African buffalo diet in a woodland and bush-dominated biome as determined by stable isotope analysis

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We examined the importance of browse and grazing in the diet of 28 African buffalo Syncerus caffer from Chobe National Park, Botswana, through analysis of stable isotope ratios of tooth collagen. Carbon isotope levels indicated that the assimilated diet was wholly dominated by grasses. Variations in nitrogen isotope values were consistent with variation in individual δ15N values being due to variations in the small proportion of non-grasses in the diet. There were no significant sex differences in diet.

Key words: African buffalo, diet, stable isotope analysis.

African buffalo (Syncerus caffer Sparrman, 1779) are normally considered to be almost pure, or ‘hyper’-grazers (Sinclair 1977; Skinner & Smithers 1991; Prins 1996). However, in some areas buffalo have been thought to incorporate a substantial element of browse into their diets (Gagnon & Chew 2000; Landman & Kerley 2001). At Chobe National Park (CNP), Botswana, buffalo are frequently observed browsing, e.g. a herd removed 30% of the leaves in a 1 ha stand of Combretum zanzibarensis in a single feeding bout (C. Skarpe, pers. comm. and unpubl. data; D.J.H. & M.M., pers. obs.). The importance of browse in the diet was unclear, however. Visual observations are biased towards open and fringe habitats and daylight hours. Dung analyses are biased towards indigestible plant remains and may underestimate the proportion of more digestible plants in the assimilated diet (Taolo 2003).

Terrestrial plants obtain carbon from atmospheric CO2. However, almost all grasses and most sedges in dry tropical regions, such as Chobe, use the C4 photosynthetic pathway, while browse species use the C3 pathway (Cerling et al. 1993; Ehleringer et al. 1997; Stock et al. 2004). This results in grasses and browse plants having different isotopic signatures, C4 plant tissue being c. 14‰ richer in 13C (Boutton 1991; Ehleringer 1991). δ15N values of terrestrial plants vary widely, from ~8 to +18‰. This is influenced mainly by the δ15N content of the soil, whether the plant fixes atmospheric nitrogen, and the systematic enrichment of deep-rooted as opposed to shallow-rooted plants (Shearer & Kohl 1989; Virginia et al. 1989). Tissues of consumers directly reflect isotopic proportions in the diet (DeNiro & Epstein 1978; Kelly 2000). Analysis of body tissue can therefore be used to investigate the proportions of assimilated food from grasses and from browse plants in the diets of herbivores living in dry tropical climates. Tooth collagen is convenient, as teeth are easily recovered, the cementum and dentine in which collagen is found are metabolically active and reflect lifetime diet, and teeth are very stable in post-mortem tissue content (Cerling et al. 1999). We present data on the diet of buffalo at Chobe as determined by isotopic analysis of carbon and nitrogen in tooth collagen.

Twenty-eight buffalo teeth from different individuals (15 females, 11 males, and two juveniles) were collected from skulls in the field, or from the CNP research department skull collection. All skulls originated from the Chobe riverfront population, composed of three distinct herds and groups of bachelor males (Halley et al. 2002), which migrate 10–40 km southwards into the interior of the park during the wet season (Taolo 2003). The area is dominated by savanna woodland and bush biomes (Skarpe et al. 2004), with open grassland restricted to the seasonally flooded riverfront area.

A subsample of 2–2.5 g of each tooth was separated, cleaned, and crushed. Apatite (the hard, mineralized outer layer) was removed by sieving though a 425 µm sieve. The resulting powder was crushed further to >250 µm. About 1 g (range: 0.88–1.14 g) was further processed to chemically separate collagen.

0.4–0.8 mg of collagen from each sample was loaded into standard tin cups and pelletized.
Pellets were placed in a Finnigan MAT 252 gas injection mass spectrometer apparatus housed at the Graduate School of Environmental Earth Sciences at the University of Hokkaido, for analysis of carbon and nitrogen isotopic ratios. Pellets were vapourized by standard quartz combustion methods (Minagawa et al. 1984), and isotope ratios analysed following standard IRM-GC/MS techniques (Brand 1996).

The δ13C carbon isotope ratio, expressed as parts per thousand (‰) relative to the standard PDB limestone (Craig 1957), is presented in Fig. 1. Inset bars indicate the range of 13C ratios found for C3 and C4 plants (Boutton 1991; Ehleringer 1991). The overall mean value was –9.96 ± 0.79‰.

There was no significant sex difference in carbon ratios, males having a mean ratio of –10.1 ± 0.91‰ and females –9.79 ± 0.70‰ (t = −1.03, P = 0.39, 24 d.f.). The mean value was +6.79 ± 1.25‰ compared with atmospheric nitrogen. Again, there were no sex differences: males +6.79 ± 1.25‰, females +6.52 + 1.42‰; t = 0.5 P = 0.4, 24 d.f.). However, δ13C and δ15N values were significantly negatively correlated (Fig. 2).

There is often a small but consistent variation, or ‘fractionation’, between δ13C values of plants and δ13C values of resulting animal tissue. Fractionation can vary slightly depending on the tissue, but in mammals is generally within 6‰ of the diet (Tieszen & Boutton 1989).

Field studies of mammals indicate bone collagen δ13C is enriched +4–6‰ relative to diet (Van der Merwe 1982; Ambrose 1993; Kelly 2000). Results from sika deer (Cervus nippon), another large ungulate (Halley et al., in press) indicate that δ13C values of bone and tooth collagen from the same individuals do not differ (while the δ15N value of tooth collagen is c. 1.35‰ enriched compared to bone collagen). Our unmodified δ13C values are at the upper end or higher than the range expected for C4 plants; however, allowing for enrichment of 4–6‰ would place these values at the lower end or slightly below the C4 range. In either case, the major conclusion is clear: the assimilated diet of African buffalo is dominated by C4 plants, and the traditional view of buffalo as bulk grazers is confirmed for the Chobe population. Histological analysis of dung from the same population (Taolo 2003) corroborates this finding, 90–93% of identifiable remains in dung being of C4 grasses and the remainder various C3 forbs and leaves (no sedges or C3 grasses were recorded). Observations of

![Fig. 1. Frequencies of δ13C ratios of tooth collagen from 28 African buffalo. Horizontal bars indicate the δ13C ratios found in C3 (browse) and C4 (grass) plants. Studies suggest a trophic fractionation of +4–6‰ in the buffalo carbon ratio will have occurred during the assimilation process (see text).](image-url)
browsing, as previously mentioned, are biased to open, edge habitats and to daylight, and probably reflect casual browsing as buffalo emerge from, or return to, shaded bush and woodland habitats where they rest and ruminate, from grasslands where they graze at the night. Landman & Kerley (2001) also noted that buffalo at Addo National Park, South Africa, were overwhelmingly grazers, despite the impression of wildlife managers that browsing was important in the diet.

\[ ^{15}N \] Values reported here may have arisen from a combination of factors (see introduction) and in themselves say little about the diet of buffalo. However, the significant negative correlation in \( ^{13}C \) and \( ^{15}N \) values suggests that the range of \( ^{13}C \) values represents a real variation between animals in the proportions of different plants consumed, and is consistent with both lower \( ^{13}C \) values and higher \( ^{15}N \) values resulting from a larger (albeit always minor) proportion of browse in the diet – C3 browse plants being more negative in \( ^{13}C \) and enriched in \( ^{15}N \) (as deeper rooted) than C4 grasses.

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