherford, 2006). With the exception of the Prieska site (PRI: a rocky gorge) all of the Nama Karoo sites were associated with isolated rock outcrops (koppies).