

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

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1 **Abstract**

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

17

18 **Keywords:** Dassie, urine,  $\text{C}_3/\text{C}_4$  plants, herbivore, carbon, nitrogen

19

20 **Highlights**

- 21 • Rock hyraxes are generally browsers, but will graze when grass is available.
- 22 • Significant correlation between foliar (dietary)  $\delta^{15}\text{N}$  and faecal  $\delta^{15}\text{N}$ .
- 23 • Significant correlation between faecal  $\delta^{15}\text{N}$  and hyraceum  $\delta^{15}\text{N}$ .
- 24 • Diet-faecal  $\delta^{15}\text{N}$  offset uncorrelated with climate.
- 25 • Significant correlations between faecal  $\delta^{15}\text{N}$ , foliar  $\delta^{15}\text{N}$  and aridity index.

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27

## 28 **Introduction**

29 The communal latrines (middens) of the rock hyrax (*Procavia capensis*) have emerged as a key  
30 palaeoenvironmental archive for desert regions in southern Africa (Scott and Bousman, 1990; Gil-  
31 Romera et al., 2006; Chase et al., 2012). Several studies have developed palaeoclimatic records using  
32 sequential analysis of stable carbon and nitrogen isotopes through stratified hyraceum, the  
33 crystallised urinary material (cf. faecal pellets) that forms many hyrax middens (Scott and Vogel, 2000;  
34 Chase et al., 2009; 2010; 2011; 2012; 2013; 2015a; 2015b). Changes in hyraceum isotopic signals have  
35 been inferred to largely relate to the stable isotope composition of the animal's diet and thus, to  
36 environmental controls on plant isotopic composition in the midden environs (Chase et al., 2012). It  
37 has been argued that this interpretation is supported by facets of the midden geochemistry (Carr et  
38 al., 2010) and by: 1) the close correlations in temporal isotopic trends between discrete midden  
39 (colony) records (Chase et al., 2010); 2) correlations of such trends with independent  
40 palaeoenvironmental archives, which furthermore show the isotopically opposite responses to those  
41 predicted by dominantly metabolic controls on urine stable isotope composition (Chase et al., 2009;  
42 2011, 2013; 2015b); and 3) good correlations between isotope and pollen data from the same midden  
43 (Chase et al., 2015a; Chase et al. 2015b).

44 Notwithstanding, the fundamental isotope systematics of the diet-herbivore system within  
45 rock hyrax habitats remain to be fully elucidated. Observational data pertaining to feeding behaviour  
46 exist for several hyrax species (*Procavia johnstoni* and *Heterohyrax brucei*; Hoeck, 1975), including  
47 *Procavia capensis* (Lensing, 1983; Fourie, 1983), but isotopic data from materials other than hyraceum  
48 are limited (e.g. DeNiro and Epstein, 1978). The aim of the present work is to significantly expand our  
49 understanding of the dietary variability and the isotope ecology of the rock hyrax (*Procavia capensis*)  
50 via an extensive study of stable carbon and nitrogen isotopes relating to the animal's diet (derived  
51 from faecal pellets) and to their potential diet (derived from plants around hyrax colonies) across a  
52 range of climatic conditions. The latter data are also of wider value as systematically-derived  $\delta^{13}\text{C}$  and  
53  $\delta^{15}\text{N}$  data from contemporary soils and plants in southern Africa are still relatively limited (cf. Heaton  
54 et al., 1986; Aranibar et al. 2008). Such data provide important benchmarking and calibration  
55 information for various aspects of palaeoenvironmental research in this region (e.g. Codron et al.  
56 2013).

## 57 **Carbon and nitrogen isotopes in faeces**

58 The stable carbon and nitrogen isotope compositions of animal tissues (e.g. hair and bone) and faecal  
59 matter provide insights into herbivore diet (Ambrose and DeNiro, 1986a; Codron et al., 2005; Codron  
60 and Codron, 2009; Botha and Stock, 2005; Sponheimer et al., 2003a). An assessment of dietary

61 preferences using faeces is particularly useful as information is obtained without disturbing the animal  
62 and, unlike hard tissue it allows insights into feeding behaviour and dietary variability (Sponheimer et  
63 al., 2003a; Codron et al 2005). In much of southern Africa, warm growing season, aridity-adapted C<sub>4</sub>  
64 grasses are preferentially consumed by grazers and exhibit leaf tissue  $\delta^{13}\text{C}$  in the range -10 to -14‰.  
65 C<sub>3</sub> plant tissue  $\delta^{13}\text{C}$  typically measures -28 to -25‰ (Vogel et al., 1978; Codron et al., 2005; 2013).  
66 Given such a separation, analysis of herbivore faecal  $\delta^{13}\text{C}$  allows grazing, browsing and mixed feeding  
67 behaviours to be differentiated (Sponheimer et al. 2003a; Codron and Codron, 2009).

68 The nitrogen isotope signature of herbivore faeces is more complex to interpret. Body tissue  
69  $\delta^{15}\text{N}$  may be affected by several factors, including trophic level (Schoeninger and DeNiro, 1984), diet  
70 (plant isotopic composition, food quality, protein content (Sponheimer et al., 2003b/c)) and  
71 physiology (e.g. water stress (Ambrose and DeNiro, 1986b; Ambrose, 1991) or hind / foregut  
72 fermentation (Sealy et al., 1987; Codron et al., 2009)). A tendency for higher herbivore body tissue  
73  $\delta^{15}\text{N}$  under arid conditions has been associated with physiological processes related to water  
74 conservation. Specifically, it has been proposed that drought-tolerant herbivores excrete more <sup>14</sup>N-  
75 enriched urea and thus have higher body tissue  $\delta^{15}\text{N}$  under conditions of drought stress (Ambrose and  
76 DeNiro, 1986a; Ambrose and DeNiro, 1986b; Ambrose and DeNiro, 1987; Sealy et al., 1987). Such  
77 physiological explanations were originally motivated by the combined observations of a negative  
78 correlation between rainfall and  $\delta^{15}\text{N}$  in bones and the apparent absence of any relationship between  
79 plant (i.e. diet)  $\delta^{15}\text{N}$  and rainfall (Ambrose and DeNiro, 1987; Heaton et al., 1986). Subsequently,  
80 multiple studies have demonstrated significant, albeit scattered, relationships between foliar  $\delta^{15}\text{N}$  and  
81 aridity (e.g. Craine et al., 2009; Hartman and Danin, 2010; Murphy and Bowman; 2006; Szpac et al.,  
82 2013), and others have specifically considered the relationship between plant and herbivore  $\delta^{15}\text{N}$ ,  
83 finding that both increase with aridity, with a 2-3‰ offset attributable to trophic level enrichment,  
84 but no progressive increase in herbivore  $\delta^{15}\text{N}$  relative to plant  $\delta^{15}\text{N}$  (Schwarcz et al., 1999; Hartman,  
85 2011; Murphy and Bowman, 2006). While the precise mechanisms for such enrichment in plants (i.e.  
86 dietary source) are still debated (Craine et al., 2015) these findings imply that body tissue  $\delta^{15}\text{N}$  in  
87 herbivores is potentially influenced by diet.

88 Rock hyraxes are generally independent of water (i.e. drought-tolerant), but when available,  
89 they will drink freely (Skinner and Chimimba, 2005). In South Africa hyrax bone collagen  $\delta^{15}\text{N}$  has been  
90 reported to be relatively high compared to other herbivores (up to 17‰; Sealy et al., 1987). In  
91 hyraceum from rock hyrax middens  $\delta^{15}\text{N}$  ranges from -2‰, (at the De Rif midden in the Cederberg  
92 Mountains north of Cape Town; Chase et al., 2011) to +20‰ (at Austerlitz in the arid northern Namib  
93 Desert; Chase et al., 2010) and can vary by up to 5‰ within stratified hyraceum during the Holocene

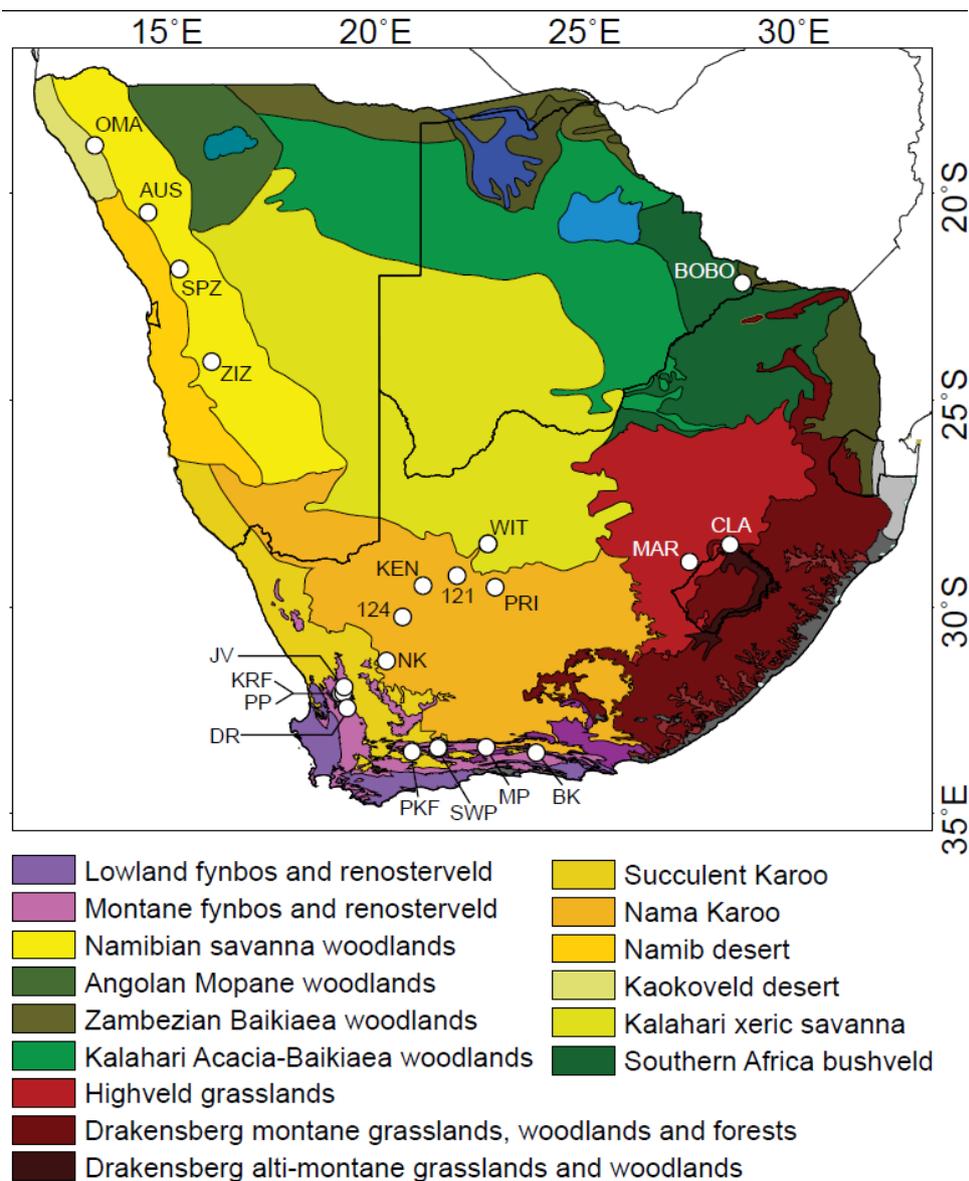
94 (e.g. Chase et al., 2009; 2015a). As  $\delta^{15}\text{N}$  analysis of hyrax middens has become an important  
95 component of recent palaeoenvironmental studies, there is an impetus to refine our understanding  
96 of  $\delta^{15}\text{N}$  dynamics in rock hyraxes and their ecosystems. More generally, control(s) on herbivore tissue  
97  $\delta^{15}\text{N}$  remain to be fully elucidated (e.g. Hartman 2011). As a first step to addressing this we assess: 1)  
98 the natural variability in hyrax faecal  $\delta^{15}\text{N}$  within and between hyrax colonies, 2) the relationship  
99 between faecal  $\delta^{15}\text{N}$  and dietary  $\delta^{15}\text{N}$  (i.e. foliar  $\delta^{15}\text{N}$  from plants surrounding colonies), and 3) the  
100 relationship between faecal  $\delta^{15}\text{N}$  and hyraceum  $\delta^{15}\text{N}$ . These are considered across a variety of biomes  
101 and climatic zones in southern Africa. Although a total understanding of  $^{15}\text{N}$  dynamics in any animal  
102 may require laboratory experimentation (e.g. Sponheimer et al., 2003a, 2003b), we can hypothesise  
103 that if  $\delta^{15}\text{N}$  variability within hyrax middens is largely an environmental signal derived from the  
104 animal's diet, modern faecal and hyraceum  $\delta^{15}\text{N}$  should correlate with dietary (local vegetation)  $\delta^{15}\text{N}$   
105 (with some as yet undetermined trophic level offset).

## 106 **Methods and materials**

### 107 **Study sites and sampling**

108 Rock hyrax faecal pellets were collected from 21 sites across southern Africa. These sites span both  
109 the summer and winter rainfall zones (**Table 1 and Figure 1**) and include sites in the Fynbos, Savanna,  
110 Succulent Karoo, Grassland and Nama Karoo biomes. Sites in the Fynbos biome are all located in the  
111 montane fynbos of the Cape Fold Belt Mountains. Sites in the west of the biome (De Rif [DR], Pakhuis  
112 Pass [PP], and Kliprandfontein [KRF]; **figures 1 and 2f**) lie in the Cederberg Mountains and are  
113 characterised by >75% winter rainfall and shrubby  $\text{C}_3$  vegetation containing largely asteraceous,  
114 restioid and proteoid elements. Fynbos sites in the southern Cape Fold Belt Mountains  
115 (Seweweekspoort [SWP] Meiringspoort [MP], Baviaanskloof [BK], Papkuilsfontein [PKF]) experience  
116 more summer rainfall, with a greater presence of succulents and some  $\text{C}_4$  grasses on nearby finer  
117 grained substrates (Mucina and Rutherford, 2006). Several middens (SWP1-3) are present at  
118 Seweweekspoort, each with different aspects and altitudes within the rock faces of the  
119 Seweweekspoort valley (Chase et al., 2013). Here, three separate sets of faecal pellet samples were  
120 collected in association with the middens SWP-1, SWP-2 and SWP-3 (**Figure 3a**). 1) SWP-1 is  
121 surrounded by a mosaic of environments, ranging from exposed north-facing rocky slabs to a more  
122 sheltered and densely vegetated drainage line, 2) SWP-2 occupies an exposed cliff with shallow soils  
123 and low water retention potential, 3) SWP-3 is located at the valley bottom, in an area of relatively  
124 high water availability and limited potential evapotranspiration. Similarly, the two middens at  
125 Baviaanskloof (BK1 and BK2) are located either side of the NW/SE orientated Baviaanskloof valley,

126 with BK2 the more shaded. An additional site, Jaagvlakte (JV), lies near to the Doring River within the  
 127 Succulent Karoo Biome, albeit close to the Fynbos Biome (**Figures 1 and 2e**).



128

129 **Figure 1:** Study locations with associated vegetation communities (from Mucina and Rutherford,  
 130 2006). Site Key: AUS = Austerlitz; BK = Baviaanskloof; Bobo = Bobonong; CLA = Clarens; DR = De Rif; JV  
 131 = Jaagvlakte; KEN = Kenhardt; KRF = Kliprandfontein; MAR = Marikabi; MP = Meiringspoort; NK =  
 132 NK2010 (see also Carr et al., 2013); OMA = Omanyne; PP= Pakhuis Pass; PKF = Papkuilsfontein; PRI =  
 133 Prieska; SPZ=Spitzkoppe; SWP = Seweweekspoort; WIT = Witsand; ZIZ = Zizou. 121 and 124 = sites Mk  
 134 121 and Mk 124 (un-named Nama Karoo koppies).

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137           None of the Nama Karoo sites were associated with midden accumulations, but they hosted  
138 extant hyrax colonies and their inclusion provided an opportunity to expand the range of  
139 environmental conditions considered within the study. These sites, which are located at the western  
140 margins of the summer rainfall zone, include a significant proportion of C<sub>4</sub> grasses (particularly  
141 *Stipagrostis* sp.). Nama Karoo vegetation in general displays a diversity of plant growth forms, and  
142 includes a range of annuals, geophytes and succulents (Mucina and Rutherford, 2006). With the  
143 exception of the Prieska site (PRI: a rocky gorge) all of the Nama Karoo sample sites were associated  
144 with isolated rock outcrops (koppies). Samples from the Savanna Biome cover a wide geographical  
145 range, from eastern Botswana (Bobonong; Bobo), to northern and central Namibia (Austerlitz,  
146 Spitzkoppe, Zizou and Omanyne [coded AUS, SPZ, ZIZ and OMA respectively]) and into the Northern  
147 Cape of South Africa (Witsand; WIT) (**Figure 1**). The most arid locale of these sites is Omanyne in the  
148 Kaokoveld desert. The Grassland Biome is represented by the Marakabi site (MAR) to the west of  
149 Clocolan in the Free State (associated with an unpublished midden record) and by the Clarens site  
150 (CLA), which is close to several middens described by Scott (1990). The Grassland Biome, associated  
151 with the Highveld and Drakensberg highlands can be distinguished from savanna by the strong  
152 structural dominance of grasses and notably by much cooler winter temperatures (Mucina and  
153 Rutherford, 2006). The Clarens locale did not preserve middens, but the faecal pellet samples (CLA1-  
154 CLA3) were acquired from closely located accumulations (several hundred metres apart) in an  
155 extensive north-facing escarpment 3 km north of the town of Clarens. The samples from Marikabi  
156 (MAR) were associated with a large midden in a rockshelter near to the top of a steep rock face. Here  
157 several separate bags of pellets were collected from accumulations within the (30-40 m across)  
158 rockshelter. Several of these sites, namely De Rif (DR - Fynbos), Seweweekspoort (SWP - Fynbos),  
159 Pakhuis Pass (PP - Fynbos), Spitzkoppe (SPZ - Savanna) and Austerlitz (AUS - Savanna) are associated  
160 hyrax middens for which there is additional published information (Chase et al., 2009, 2010, 2011,  
161 2013, 2015b; Scott and Woodbourne, 2007a; 2007b).



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**Figure 2:** Photo montage of midden sites A) Spitzkoppe (SPZ, Savanna Biome) showing the upper slope below SPZ1-2, SPZ1-3 and SPZ1-5 (Chase et al., 2009) midden; B) Zizou (ZIZ, Savanna Biome; note white hyraceum staining of the rocks in the centre of the image); C) Witsand (Wit, Savanna Biome; note shading in the lower left of the valley; D) Omanyne (OMA, Savanna Biome; view down slope from immediately below the midden; E) The landscape around Jaakvlakte (JV) – the midden is located in the rocky valley sides; F) De Rif (DR) and the associated montane fynbos of the Cederberg Mountains.

170 As well as assessing geographic-climatic trends in faecal  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , we also sought to  
171 address how much isotopic variability is generated by individual feeding behaviour and how much  
172 inter-plant (dietary) isotopic variability exists at some sites. Food source (foliar)  $\delta^{15}\text{N}$  variability will  
173 probably reflect the impact of species effects and micro-scale variability in hydrological and edaphic  
174 conditions on the rocky slopes occupied by hyraxes, but this variability remains un-quantified. To  
175 address this at several savanna sites, *viz.* Spitzkoppe (2013 and 2014), Omanyne (2014) and Zizou  
176 (2014), faecal pellets and plants were intensively sampled around the middens and on surrounding  
177 rock slopes. At Spitzkoppe, it was possible to sample multiple small piles of pellets, which might reflect  
178 recent feeding by one or a small number of individuals (typically 10-15 individual pellets). These were  
179 sampled systematically down-slope from the midden to the surrounding savanna plains (**Figure 2**).  
180 Additionally, several sites were sampled in multiple years; namely Pakhuis Pass (PP; Fynbos),  
181 Spitzkoppe (SPZ; Savanna) and Omanyne (OMA; Savanna) (**Figure 1; Table 1**). We sought fresh looking  
182 pellets occupying exposed rock surfaces that were unlikely to have remained undisturbed for any  
183 length of time (e.g. it is unlikely that pellets persist in exposed locations through the rainy season), but  
184 given how quickly the pellets dry out in these environments the true degree of “freshness” was  
185 difficult to assess.

186 Plant sampling was carried out at seven sites. Four of those sites (De Rif, Pakhuis, Jaagvlakte  
187 and NK2010) lie close to middens or hyrax colonies, but were originally sampled as part of a separate  
188 study concerning plant and soil geochemistry (see Carr et al., 2013 and 2014 for details). At these sites,  
189 plants were obtained from 10x10 m vegetation survey plots and one representative specimen of every  
190 plant species was sampled. At Zizou, Spitzkoppe and Omanyne in the savanna biome plant sampling  
191 in 2013 and 2014 was specifically concerned with an assessment of hyrax dietary variability. Here  
192 samples were obtained from numerous individual plants (regardless of repeat sampling of the same  
193 species) within a 100 m radius of the midden. This included plants on the rocky slopes near the midden  
194 and some plants on the surrounding plains. It is recognised that these sampling approaches are  
195 different and that this may impact the comparability, but this issue is offset by the greater  
196 geographic/environment range afforded by the combination of data from these sites and the general  
197 paucity of foliar  $\delta^{15}\text{N}$  data in South Africa and Namibia (cf. Heaton, 1987). All plant samples were air  
198 dried in the field, stored in paper bags and freeze dried in the UK.

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## 200 **Laboratory and data analyses**

201 Freeze-dried individual pellets, or mixtures of leaves from the same plant specimen were  
202 homogenised, sub-sampled and encapsulated in tin cups. Each pellet and leaf mixture was measured

203 in triplicate. Total carbon (TC), Total nitrogen (TN) and  $\delta^{13}\text{C}_{\text{TC}}$  and  $\delta^{15}\text{N}_{\text{TN}}$  were determined using a  
204 SerCon ANCA GSL elemental analyser interfaced to a SerCon Hydra 20–20 continuous flow isotope  
205 ratio mass spectrometer. Typical measurement reproducibility was better than  $\pm 0.1\text{‰}$  for  $\delta^{13}\text{C}$  and  
206  $\pm 0.2\text{‰}$  for  $\delta^{15}\text{N}$ . Climatic data were obtained from WorldClim 1.4 (Hijmans et al., 2005), with site  
207 aridity indices derived following Trabucco and Zomer (2009). Statistical analyses were performed  
208 using Prism 6 and SigmaPlot.

## 209 Results

### 210 Faecal C and N content

211 The total carbon and nitrogen contents of hyrax faecal pellets are broadly consistent across the biomes  
212 (**Figures S1 and S2**). Faecal N content is typically 2-3 %, although several savanna sites such as  
213 Austerlitz (average  $3.5 \pm 0.9\%$ ) and Zizou, as well as NK2010 in the Nama Karoo (averages  $1.4 \pm 0.6\%$   
214 and  $1.5 \pm 0.3\%$  respectively) show some deviation from this. C/N ratios similarly show limited  
215 variability (typically 15-30), although some individual sites such as Zizou ( $33 \pm 11$ ) differ markedly in  
216 comparison to other sites in the same (savanna) biome (e.g. Austerlitz;  $14 \pm 4$ ). For sites sampled in  
217 multiple years (Omanyne 2008/2014, Spitzkoppe 2013/2014 and Pakhuis Pass 2008/2013) inter-  
218 annual differences in faecal N and C/N ratios are observed (**Table S1; Figure S1**). Inter-annual  
219 differences in faecal N content are statistically significant at Omanyne and Spitzkoppe (Mann-Whitney  
220  $U = 194.5$ ,  $p < 0.0001$  and Mann-Whitney  $U = 362$ ,  $p < 0.0001$ , respectively) and less for the 2008/2013  
221 samples Pakhuis Pass (Mann-Whitney  $U = 41.5$ ,  $p = 0.016$ ) (**Table S1**).

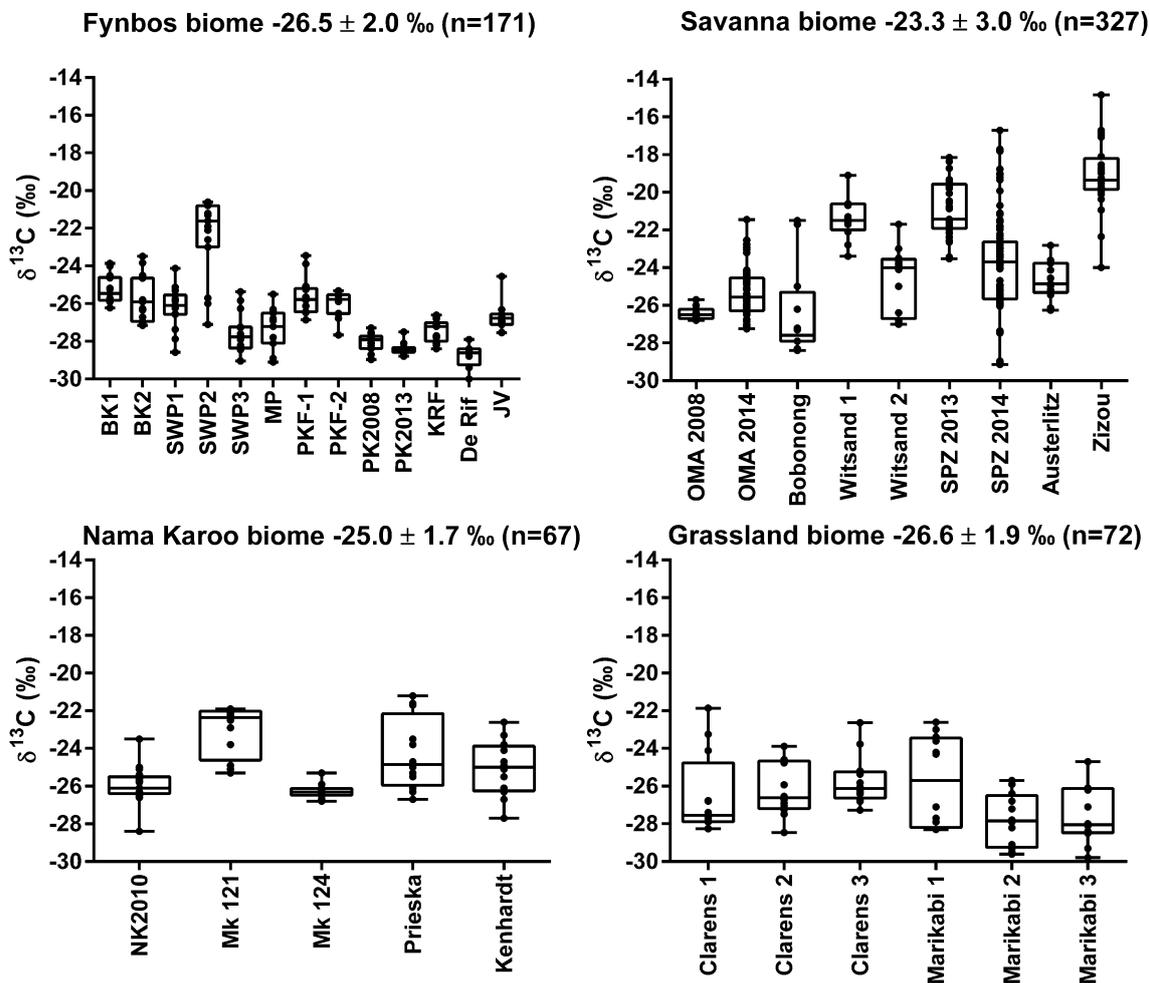
222

### 223 Stable carbon isotopes

#### 224 Fynbos Biome

225 Faecal  $\delta^{13}\text{C}$  data from all sites in the western Fynbos Biome (i.e. PP, KRF and DR) is typically -26 to -  
226  $28\text{‰}$  and the results from these sites are statistically indistinguishable. This contrasts with the eastern  
227 Fynbos Biome sites (BK1, BK2, MP1, PKF and SWP), which show greater intra- (MP, SWP) and inter-  
228 site variation (**Figure 3**). The BK1 and BK2  $\delta^{13}\text{C}$  data are comparable ( $-25.2 \pm 0.7\text{‰}$  and  $-25.8 \pm 1.2\text{‰}$ ),  
229 with BK2 (shaded) marginally lower (the difference is not statistically significant). In terms of temporal  
230 variation, the 2008 data from Pakhuis Pass are indistinguishable from the 2013 data (means:  $-26.1 \pm$   
231  $0.4\text{‰}$  and  $-26.4 \pm 0.4\text{‰}$ ,  $n = 15$  and  $n = 12$ , respectively). Overall, with the exception of SWP-2, faecal  
232  $\delta^{13}\text{C}$  for all fynbos sites is in the anticipated range of pure  $\text{C}_3$  plant diets. Jaakvlakte (JV) within the

233 Succulent Karoo Biome has an average faecal  $\delta^{13}\text{C}$  of  $-26.7 \pm 0.7\text{‰}$ , which is close to the Fynbos Biome  
 234 average of  $-26.5 \pm 2.0\text{‰}$  (the latter is  $-26.9 \pm 1.4\text{‰}$  if the outlier SWP-2 site is excluded).



235  
 236 **Figure 3:** Box and whisker plots for faecal  $\delta^{13}\text{C}$ . Plots show inter-quartile range, maximum and  
 237 minimum values and all data points. For convenience the site JV (Jaagvlakte) has been plotted with  
 238 sites from the (geographically close) Fynbos biome, although this specific site is actually located in the  
 239 Succulent Karoo biome.

240  
 241 **Nama Karoo Biome**

242 Average faecal  $\delta^{13}\text{C}$  in the Nama Karoo biome ( $-25.0 \pm 1.7\text{‰}$ ) is higher than the Fynbos Biome and  
 243 intra-site variability in the Nama Karoo is also somewhat higher than that of the Fynbos Biome, with  
 244 individual pellets at some sites reaching  $\delta^{13}\text{C}$  values of  $-22\text{‰}$ . In general  $\delta^{13}\text{C}$  is however rather  
 245 invariant across the five sites (**Figure 3b**) with the exception of the tightly clustered data at Mk-124.

## 246 Savanna Biome

247 Given the significance of middens as palaeoenvironmental archives for the savannas of central and  
248 northern Namibia (Chase et al., 2010; Chase et al., 2009; Gil-Romera et al., 2006; Gil-Romera et al.,  
249 2007; Scott, 1996; Scott et al., 2004) this region was studied in some detail. Overall, like the Nama  
250 Karoo,  $\delta^{13}\text{C}$  is often (e.g. Omanyne, Bobonong, Austerlitz; **Figure 3c**) within the range anticipated for  
251 pure  $\text{C}_3$  vegetation. However, the contribution of  $\text{C}_4$  vegetation to the animal's diet is readily apparent  
252 at several savanna sites, both from the isotope data (in terms of both average values and inter/inter  
253 site variability) (**Figure 3c**) and from observations of grazed grasses at sites such as Spitzkoppe and  
254 Zizou.

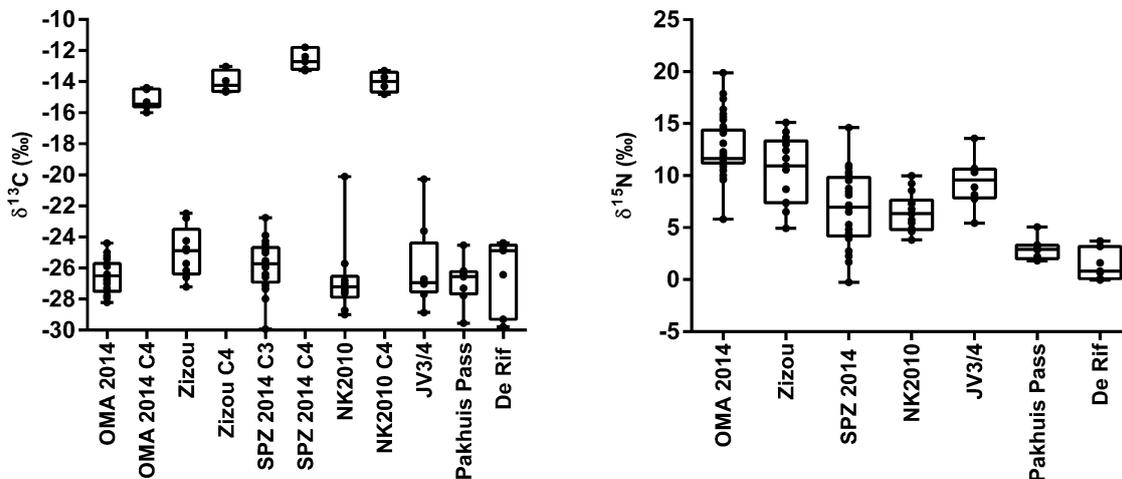
255 Spitzkoppe (**Figure 2a**), Omanyne (**Figure 2d**) and Zizou (**Figure 2b**) were the most intensively  
256 sampled sites. The highest site average faecal  $\delta^{13}\text{C}$  is seen at Zizou (2014;  $-19.5 \pm 0.5\text{‰}$ ,  $n = 48$ ) and  
257 the spread of pellet  $\delta^{13}\text{C}$  is quite broad. At Spitzkoppe, 36 pellets from three different accumulations  
258 sampled in 2013 (average  $-20.9 \pm 1.5\text{‰}$ ) and 96 pellets from 12 piles in sampled 2014 (average  $-23.7$   
259  $\pm 2.6\text{‰}$ ) were analysed. The inter-annual  $\delta^{13}\text{C}$  difference is significant (Mann-Whitney  $U = 551$ , two  
260 tailed  $p < 0.0001$ ), although it should be noted that the 2014 samples were deliberately sampled to  
261 capture potential variability at a single site (**Figure 3c**), whereas the 2013 samples were all collected  
262 from accumulations close to the midden itself. Relative to other savanna sites, faecal  $\delta^{13}\text{C}$  at Omanyne  
263 is relatively low in both 2008 and 2014, averaging  $-26.4 \pm 0.4 \text{‰}$  ( $n=15$ ) and  $-25.3 \pm 1.3 \text{‰}$  ( $n = 81$ )  
264 respectively. The difference between the two years is statistically significant (Mann-Whitney  $U = 214$   
265 two tailed  $p < 0.0001$ ). Witsand (WIT), which is located in an embayment in a rocky west-facing  
266 escarpment provides a useful demonstration of micro-climatic effects (cf. Chase et al., 2013) in that  
267 there are clear differences (Mann-Whitney,  $U = 4.5$  two tailed  $p < 0.0001$ ) between the cliff top  
268 (exposed;  $-21.4 \pm 1.1\text{‰}$   $n=12$ ) and cliff-bottom (shaded;  $-24.7 \pm 1.7\text{‰}$   $n=12$ ) pellet accumulations  
269 (**Figure 2C**).

## 270 Grassland Biome

271 At the Clarens (CLA) site there is no significant difference in  $\delta^{13}\text{C}$  between the three sampled pellet  
272 accumulations (Kruskal-Wallis Test Stat 4.22,  $p = 0.12$ ) and the site average for all pellets is  $-26.1 \pm$   
273  $1.7\text{‰}$ ;  $n=36$ ; **Figure 3d**). At Marikabi the average  $\delta^{13}\text{C}$  for the three collections of pellets ranges from  
274  $-25.7 \pm 2.3 \text{‰}$  ( $n=12$ ) to  $-27.8\text{‰} \pm 1.4\text{‰}$  ( $n=12$ ), but as at Clarens, there is no significant difference in  
275  $\delta^{13}\text{C}$  between the faecal pellet collections (Kruskal-Wallis Test Stat = 4.92,  $p = 0.09$ ). Overall, the data  
276 suggest a  $\text{C}_3$  diet, although there is more scatter in  $\delta^{13}\text{C}$  for the Grassland Biome than the Fynbos  
277 Biome (**Figure 3d**), perhaps suggesting a more diverse diet or range of plant foliar  $\delta^{13}\text{C}$ .

278 **Foliar  $\delta^{13}\text{C}$**

279 Plant samples were obtained for seven sites in the Fynbos, Succulent Karoo, Nama Karoo and Savanna  
 280 biomes (**Table 1; Figure 4**). Here we focus on the analysis of foliar material, although we recognise  
 281 that other plant parts may be consumed by hyraxes, and such data will be presented elsewhere. Plants  
 282 from the Cederberg in the western Fynbos Biome were obtained from De Rif (DR) and Pakhuis Pass  
 283 (PP). Foliar  $\delta^{13}\text{C}$  at De Rif is higher and exhibits a wider range ( $-26.3 \pm 2.3\text{‰}$   $n = 7$ ) than faecal  $\delta^{13}\text{C}$  ( $-$   
 284  $28.8 \pm 0.7\text{‰}$   $n = 12$ ), a pattern repeated at Pakhuis Pass (foliar average  $-27.0 \pm 0.7\text{‰}$   $n = 6$ ; faecal  
 285 average  $-28.2 \pm 0.5\text{‰}$   $n = 27$ ) and Jaagvlakte (JV; foliar average  $-26.0 \pm 2.7\text{‰}$   $n = 8$ ; faecal average  $-$   
 286  $26.7 \pm 0.7\text{‰}$   $n = 15$ ). Plants in the Nama Karoo and Savanna biomes exhibit bimodal foliar  $\delta^{13}\text{C}$   
 287 distributions, reflecting their mixed  $\text{C}_3/\text{C}_4$  vegetation communities. As anticipated, at NK2010 all  
 288 sampled grasses utilised the  $\text{C}_4$  photosynthetic pathway (average  $\delta^{13}\text{C}$   $-14.0 \pm 0.7\text{‰}$   $n = 4$ ). The  
 289 resulting site average foliar  $\delta^{13}\text{C}$  is thus associated with a large standard deviation ( $-23.0 \pm 6.3\text{‰}$   $n =$   
 290  $14$ ), reflecting this mixture of photosynthetic pathways. Faecal  $\delta^{13}\text{C}$  is lower (average  $-25.9 \pm 0.6\text{‰}$   $n$   
 291  $= 19$ ) and less scattered than the foliar data. It is only slightly higher than the mean foliar  $\delta^{13}\text{C}$  of the  
 292 non- $(\text{C}_4)$  grasses ( $-26.7 \pm 2.5\text{‰}$   $n = 10$ ) implying a minor  $\text{C}_4$  contribution to diet.



293  
 294 **Figure 4:** Foliar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data. Plots show inter-quartile range with maximum and minimum  
 295 values. For clarity  $\text{C}_4$  specimens are plotted separately from  $\text{C}_3$  plants for sites in the savanna  
 296 Karoo biomes.

297  
 298 In the Savanna Biome, 36 plants from Omanyne (OMA) were collected within 100 m of the midden.  
 299 The site average foliar  $\delta^{13}\text{C}$  is  $-23.4 \pm 5.2\text{‰}$ , but the distribution is strongly bimodal reflecting the  
 300 sampling of ten  $\text{C}_4$  grasses (**Figure 4**; average  $-15.2 \pm 0.6\text{‰}$ ) and 26  $\text{C}_3$  shrubs and trees ( $-26.6 \pm 1.1\text{‰}$ ).

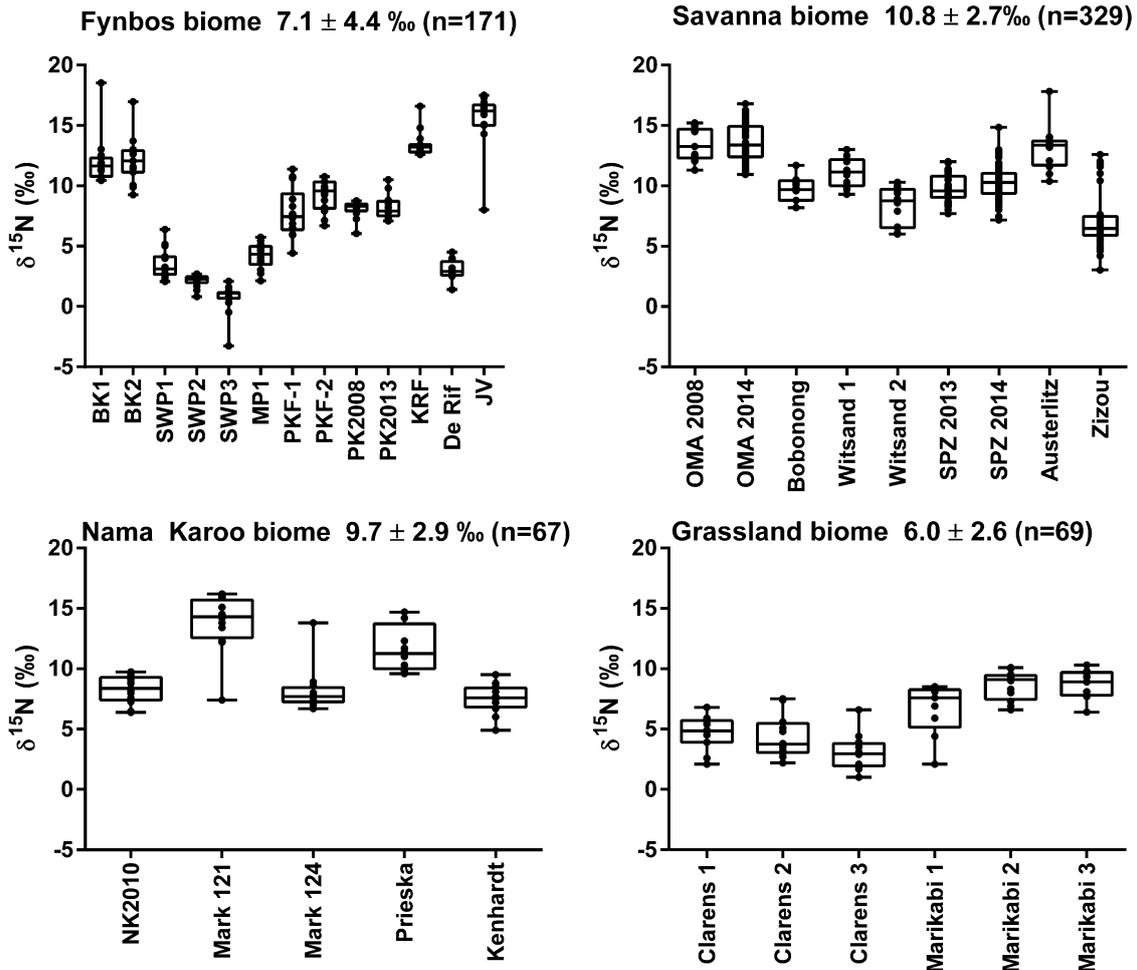
301 At Zizou (ZIZ) the average shrub/tree foliar  $\delta^{13}\text{C}$  is  $-25.0 \pm 1.6\text{‰}$  (n=9), while three C<sub>4</sub> grass specimens  
302 growing on the outcrop hosting the midden and on the flat grassy plain below (**Figure 2**) produce an  
303 average  $\delta^{13}\text{C}$  of  $-14.4 \pm 0.1\text{‰}$  (n=3). The site average faecal  $\delta^{13}\text{C}$  at ZIZ ( $-19.0 \pm 1.6\text{‰}$  n=48) therefore  
304 implies a contribution of C<sub>4</sub> grasses to the diet, consistent with observational evidence for grazing  
305 (**Figure 2**). 27 plants at Spitzkoppe (SPZ) were sampled across the rocky slopes below the midden  
306 (**Figure 2**) and these comprised a diverse mix of shrubs (Asteraceae), trees (*Ficus illcina*, *Rhus* sp., and  
307 *Olea* sp.), succulents (*Sarcostema viminale*) and grasses. In several locations the latter had been grazed  
308 upon. A specimen of the stem succulent *Sarcostema viminale* demonstrated the presence of CAM  
309 plants ( $-13.2\text{‰}$ ; n=1), while all sampled grasses were C<sub>4</sub> ( $-12.5 \pm 0.6 \text{‰}$  n=6). The foliar average  $\delta^{13}\text{C}$   
310 for the SPZ C<sub>3</sub> shrubs and trees (excluding the CAM specimen) was  $-25.8 \pm 1.6\text{‰}$  (n=20). The faecal  
311  $\delta^{13}\text{C}$  (**Figure 3**) therefore suggest that grasses/CAM form some part of the hyrax diet at this site, but  
312 there is a broad spread, particularly for the 2014 samples (average  $-23.7 \pm 2.6\text{‰}$ , range  $-29.1$  to  $-$   
313  $16.7\text{‰}$ ).

314

## 315 **Stable nitrogen isotopes**

### 316 **Fynbos Biome**

317 There is considerable variability in faecal  $\delta^{15}\text{N}$  for the Fynbos Biome (**Figure 5a**). The site averages  
318 range from  $13.4 \pm 1.1\text{‰}$  (KRF) to  $0.7 \pm 1.2\text{‰}$  (SWP-3) with maximum and minimum individual pellet  
319 values of  $18.5\text{‰}$  (BK1) and  $-3.3\text{‰}$  (SWP-3). Despite its outlier position for  $\delta^{13}\text{C}$ , SWP-2 produced an  
320 average  $\delta^{15}\text{N}$  close to SWP-1 and SWP-3. The presence of one or two outliers within otherwise tightly  
321 clustered datasets (e.g. BK1, KRF, SWP-3; **Figure 5a**) is a noteworthy feature in the Fynbos faecal  $\delta^{15}\text{N}$   
322 data; something less apparent in other biomes (**Figure 5**) and the  $\delta^{13}\text{C}$  data (**Figure 3**). As with  $\delta^{13}\text{C}$ ,  
323 repeat sampling in 2008 and 2013 at Pakhuis Pass (PP) produced indistinguishable results ( $8.1 \pm 0.7\text{‰}$   
324 (n=15) and  $8.3 \pm 1.0\text{‰}$  (n=12)). In the Succulent Karoo, the highest site average faecal  $\delta^{15}\text{N}$  of any site  
325 in the study is observed at Jaagvlakte (JV;  $15.5 \pm 2.3\text{‰}$  n = 15).



326  
 327 **Figure 5:** Box and whisker plots for faecal  $\delta^{15}\text{N}$ . Plots show inter-quartile range with maximum and  
 328 minimum values. For convenience the site JV (Jaagvlakte) has been plotted with sites from the  
 329 (geographically close) Fynbos biome, although this specific site is itself located in the Succulent  
 330 Karoo

### 331 Nama Karoo Biome

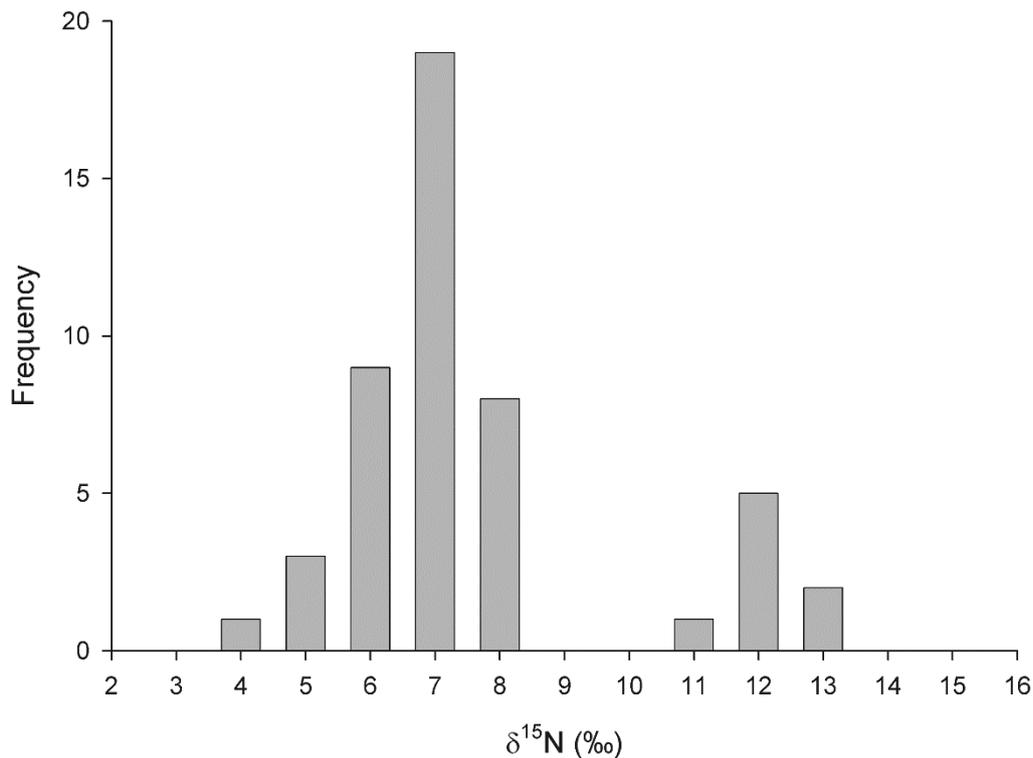
332 Faecal  $\delta^{15}\text{N}$  is higher in the Nama Karoo than in the Fynbos Biome (biome average  $9.7 \pm 2.9\text{‰}$ ) and  
 333 there is markedly less inter-site variability (**Figure 5**). Some intra-site variability is apparent, but in the  
 334 case of Mk121 and Mk124 this is influenced by individual outlier pellet values.

### 335 Savanna Biome

336 In the savanna site average  $\delta^{15}\text{N}$  (**Figure 5c**) ranges from  $13.6 \pm 1.6\text{‰}$  (Omanyne 2014,  $n=81$ ) to  $7.1 \pm$   
 337  $2.2\text{‰}$  (Zizou  $n=48$ ). The 2008 and 2014 data for Omanyne are identical ( $13.5 \pm 1.4\text{‰}$   $n=15$  and  $13.6 \pm$   
 338  $1.6\text{‰}$   $n=81$  respectively). The 2013 and 2014 data from Spitzkoppe differ slightly ( $9.7 \pm 1.1\text{‰}$   $n = 41$   
 339 and  $10.3 \pm 1.3\text{‰}$   $n = 96$  respectively) and this difference is statistically significant (Mann-Whitney U  
 340  $=1457$  two tailed  $p = 0.016$ ). The data from Zizou show a bimodal faecal  $\delta^{15}\text{N}$  distribution (modes of  
 341  $6.2 \pm 0.1\text{‰}$   $n = 40$  and  $11.6 \pm 0.7\text{‰}$   $n = 8$ ; **Figure 6**).The majority of faecal pellets are associated with

342 the lower mode. The higher  $\delta^{15}\text{N}$  mode is associated with a higher faecal N content (%N average of  
343  $2.5 \pm 0.9\%$  compared to  $1.1 \pm 0.2\%$ ) but  $\delta^{13}\text{C}$  values ( $-19.6\text{‰}$ ) comparable to the lower mode. As with  
344  $\delta^{13}\text{C}$ , the upper and lower sites from Witsand show a statistically significant difference (Mann-Whitney  
345  $U=10.5$ , two tailed  $p < 0.001$ ), with the more exposed cliff top site averaging of  $11.2 \pm 1.2\text{‰}$  and the  
346 lower site  $8.3 \pm 1.6\text{‰}$ .

347



348

349 **Figure 6:** Zizou faecal pellet  $\delta^{15}\text{N}$  distribution

### 350 **Grassland Biome**

351 The Grassland Biome (**Figure 5d**) shows a clear distinction between the Marikabi (MAR;  $6.6 \pm 2.2$  to  
352  $8.8 \pm 1.3\text{‰}$ ) and Clarens sites (CLA sampling averages  $3.1 \pm 1.4$  to  $4.7 \pm 1.4\text{‰}$ ), although intra-site  
353 variability is comparable to other sites in the study (ranges of 2-6 ‰). As with  $\delta^{13}\text{C}$ , there are no  
354 significant differences between the three pellet accumulations sampled at each site.

### 355 **Plant foliar $\delta^{15}\text{N}$**

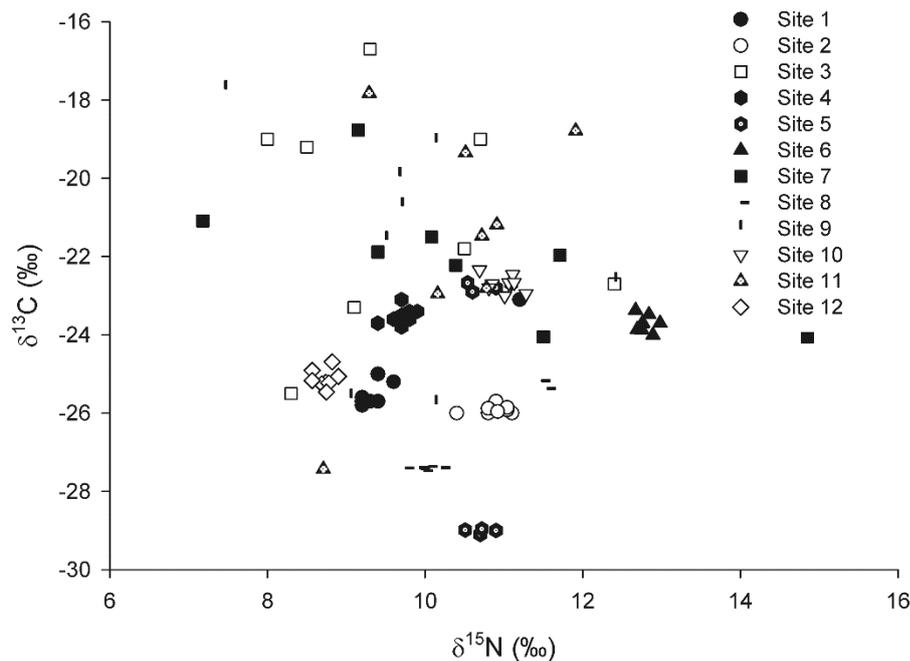
356 Scatter in foliar  $\delta^{15}\text{N}$  is greater than that observed in the faecal pellets (**Figure 4**). Site averages vary  
357 from a minimum of  $1.4 \pm 1.5\text{‰}$  ( $n=7$ ) at De Rif (DR; Fynbos Biome) to a maximum of  $12.5 \pm 1.6\text{‰}$  ( $n =$   
358 36) in the Savanna Biome (Omanyne). Foliar  $\delta^{15}\text{N}$  at the two fynbos sites is substantially lower than

359 the other biomes (DR  $1.4 \pm 1.5\text{‰}$  n = 7; PP  $2.9 \pm 1.0\text{‰}$  n = 8). Savanna foliar  $\delta^{15}\text{N}$  shows considerable  
360 variability (**Figure 4**). Interestingly, at Spitzkoppe, Zizou, NK2010 and Omanyne  $\delta^{15}\text{N}$  tends to be lower  
361 in  $\text{C}_4$  grasses compared to the  $\text{C}_3$  plants (**Table 2**). The difference is most striking at Zizou (Mann-  
362 Whitney U=0 Two tailed  $p=0.003$ ; **Table 2**) although it is also statistically significant at Spitzkoppe and  
363 Zizou. Similarly, in the Nama Karoo foliar  $\delta^{15}\text{N}$  at NK2010 is bimodal distributed, with the four  
364 specimens of  $\text{C}_4$  grass associated with the lower mode ( $4.5\text{‰}$ ; Mann-Whitney U=8 Two tailed  $p=0.03$ ).  
365 Foliar N content is also very variable (**Figure S3**) and in the Fynbos biome (DR and PP), foliar N is low  
366 compared to other biomes (**Table 2**). In the savanna biome foliar N content is also significantly lower  
367 in  $\text{C}_4$  grasses compared ( $\text{C}_3$ ) shrubs and trees at the same site (e.g. Codron et al. 2005) (**Table 2**).

368

### 369 **Faecal stable isotope variability at a single site**

370 At the intensively-sampled Spitzkoppe site it was possible to observe the isotopic variability of multiple  
371 small pellet piles, which we hypothesised were deposited by a limited number of individuals during  
372 short periods of recent feeding. There are marked differences in  $^{13}\text{C}$  and  $^{15}\text{N}$  content between  
373 individual pellet accumulations; some piles have tightly clustered  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  while others have very  
374 broad ranges (**Figure 7**). Narrow  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ranges are seen at pellet piles 2, 4, 6 and 13 and imply  
375 feeding associated with a singular or restricted range of plant browse. None of these tightly clustered  
376 sites exhibit  $\delta^{13}\text{C}$  greater than  $-23\text{‰}$ , consistent with the upper range  $\text{C}_3$  plant foliar data  $\delta^{13}\text{C}$  (**Figure**  
377 **4**). Flexibility in feeding is apparent however, as several pellet piles comprised a mix of pellets that  
378 contain largely  $\text{C}_4$  plant-derived matter *and* also pellets composed largely of  $\text{C}_3$ -derived plant matter  
379 (e.g. sites 3 and 9). In some cases, the impact of the aforementioned tendency for lower  $\delta^{15}\text{N}$  in  $\text{C}_4$   
380 grasses at this site (**Table 2**) is also apparent (e.g. sites 3 and 7). The distance from the midden  
381 increases with site number, but there is no tendency in these data for the scatter to be greater in  
382 pellet piles further from the midden.



383

384 **Figure 7:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from individual pellet piles sampled down the slope from the Spitzkoppe  
 385 midden. No pellet pile is indicative of focused  $\text{C}_4$  grass feeding

386

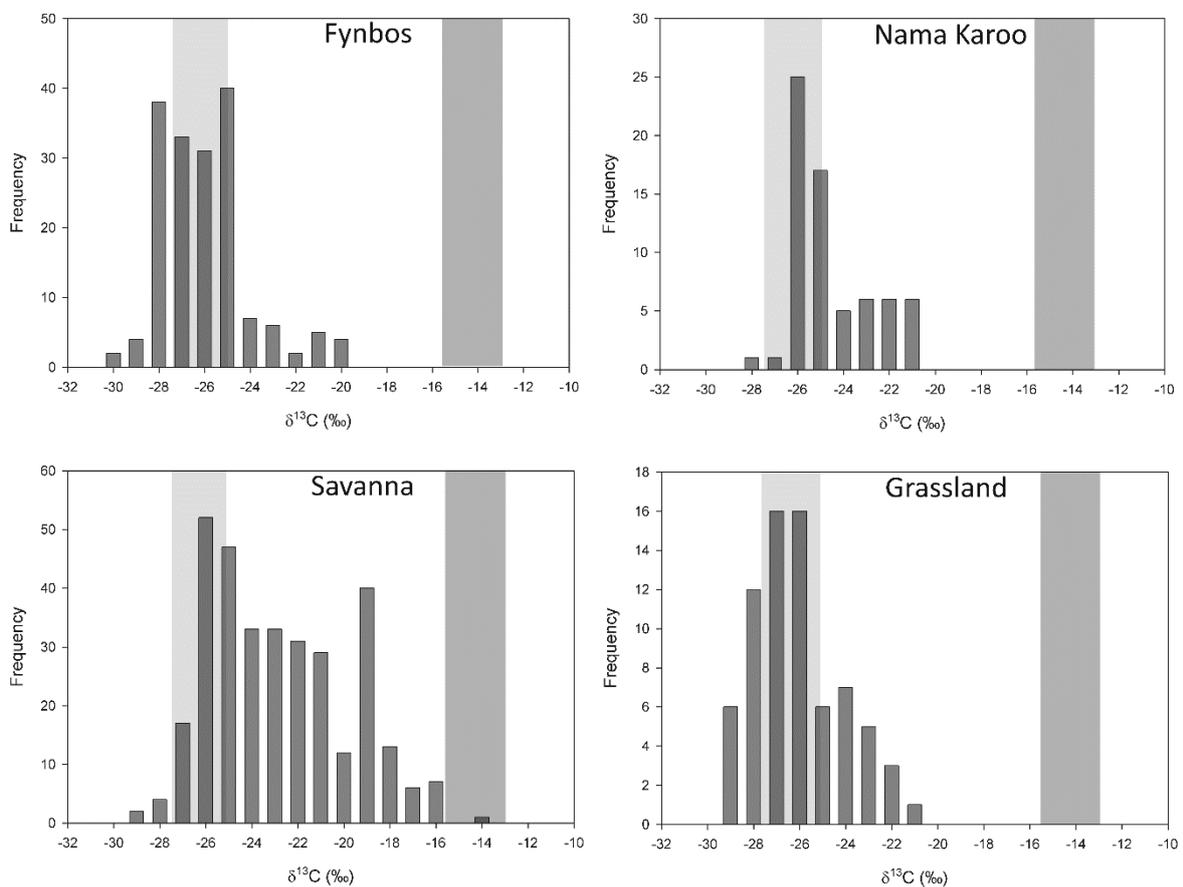
## 387 Discussion

388 In this study we sought to 1) address dietary variability via the analysis of faecal  $\delta^{13}\text{C}$ , and 2) address  
 389 controls on animal tissue  $\delta^{15}\text{N}$  within the hyrax ecosystem. Overall, the data demonstrate considerable  
 390 variability in the stable carbon and nitrogen isotope composition of rock hyrax faecal pellets, as well  
 391 as considerable intra/inter-site variability in foliar  $\delta^{15}\text{N}$  and foliar  $\delta^{13}\text{C}$ .

### 392 Faecal $\delta^{13}\text{C}$ , grazing and browsing

393 Faecal  $\delta^{13}\text{C}$  responds to anticipated variability in foliar  $\delta^{13}\text{C}$  across the southern African biomes (e.g.  
 394 Vogel et al., 1978; Still and Powell 2010) and we observe obvious differences between the Fynbos ( $\text{C}_3$   
 395 vegetation), Succulent Karoo ( $\text{C}_3/\text{CAM}$  vegetation) and the Savanna / Nama Karoo Biomes, in terms of  
 396 both average faecal  $\delta^{13}\text{C}$  and faecal  $\delta^{13}\text{C}$  range. Faecal  $\delta^{13}\text{C}$  has been shown to effectively characterise  
 397 the feeding behaviour of herbivores (Ambrose, 1986; Tieszen et al., 1979). Proposed faecal  $\delta^{13}\text{C}$  for  $\text{C}_3$   
 398 browsers,  $\text{C}_4$  grazers and mixed feeders are  $-26.3 \pm 1.0\text{‰}$ ,  $-14.3 \pm 1.2\text{‰}$  and  $-19.6 \pm 3.7\text{‰}$ , respectively  
 399 (Codron and Codron, 2009). These ranges are plotted with our data in **Figure 8**, from which we infer  
 400 dominantly browsing behaviour. Only 10% of the 653 pellets analysed had measured  $\delta^{13}\text{C}$  values  $\geq 19$   
 401 ‰. In the Fynbos, as anticipated, faecal  $\delta^{13}\text{C}$  implies a  $\text{C}_3$  diet. We find do not find evidence for the

402 substantial consumption of CAM plants within the Fynbos, with the possible exception of SWP-2,  
 403 which accounts for every data point higher than -24 ‰ in the Fynbos biome (**Figure 8a**). This may  
 404 reflect the shallow soils surrounding the site and the occurrence of associated succulent plants at this  
 405 locale. Rock hyraxes have been observed to feed on CAM plants (several species of *Aloe*) in the Eastern  
 406 Cape Province, but this represented a minor contribution to diet and was restricted to drier months  
 407 of the year (Fourie, 1983). In the other biomes faecal  $\delta^{13}\text{C}$  values of between -23 and -16‰ suggest  
 408 mixed-feeding, most obviously in the Savanna (e.g. **Figure 7**). In the Grassland Biome, the generally  
 409 low faecal  $\delta^{13}\text{C}$  for Clarens and Marikabi are consistent with prior observations in this region that  
 410 implied limited grass consumption (Scott and Vogel, 2000). This was thought to reflect the unpalatable  
 411 nature of “sour grass” in this region and cooler conditions relative to the rest of the summer rainfall  
 412 zone (*ibid*).



413  
 414 **Figure 8:** All measured pellet  $\delta^{13}\text{C}$  presented by biome. Grey bands show the pure grazer (dark grey)  
 415 and browser (light grey)  $\delta^{13}\text{C}$  ranges proposed by Codron and Codron (2009).

416

417 For sites with foliar  $\delta^{13}\text{C}$  data (**Table 2**) the proportion of  $\text{C}_3/\text{C}_4$  consumption can be estimated  
418 from the faecal  $\delta^{13}\text{C}$ ; after first correction for a  $-0.8\text{‰}$  offset between dietary and faecal  $\delta^{13}\text{C}$   
419 (Sponheimer et al. 2003a). At Omanyne, hyrax diet in 2008 and 2014 was dominated by  $\text{C}_3$  vegetation  
420 (90% and 80% respectively). At Zizou, the July 2014 data indicate mixed feeding, with average faecal  
421  $\delta^{13}\text{C}$  ( $-19.0 \pm 1.6\text{‰}$ ) implying  $\sim 40\%$   $\text{C}_3$  plant contribution to diet. At Spitzkoppe the  $\text{C}_3$  contribution was  
422  $\sim 56\%$  ( $n=36$ ) in May 2013 and  $\sim 77\%$  in July 2014 ( $n=96$ ). At NK2010  $\text{C}_3$  consumption was  $\sim 82\%$  ( $n=15$ ).  
423 These data therefore indicate some variability, even within the same biome (savanna). Some of this  
424 can be accounted for with consideration of the site settings. For example, at Omanyne the dominantly  
425  $\text{C}_3$  diet probably reflects the location of the midden on a steep rocky slope dominated by shrubs and  
426 trees with few grasses within a 50 m feeding radius of the midden (**Figure 2d**). By contrast, Zizou is  
427 located on a small outcrop and lies immediately adjacent to a wide grassy plain, well within the  
428 animal's feeding range (**Figure 2b**). The more substantial contribution of grasses to diet here is  
429 therefore unsurprising and is supported by the grazed appearance of the grasses around the site. The  
430 rocky slopes at Spitzkoppe support a mixture of localised grasses, abundant shrubs and several species  
431 of tree, with a mixed diet implied by the faecal  $\delta^{13}\text{C}$  data. Grasses only dominate on the plains  
432 surrounding Spitzkoppe (**Figure 2a**), which are beyond the safe foraging distance for hyraxes  
433 occupying the rock slopes (Kotler et al., 1999). The trees also include one species (*Olea europaea*)  
434 previously reported to be a significant contributor to the rock hyrax diet (Fourie, 1983).

435 Questions of dietary preference must be considered in the context of the temporal availability  
436 of plant type, and observations of animal behaviour (e.g. Lensing, 1983; Fourie, 1983). It has, for  
437 example, been shown that the foraging range can fluctuate seasonally, depending on food availability  
438 (Brown and Downs, 2005). Lensing (1983) demonstrated that despite a diverse diet, as much as 90%  
439 of an individual's stomach contents can comprise 2-4 plant species. Fourie (1983) similarly observed  
440 that just 10 species (mostly trees and shrubs) accounted for  $\sim 83\%$  of hyrax food consumption in the  
441 Eastern Cape Province of South Africa. Here we observe that the range in faecal  $\delta^{13}\text{C}$  is generally lower  
442 (typical standard deviations for pellet piles are  $\pm 1.5\text{‰}$ ) than foliar  $\delta^{13}\text{C}$  variation (typical site standard  
443 deviations are  $\pm 3.0\text{‰}$ ).

444 In terms of temporal variability, while trees and shrubs may access to deeper water resources,  
445 in arid regions with seasonal and restricted growing seasons, the period of elevated protein and water  
446 content (and thus palatability) in grasses is restricted to a few weeks of the year (Grunow et al., 1970).  
447 Observations of *P. capensis* behaviour and analysis of their stomach contents (Lensing, 1983; Fourie,  
448 1983; Skinner and Chimimba, 2005) suggests that the rock hyrax is an opportunistic feeder, and that  
449 grazing only comprises a substantial proportion of diet early in the wet season, when fresh grass is

450 sprouting. This period was observed to last for a matter of weeks in Namibia (Lensing, 1983) and to  
451 end quickly as grass protein content falls in response to peak summer temperatures (Fourie, 1983).  
452 Supporting this, we note that the N (approximation of protein) content of grasses sampled in the  
453 savanna biome, which here were mostly sampled at the end of the wet season /early dry season (**Table**  
454 **1**) is lower than that of the shrubs and trees at the same sites (**Table 2**). The role of foliar N content in  
455 influencing seasonal grazing and browsing has been noted for other herbivores (Botha and Stock,  
456 2005).

457         Observational data suggest that while they may graze during times when fresh grasses are  
458 available (Hoeck, 1975; Sale, 1965) – and grasses can reach as much as 40-60% of food intake (see  
459 Fourie 1983) – hyraxes are required to browse in many instances, exploiting various plant species and  
460 parts, depending on conditions and their needs (Skinner and Chimimba, 2005). The isotopic and %N  
461 data here are essentially consistent with this. For example, the 2013/2014 faecal  $\delta^{13}\text{C}$  and %N data  
462 from Spitzkoppe imply a differences in food sources for different years (**Figure 7**). The differences in  
463  $\text{C}_3/\text{C}_4$  consumption for 2013 and 2014 may, to some extent, reflect our differing sampling strategies  
464 (see above), but summer in 2014 was reported to have been drier than previous years by local  
465 residents, commensurate with a greater reliance on browse and the lower faecal  $\delta^{13}\text{C}$ / higher %N  
466 (**Figure S1**). Precisely how seasonality impacts our data more generally is difficult to assess, partly  
467 because the identification of fresh pellets is challenging. Nonetheless, assuming that most samples  
468 were deposited shortly prior to sampling (within weeks), it is possible that  $\text{C}_4$  grass palatability may  
469 have been higher earlier in wet (summer) season (Lensing, 1983) (**Table 1**). The maximum contribution  
470 of  $\text{C}_4$  grasses may be higher than our estimates imply.

471         The question of whether these faecal data are mirrored in the hyraceum (hyrax midden)  $^{13}\text{C}$   
472 content is important. For sites hosting hyrax middens with recent (last century) midden accumulation  
473 (**Table S2**), we observe that faecal  $\delta^{13}\text{C}$  is almost always lower than hyraceum  $\delta^{13}\text{C}$  (average offset  $1.3$   
474  $\pm 1.1\text{‰}$ ). The relationship between these two variables across multiple site/environments is difficult  
475 to assess as most data points cluster between  $-25$  and  $-26\text{‰}$ , with the single higher value for  
476 Spitzkoppe. However, the higher faecal  $\delta^{13}\text{C}$  ( $-20.9 \pm 1.5\text{‰}$ ) at Spitzkoppe is mirrored in the hyraceum  
477  $\delta^{13}\text{C}$  ( $-20.1 \pm 1.2\text{‰}$ ; average of six samples spanning the last 120 years) (**Table S2**). In summary, faecal  
478  $\delta^{13}\text{C}$  suggests that where a mixed  $\text{C}_3/\text{C}_4$  diet is available the rock hyrax will graze, depending on  
479 seasonal grass palatability and probably, protein content, but that for much of the year they are  
480 restricted to browsing. At several sites, it is also apparent that the landscape around the hyrax colony  
481 and associated spatio-temporal variability of palatable vegetation may account for inter-site  
482 differences in the pellet isotopic signature.

483

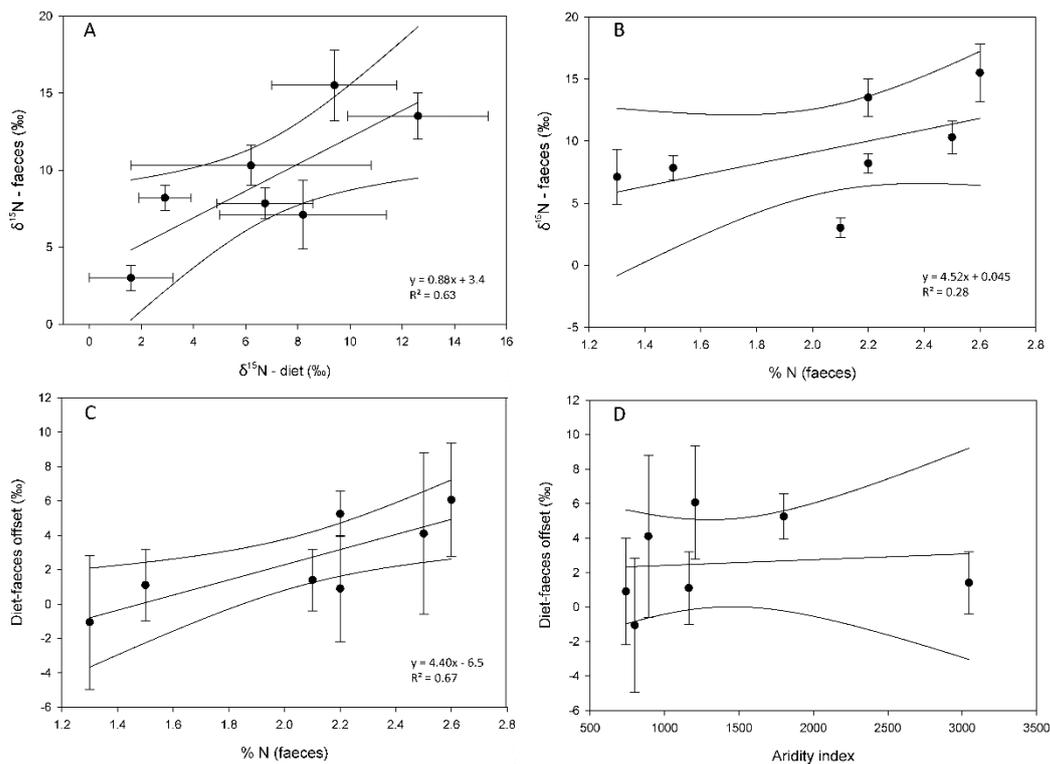
## 484 Nitrogen isotopes

485 While the utility of faecal  $\delta^{13}\text{C}$  as a means to infer diet is established, the interpretation of faecal  $\delta^{15}\text{N}$   
486 is more challenging (Codron and Codron, 2009). In this study, considerable inter-site variability in  
487 faecal  $\delta^{15}\text{N}$  is observed. Faecal  $\delta^{15}\text{N}$  at some sites is higher than values (albeit from different  
488 environments) for browsing and grazing African herbivores (Codron et al., 2005; Codron and Codron,  
489 2009), but these findings are not inconsistent with previous reports of high hyrax tissue  $\delta^{15}\text{N}$  (Ambrose  
490 and De Niro, 1986a; Sealy et al., 1987).

491           Given the range of potential environmental and physiological controls on animal tissue  $\delta^{15}\text{N}$ ,  
492 even for herbivores fed the same diet (Sponheimer et al., 2003b; Codron et al. 2012), the  
493 interpretation of this variability is complex (e.g. Ambrose and DeNiro, 1986a; Hartman and Danin,  
494 2010; Murphy and Bowman, 2006). A first step is to compare the faecal  $\delta^{15}\text{N}$  with the food source. As  
495 might be anticipated (Hartman, 2011; Hartman and Danin, 2010; Murphy and Bowman, 2006), due to  
496 the range in soil conditions, water availability and plant types in the complex micro-topography of  
497 rock hyrax habitats there is marked scatter in foliar  $\delta^{15}\text{N}$  (**Figure 4; Table 3**). We observe over 20‰  
498 variation in the complete foliar  $\delta^{15}\text{N}$  dataset and up to 15‰ in single biomes and single sites (e.g.  
499 Omanyne and Spitzkoppe). Such foliar  $\delta^{15}\text{N}$  variability is not unprecedented (e.g. Craine et al., 2012).  
500 We also observe a tendency for  $\text{C}_4$  grass  $\delta^{15}\text{N}$  to be lower than  $\text{C}_3$  shrub/tree  $\delta^{15}\text{N}$  at the same site  
501 (**Table 2**). This difference is not significant at all sites. Inconsistent differences in foliar  $\delta^{15}\text{N}$  for  
502 different photosynthetic pathways have been reported (e.g. Aranibar et al., 2008; Hartmann and  
503 Danin 2010; Murphy and Bowman, 2006), with no differences reported in some studies (Heaton,  
504 1987).

505           When individual sites are considered, faecal  $\delta^{15}\text{N}$  is generally higher than foliar (dietary)  $\delta^{15}\text{N}$   
506 (**Table 3**) (e.g. Ambrose and DeNiro, 1986; Sutoh et al., 1987; Sponheimer et al. 2003c). As observed  
507 with  $\delta^{13}\text{C}$ , intra-site *variability* (i.e. standard deviations; **Table 3**) in faecal  $\delta^{15}\text{N}$  is substantially (~50%)  
508 lower than foliar  $\delta^{15}\text{N}$ , most likely indicating selective feeding (see above) and homogenisation within  
509 the digestive tract. We observe a (non-significant) positive correlation between site average faecal  
510  $\delta^{15}\text{N}$  and site average foliar  $\delta^{15}\text{N}$  ( $r^2 = 0.50$ ,  $p=0.08$   $n=7$ ). However, *dietary*  $\delta^{15}\text{N}$  need not be equivalent  
511 to the simple site average foliar  $\delta^{15}\text{N}$ . For instance, we have observed at several sites that foliar  $\delta^{15}\text{N}$   
512 is significantly lower for  $\text{C}_4$  grasses (**Table 2**). At Zizou, the mean foliar  $\delta^{15}\text{N}$  (10.5‰) differs from the  
513 estimated *dietary*  $\delta^{15}\text{N}$  (8.2‰); the latter being determined from the average foliar  $\delta^{15}\text{N}$  weighted by  
514 the proportion of grass consumption (as derived from the faecal  $\delta^{13}\text{C}$ ). The difference induced by such  
515 an adjustment is 0.9 ‰ for Spitzkoppe (based on 2014 pellet data), 0.3‰ at NK2010 and negligible at

516 Omanyne (0.1‰), where there is no difference between C<sub>4</sub> grass and C<sub>3</sub> foliar δ<sup>15</sup>N. Analysis using the  
 517 estimated dietary δ<sup>15</sup>N indicates a significant correlation ( $r^2=0.63$ ,  $p=0.03$   $n=7$ ) between dietary δ<sup>15</sup>N  
 518 and faecal δ<sup>15</sup>N with a predicted  $3.4 \pm 2.3$  ‰ diet-faeces offset (**Figure 9**) and a gradient not  
 519 significantly different from 1 ( $0.88 \pm 0.3$ ). A comparable strength of relationship between faecal and  
 520 foliar δ<sup>15</sup>N was reported by Díaz et al. (2016) for camelid and rodent faeces in the Atacama Desert.

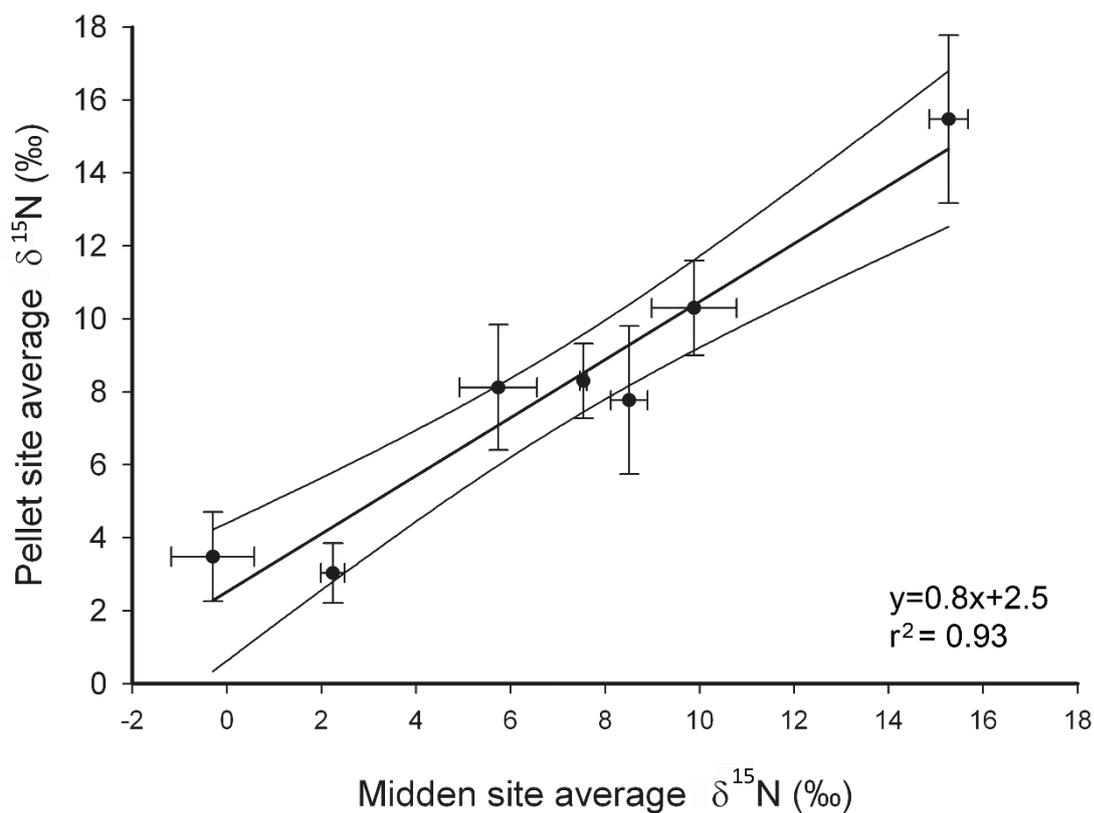


521  
 522 **Figure 9:** A) Dietary-weighted average δ<sup>15</sup>N plotted against site average faecal δ<sup>15</sup>N. Standard  
 523 deviations are plotted. B) Average %N plotted against site average faecal δ<sup>15</sup>N; C) Dietary-faeces offset  
 524 plotted against %N; D) Dietary-faeces offset plotted against aridity index (Trabucco and Zomer, 2009).  
 525 Results of ordinary least-squares regression are shown in each case.

526  
 527 In all cases, sampling biases must be kept in mind. Not all plants in the foraging range of the  
 528 hyrax colonies were sampled, and samples were not taken throughout the year. Our samples thus may  
 529 not reflect the full feeding behaviour of the hyraxes, nor the season in which the pellets were  
 530 deposited. The values presented here are only comparable in the broadest sense. However, Codron  
 531 and Codron (2009) also demonstrated a relationship between faecal and dietary δ<sup>15</sup>N for southern  
 532 African herbivores, although they noted that the relationship is not as strong as that for δ<sup>13</sup>C. While

533 there are several proposed physiological controls on herbivore tissue  $\delta^{15}\text{N}$ , the only additional control  
534 of significance for faecal  $\delta^{15}\text{N}$  identified by Codron and Codron (2009) was %N in faeces, which can be  
535 considered a proxy for dietary protein content (*ibid*). Dietary protein content has been proposed  
536 (along with water conservation strategies) to impact the faecal/urine  $^{15}\text{N}$  mass balance in drought-  
537 tolerant herbivores (Ambrose, 1991; Codron et al. 2005). In our dataset the relationship between %N  
538 in faeces and faecal  $\delta^{15}\text{N}$  is positive, but not significant ( $r^2 = 0.28$ ,  $p = 0.22$ ,  $n=7$ ; **Figure 9B**). There is,  
539 however, a significant positive correlation ( $r^2 = 0.67$   $p=0.02$   $n=7$ ) between the  $\delta^{15}\text{N}$  diet-faeces *offset*  
540 and %N in faecal pellets (**Figure 9C**). This implies a dietary protein content control (**Tables 2 and 3**).  
541 Greater isotopic diet-tissue discrimination has been reported for higher protein diets (Sponheimer et  
542 al. 2003b). Indeed, the lowest offsets are observed at Zizou and NK2010 where we observe significant  
543 consumption of grasses (which have low foliar %N; **Table 2**). Additionally, we do not observe any  
544 correlation between the diet-faecal offset and aridity (**Figure 9D**), which might be an anticipated  
545 impact of water conservation physiological responses to aridity. This finding is consistent with other  
546 studies (e.g. Ugan and Coltraine, 2011).

547 To link these findings with palaeoenvironmental studies employing hyraceum  $\delta^{15}\text{N}$  we also  
548 compared faecal  $\delta^{15}\text{N}$  with hyraceum  $\delta^{15}\text{N}$  from recently-deposited middens (**Table S2; Figure 10**). As  
549 hyraceum is considered to be largely a urinary product, it has been assumed to contain urea, which  
550 following mass-balance expectations of some physiological water conservation models may have a  
551  $\delta^{15}\text{N}$  signature anti-correlated with body tissue, or at least generally have a lower  $\delta^{15}\text{N}$  than body tissue  
552 (e.g. Sponheimer et al., 2003c and references therein). Here we compare hyraceum with faeces, within  
553 which N is assumed to be primarily derived from animal tissue (e.g. Codron et al., 2005). The number  
554 of sites with recent (we have used the last 100 years) midden accretion is limited (Chase et al., 2012),  
555 but the relationship between faeces and hyraceum  $\delta^{15}\text{N}$  for these sites is positive and highly  
556 significant. The high explanatory power of this relationship ( $r^2 = 0.93$   $p < 0.001$ ) suggests that hyraceum  
557  $\delta^{15}\text{N}$  is positively correlated with faecal  $\delta^{15}\text{N}$  across the study region, and by corollary (i.e. **Figure 9A**),  
558 correlated with dietary  $\delta^{15}\text{N}$ . Concerning the latter, at present there are only four sites with both  
559 recent hyraceum deposits and dietary (foliar)  $\delta^{15}\text{N}$  data (Spitzkoppe, Jaagvlakte, De Rif and Pakhuis  
560 Pass). However the data from these four sites indicate a positive correlation between dietary  $\delta^{15}\text{N}$  and  
561 hyraceum  $\delta^{15}\text{N}$  (Pearson's  $r = 0.96$ ,  $p = 0.04$ ).



562

563 **Figure 10:** Midden (hyraceum)  $\delta^{15}\text{N}$  (site average and standard deviation for the last ~100 years; **Table**  
 564 **S2**) plotted against site average and standard deviation of modern faecal  $\delta^{15}\text{N}$ . The sites plotted are:  
 565 Spitzkoppe, De Rif, Marikabi, Seweweekspoort (SWP-1), Jaagvlakte, Pakhuis Pass and Papkuilsfontein.

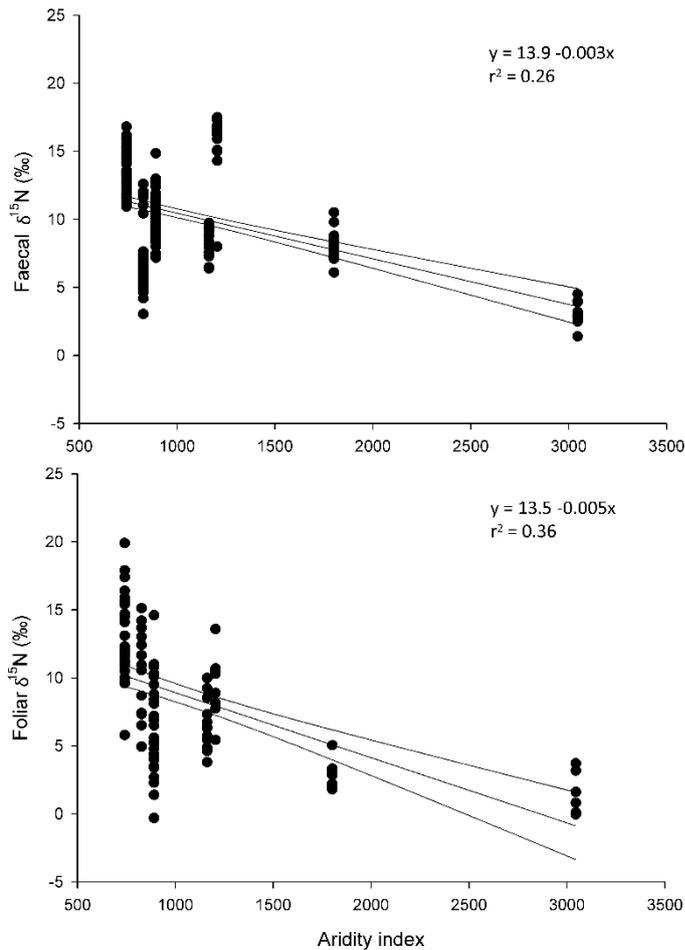
566 Overall, these findings suggest a significant role for diet (i.e. source isotopic composition and  
 567 dietary protein content) in controlling variability in both faecal and hyraceum  $\delta^{15}\text{N}$  (**Figure 9A**; **Figure**  
 568 **10**). Furthermore, the strong positive correlations between faecal and foliar  $\delta^{15}\text{N}$  with *hyraceum*  $\delta^{15}\text{N}$   
 569 imply that either: 1) the dominant control on  $\delta^{15}\text{N}$  in hyraceum is not related to metabolic effects (e.g.  
 570 Hartmann, 2011; Murphy and Bowman, 2006) and/or 2) hyraceum is not primarily composed of urea,  
 571 and the N-containing metabolic products being measured are not affected by water conservation  
 572 physiological responses. It is noteworthy that modern hyraceum  $\delta^{15}\text{N}$  is higher than dietary (foliar)  
 573  $\delta^{15}\text{N}$  (**Figure 9**) but statistically indistinguishable from faecal  $\delta^{15}\text{N}$  at the four sites with the complete  
 574 set of hyraceum, faecal and foliar  $\delta^{15}\text{N}$  data (**Table S2**). Furthermore several unrelated (to urea) N-  
 575 containing animal metabolites have been identified within hyraceum (Carr et al., 2010). While this  
 576 issue needs further study, it is possible that other N containing components of hyraceum swamp any  
 577  $^{15}\text{N}$  depleted urea, or that excreted urea is quickly converted to ammonia and volatilised (Schwarcz et  
 578 al., 1999), and hence is not preserved.

579 *Relationship to climate*

580 Palaeoenvironmental reconstructions from hyrax middens have interpreted nitrogen isotope  
581 variability within hyraceum as reflecting the impact of climatic changes on soil and plant  $\delta^{15}\text{N}$  in  
582 foraging zones around a hyrax colony (Chase et al., 2012). It has been proposed that in desert  
583 ecosystems an underlying mechanism driving foliar  $\delta^{15}\text{N}$  variation is soil water availability (Hartman,  
584 2011; Hartman and Danin, 2010; Murphy and Bowman, 2006). At the global scale, increasing foliar  
585  $\delta^{15}\text{N}$  with aridity may reflect the influence of water availability on the 'openness' of the nitrogen cycle  
586 (losses relative to the size of the total N pool) (Austin and Vitousek, 1998; Handley et al., 1999). This  
587 relationship may breakdown under conditions of the most extreme aridity (Díaz et al. 2016). The foliar  
588  $\delta^{15}\text{N}$  measurements from this study, encompassing seven sites spanning aridity index values from  
589 3045-701 (equivalent to UNEP aridity index 0.3 [semi-arid] to 0.07 [arid]) and mean annual  
590 precipitation values from 98 mm a<sup>-1</sup> to 860 mm a<sup>-1</sup> show a scattered, but negative correlation with  
591 aridity ( $r^2=0.36$   $p<0.0001$   $n=110$ ) (**Figure 11**).

592 For sites with paired foliar/faecal  $\delta^{15}\text{N}$  data (**Figure 11**) we can explore the roles of climate and  
593 metabolic affects in more detail (e.g. Heaton 1987) as it can be hypothesised that with increasing  
594 aridity any additional physiological response to water stress (resulting in the preferential excretion of  
595 <sup>15</sup>N-depleted urea via urine) will result in a steeper gradient in the relationship between faecal  $\delta^{15}\text{N}$   
596 and aridity compared to that between foliar  $\delta^{15}\text{N}$  and aridity. Previous studies have reported bone  
597 collagen  $\delta^{15}\text{N}$  to decrease by 1.1 to 1.3 ‰ per 100 mm increase in rainfall, which was inferred to be  
598 three times the gradient observed for vegetation  $\delta^{15}\text{N}$  (see Ambrose, 1991; cf. Schwarcz et al., 1999  
599 and references therein). More recent studies have implied a consistent offset between body tissue  
600 and foliar  $\delta^{15}\text{N}$  across aridity gradients, implying no significant metabolic effect (Schwarcz et al., 1999;  
601 Hartman, 2011; Murphy and Bowman, 2006). In our data (**Figure S4**), we observe gradients of  $-2.5 \pm$   
602  $0.2$  ‰ per 100 mm of rainfall for faecal  $\delta^{15}\text{N}$  and  $-3.8 \pm 0.4$  ‰ per 100 mm of rainfall for foliar  $\delta^{15}\text{N}$ . In  
603 fact, when site average  $\delta^{15}\text{N}$  values are used (as opposed to linear regression slopes derived using all  
604 measured data points) these gradients are essentially identical ( $-3.1 \pm 0.8$  ‰ per 100 mm rainfall for  
605 diet-weighted foliar  $\delta^{15}\text{N}$ ,  $-3.5 \pm 1.7$  ‰ for faecal  $\delta^{15}\text{N}$  and  $-3.4 \pm 0.8$  ‰ for site average foliar  $\delta^{15}\text{N}$ ).  
606 This is consistent with **figure 9D**. We do, however, note that our data are restricted to relatively arid  
607 environments and that these relationships may become weaker under increased humidity (Pate and  
608 Anson, 2008).

609



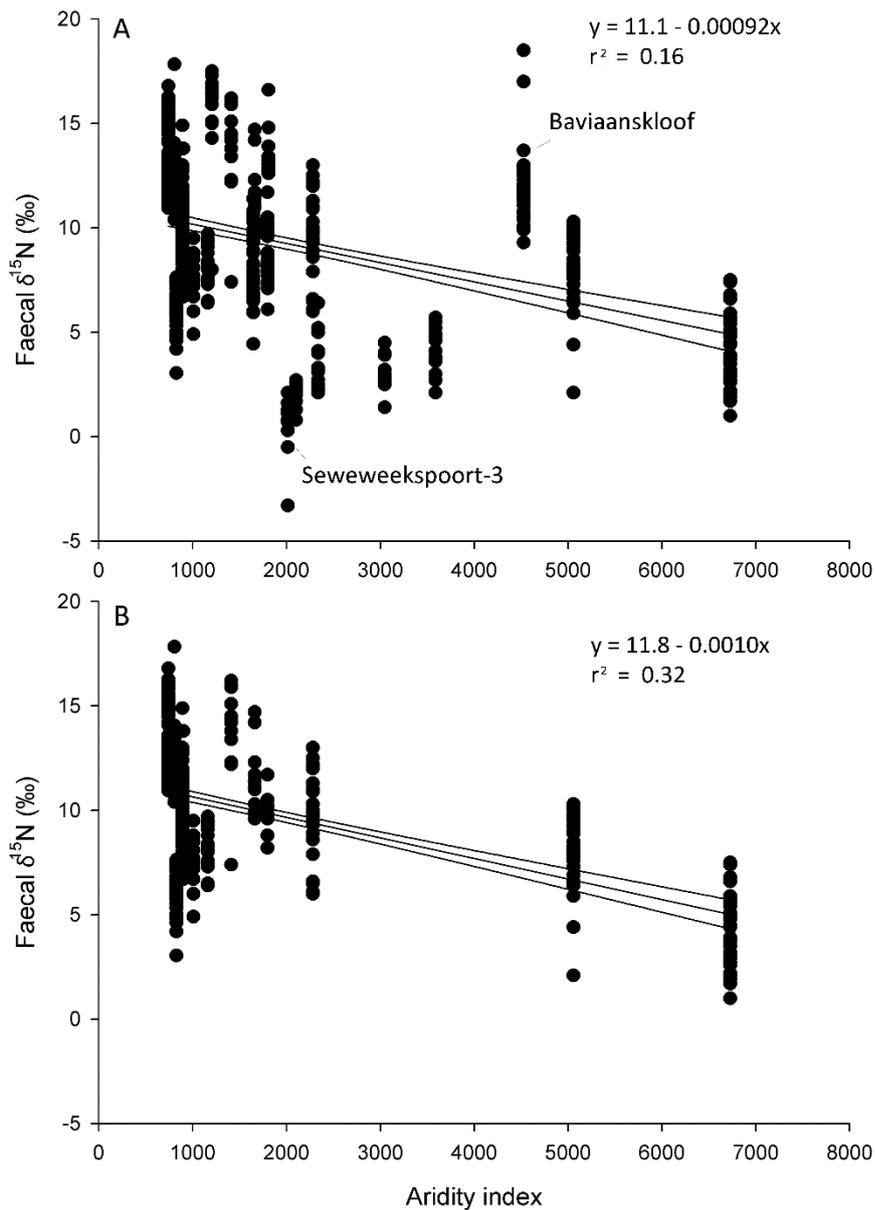
610

611 **Figure 11:** Relationship between aridity index and faecal δ<sup>15</sup>N and plant δ<sup>15</sup>N for sites where the two  
 612 were jointly sampled. The sites plotted are NK2010, Jaagvlakte, De Rif, Pakhuis Pass, Omanyne, Zizou  
 613 and Spitzkoppe. Minimising the leverage effect of the most humid site (De Rif) using log aridity index  
 614 also results statistically significant relationships ( $r^2 = 0.43$  and  $0.25$  for foliar and faecal data  
 615 respectively)

616

617 An aridity index that incorporates temperature and evaporative effects on water availability  
 618 may be a more appropriate way to consider these processes (Hartman, 2011; Murphy and Bowman,  
 619 2006). The gradients for paired faecal/foliar δ<sup>15</sup>N data using aridity index show comparable relations  
 620 to those seen using mean annual rainfall; i.e. the gradient is steeper for foliar δ<sup>15</sup>N than for faecal δ<sup>15</sup>N  
 621 (**Figure 11**), although the role of high AI outlier site (De Rif) should be kept in mind. Considering the  
 622 total faecal δ<sup>15</sup>N dataset across every site, we observe a weak, but significant ( $r^2 = 0.16$   $p < 0.00001$   
 623  $n=651$ ) negative correlation with aridity index (**Figures 11 and 12**). Two outlier sites contribute to the  
 624 low explanatory power of this relationship (**Figure 12**) – SWP-3 and Baviaanskloof (BK1&2). As noted

625 previously, the former is located in the sheltered valley bottom (see above) and the AI value may not  
626 be representative of the true water availability at this location. The inter-site scatter in faecal  $\delta^{15}\text{N}$  in  
627 the Fynbos biome has already been noted (**Figure 5**) and the relationship between faecal  $\delta^{15}\text{N}$  and  
628 climate is markedly stronger ( $r^2 = 0.30$   $p < 0.00001$   $n=465$ ) if sites from the Fynbos are excluded from  
629 the analyses (**Figure 12**). A critical caveat is that gridded climate data are limited by interpolation based  
630 on discrete, and sometimes distant, weather station data (e.g. Hijmans et al., 2005) and the precision  
631 of the data is generally resolved to 1 km or greater grid cells, which cannot adequately reflect the  
632 diversity of microclimates and local-scale variability in soil bodies (e.g. water, C and N availability). This  
633 is potentially significant in areas of high relief and variability in aspect, such as the valleys and cliffs  
634 that many midden sites are located (well-illustrated at Witsand) and is likely to particularly affect sites  
635 in the Cape Fold Belt Mountains (cf. BK1 and BK2). Thus, even if climatic factors were the sole  
636 mechanisms for determining soil/plant  $\delta^{15}\text{N}$ , the nature of climatic data employed would necessarily  
637 generate significant data scatter.



638

639 **Figure 12:** A) All faecal  $\delta^{15}\text{N}$  determinations plotted in relation to aridity index. B) All faecal  $\delta^{15}\text{N}$   
 640 determinations plotted with the exception of sites located in the Fynbos Biome. Inappropriate  
 641 attribution of the aridity index to sites in the topographically-complex Cape Fold Belt region may  
 642 account for the weaker explanatory power when including the Fynbos biome. Using log aridity index  
 643 also results statistically significant relationships ( $r^2 = 0.20$  and  $0.30$  for all sites and all non-fynbos sites  
 644 respectively)

645

## 646 **Implications for hyrax midden palaeoenvironmental research**

647 The  $\delta^{13}\text{C}$  data suggest that *P. capensis* is an opportunistic feeder, grazing when palatable grass is  
648 available, but primarily limited to browsing. This is consistent with existing observations (Lensing,  
649 1983; Fourie, 1983; Scott and Vogel, 2000), but the wider geographic spread of our data suggests such  
650 inferences are generally valid for much of the hyrax's habitat. This is also consistent with some  
651 interpretations of hyrax midden  $\delta^{13}\text{C}$  records from the Savanna Biome, whereby a model of greater  
652 wet season  $\text{C}_4$  grass consumption was extended to consider longer-term fluctuations in the  
653 duration/intensity of the wet season (Chase et al. 2009; 2010).

654 The  $\delta^{15}\text{N}$  data overall imply: 1) faeces and hyraceum  $\delta^{15}\text{N}$  are controlled largely by diet (i.e.  
655 foliar  $\delta^{15}\text{N}$  and potentially foliar N content), 2) that the previously-reported negative relationship  
656 between aridity and herbivore/foliar  $\delta^{15}\text{N}$  is observed in southern African hyrax habitats, 3) a limited  
657 role for water-conservation metabolic effects. The specific drivers of the offsets between between  
658 foliar (dietary)  $\delta^{15}\text{N}$ , faecal  $\delta^{15}\text{N}$  and hyraceum  $\delta^{15}\text{N}$  are difficult to interpret, but a substantial (though  
659 not necessarily singular) role for diet in driving hyrax faecal and midden  $\delta^{15}\text{N}$  variability is implied  
660 (**Figure 9**) by the comparable slopes of the faecal/foliar  $\delta^{15}\text{N}$ -MAP/aridity index relationships (**Figures**  
661 **9D, 11 and S4**) and the positive correlation between faecal  $\delta^{15}\text{N}$  and hyraceum  $\delta^{15}\text{N}$  (**Figure 10**). The  
662 N (protein) content of the hyrax diet may be significant (**Figure 9c**; Sponheimer et al., 2003b), but the  
663 broader impact of this latter factor is difficult to assess as it can be anticipated that the animal is able  
664 to meet its protein needs and at most sites (perhaps excepting Zizou) this can be achieved through  
665 varying the proportions of (fresh) graze and browse through time. Strong evidence for a metabolic  
666 effect is not readily apparent, although the the strong correlation between faecal  $\delta^{15}\text{N}$  and hyraceum  
667  $\delta^{15}\text{N}$ , and the comparable diet-faeces and diet-hyraceum  $\delta^{15}\text{N}$  offsets could also be explained by an  
668 absence of urea in the measured hyraceum  $\delta^{15}\text{N}$ .

669 Additionally, in the savanna biome (and NK2010 in the Nama Karoo), we observe that  $\delta^{15}\text{N}$   
670 and %N can be lower in  $\text{C}_4$  grasses compared to  $\text{C}_3$  shrubs and trees at the same site (**Table 2**), which  
671 either singularly or together may have attendant (i.e. lowering) impacts on herbivore  $\delta^{15}\text{N}$  and thus  
672 hyraceum  $\delta^{15}\text{N}$  (e.g. Sponheimer et al., 2003b). For the savanna biome as a whole faecal  $\delta^{13}\text{C}$  is  
673 negatively correlated with faecal  $\delta^{15}\text{N}$  ( $r^2=0.33$ ), although this relationship is strongly affected by the  
674 data from Zizou ( $r^2=0.14$  without Zizou) where higher grass consumption is inferred. There are weaker  
675 (Grassland;  $r^2= 0.26$ ), opposing (i.e. positive correlation and  $r^2= 0.47$ ; Nama Karoo) or insignificant  
676 (fynbos;  $r^2<0.01$ ) relationships between faecal  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in the other biomes, presumably  
677 reflecting far more minor/lack off of  $\text{C}_4$  vegetation consumption in these environments (no faecal  
678 pellet has a  $\delta^{13}\text{C}$  higher than  $-21\text{‰}$  in the Grassland or Nama Karoo biomes).

679 More data are needed to assess this (and any mechanism) robustly, given the relatively limited  
680 dataset and potential seasonal variability in grass %N and  $\delta^{15}\text{N}$  (Codron et al., 2013) and so in some  
681 environments disentangling the specific roles of  $\text{C}_4$  contribution to diet versus climate (remembering  
682 that the two are clearly not independent variables) in driving hyraceum palaeo- $\delta^{15}\text{N}$  records could be  
683 challenging. Notwithstanding, both effects are consistent with palaeoecological interpretations  
684 presented for the savanna middens. That is, as the dietary contribution of fresh and palatable  $\text{C}_4$   
685 grasses increases with water availability we would anticipate a reduction in hyraceum  $\delta^{15}\text{N}$  and an  
686 increase  $\delta^{13}\text{C}$  (as is observed; Chase et al., 2009; 2010). However, the data demonstrate a need to  
687 consider the context of each individual midden as the proportional contribution of grasses to diets in  
688 the savanna biome can be variable (e.g. Zizou). The dietary data presented thus far are derived only  
689 from foliar  $\delta^{15}\text{N}$  and further work concerning other plant parts may allow these relationships to be  
690 refined.

691 In the Fynbos, diet is dominated by  $\text{C}_3$  vegetation and with the exception of SWP-2 there is  
692 little evidence of CAM plant consumption. The SWP-2 data suggest that this cannot always be  
693 discounted, and minor (< 1% of consumed material) consumption of CAM plants (*Aloe*) has been  
694 observed in the dry season (Fourie, 1983). In terms of hyraceum isotope records, the resulting shift in  
695  $\delta^{13}\text{C}$  due to CAM consumption would likely parallel the impact of water-use efficiency changes in  $\text{C}_3$   
696 plants (Chase et al., 2011), and long-term trends in midden records (pollen and isotopes) have  
697 indicated potentially increased CAM plant representation during certain periods (Chase et al., 2015b).

698 Finally, the importance of the time/space averaging effects, as occurs when sampling  
699 hyraceum, is demonstrated. The inter-sample scatter in hyraceum  $\delta^{13}\text{C}/\delta^{15}\text{N}$  (**Table S2**; site standard  
700 deviations of  $\sim 0.5\text{‰}$ ) is lower than the total scatter in faecal  $\delta^{13}\text{C}/\delta^{15}\text{N}$  (site standard deviations of  
701  $\sim 1.5\text{‰}$ ), which is in turn lower than the variability in foliar  $\delta^{13}\text{C}/\delta^{15}\text{N}$  (site standard deviations of  
702  $\sim 2.5\text{‰}$ ). The scatter in foliar  $\delta^{15}\text{N}$  probably reflects a combination plant species effects and local  
703 topographic/hydrological/soil nutrient (N availability) controls on soil  $\delta^{15}\text{N}$  (Craine et al., 2012;  
704 Handley et al., 1999; Ugan and Coltraine, 2011).

## 705 **Conclusions**

706 These data represent a first attempt to refine, from the perspective of stable isotopes, our  
707 understanding of rock hyrax diet and behaviour. This is of particular interest given the use of rock  
708 hyrax middens as arid zone palaeoenvironmental archives. Faecal  $\delta^{13}\text{C}$  demonstrates that the rock  
709 hyrax is largely a browser but is (probably) an opportunistic mixed feeder, consuming  $\text{C}_4$  grasses during  
710 periods of the year when this food source is available/most nutritious. This is consistent with

711 observations of animal behaviour. *Inter*-site faecal  $\delta^{15}\text{N}$  variability is large, particularly in the Fynbos.  
712 The absolute values of faecal  $\delta^{15}\text{N}$  are high relative other African herbivores, but they correlate with  
713 dietary (foliar)  $\delta^{15}\text{N}$ , with an offset consistent with expected trophic level enrichment. The diet-faeces  
714  $\delta^{15}\text{N}$  offset - which is predicted to increase with aridity if water-conservation metabolic effects have a  
715 significant impact on the  $\delta^{15}\text{N}$  of animal tissue - is uncorrelated with climate, but is correlated with %N  
716 in faecal pellets. Faecal  $\delta^{15}\text{N}$  (and thus foliar  $\delta^{15}\text{N}$ ) correlates strongly with hyraceum  $\delta^{15}\text{N}$ . Foliar  $\delta^{15}\text{N}$   
717 data are available for seven sites across three biomes and correlate significantly (albeit with scatter)  
718 with aridity. Together these observations do not presently imply a substantial role for water-  
719 conservation metabolic processes in driving hyraceum  $\delta^{15}\text{N}$  variation and/or that measured nitrogen  
720 within hyraceum is representative of body tissue N other than urea N. The data presently available for  
721 modern hyrax habitats are thus broadly in agreement interpretations of hyraceum  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$   
722 records in palaeoenvironmental reconstructions.

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903 **Table Captions**

904

905 **Table 1:** Site information and coordinates. Sites are listed by biome with vegetation types obtained  
 906 from Mucina and Rutherford (2006) with the exception of sites marked <sup>1</sup>, which were derived from  
 907 the World Wildlife Fund (2016) Ecoregions.

908

909 **Table 2:** C<sub>3</sub> and C<sub>4</sub> plant foliar δ<sup>13</sup>C and δ<sup>15</sup>N. Differences in δ<sup>15</sup>N and %N between C<sub>3</sub> and C<sub>4</sub> plants at  
 910 Spitzkoppe, Zizou, Omanyne and NK2010 are all statistically significant (i.e. Mann-Whitney p <0.05)  
 911 except for Omanyne δ<sup>15</sup>N (Mann-Whitney U = 100.5, two tailed p=0.3). \*Excluding CAM specimen for  
 912 δ<sup>13</sup>C.

| Site              | C <sub>4</sub> plant δ <sup>13</sup> C (‰) | C <sub>4</sub> plant δ <sup>15</sup> N (‰) | C <sub>4</sub> plant % N | C <sub>3</sub> plant δ <sup>13</sup> C (‰) | C <sub>3</sub> plant δ <sup>15</sup> N (‰) | C <sub>3</sub> plant % N |
|-------------------|--|--|--------------------------|--|--|--------------------------|
| Omanyne (OMA)     | -15.2 ± 0.6                                | 11.3 ± 2.2                                 | 1.0 ± 0.2                | -26.6 ± 1.1                                | 13.0 ± 2.8                                 | 2.5 ± 0.7                |
| Spitzkoppe* (SPZ) | -12.5 ± 0.6                                | 3.9 ± 1.5                                  | 0.3 ± 0.1                | -25.8 ± 1.6                                | 7.1 ± 3.5                                  | 2.0 ± 0.9                |
| Zizou (ZIZ)       | -14.0 ± 0.7                                | 6.6 ± 0.4                                  | 0.6 ± 0.2                | -25.0 ± 1.6                                | 12.3 ± 2.0                                 | 1.9 ± 0.9                |
| NK2010            | -14.0 ± 0.7                                | 4.5 ± 0.5                                  | 0.5 ± 0.2                | -27.4 ± 1.0                                | 7.3 ± 1.5                                  | 1.6 ± 0.5                |
| De Rif (DR)       | -  | -  | -                        | -26.3 ± 2.3                                | 1.4 ± 1.5                                  | 0.7 ± 0.2                |
| Pakhuis Pass (PP) | -  | -  | -                        | -26.8 ± 1.4                                | 2.9 ± 1.0                                  | 0.7 ± 0.2                |
| Jaagvlakte (JV)   | -  | -  | -                        | -26.0 ± 2.7                                | 9.4 ± 2.4                                  | 2.0 ± 0.6                |

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919 **Table 3:** Comparison of faecal and foliar (dietary)  $\delta^{15}\text{N}$  for sites with detailed plant sampling. \*refers  
 920 to sites with differing  $\delta^{15}\text{N}$  in  $\text{C}_3$  and  $\text{C}_4$  plants where foliar  $\delta^{15}\text{N}$  is weighted by proportional  
 921 consumption of  $\text{C}_3/\text{C}_4$  grasses to derive a dietary  $\delta^{15}\text{N}$  estimate (see text).

| Site                        | Biome           | Average foliar (dietary) $\delta^{15}\text{N}$ (‰) (n) | Average faecal $\delta^{15}\text{N}$ (‰) (n) | Average faecal N content (%) | Diet-faeces offset (‰) |
|-----------------------------|-----------------|--|--|------------------------------|------------------------|
| NK2010*                     | Nama Karoo      | 6.7 ± 1.8 (14)   | 7.8 ± 1.1 (19)                               | 1.5 ± 0.3                    | <b>1.1 ± 2.1</b>       |
| Jaagvlakte (JV)             | Succulent Karoo | 9.4 ± 2.4 (8)  | 15.5 ± 2.3 (15)                              | 2.6 ± 1.0                    | <b>6.1 ± 3.3</b>       |
| De Rif (DR)                 | Fynbos          | 1.4 ± 1.5 (7)  | 3.0 ± 0.8 (12)                               | 2.1 ± 0.4                    | <b>1.6 ± 1.8</b>       |
| Pakhuis Pass (PP 2008/2013) | Fynbos          | 2.9 ± 1.0 (8)  | 8.2 ± 0.8 (27)                               | 2.3 ± 0.3                    | <b>5.3 ± 1.3</b>       |
| Omanyne* (OMA)              | Savanna         | 12.5 ± 2.7 (36)  | 13.5 ± 1.5 (81)                              | 2.2 ± 0.4                    | <b>1.0 ± 3.1</b>       |
| Zizou* (ZIZ)                | Savanna         | 8.2 ± 3.2 (13)   | 7.1 ± 2.2 (48)                               | 1.4 ± 0.6                    | <b>-1.1 ± 3.9</b>      |
| Spitzkoppe* (SPZ)           | Savanna         | 6.2 ± 3.5 (26)   | 10.3 ± 1.3 (96)                              | 2.5 ± 0.4                    | <b>4.1 ± 3.7</b>       |
| Average                     |                 |  |  |                              | <b>2.6 ± 2.6</b>       |

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