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Extensive browsing by a conventional grazer? Stable carbon isotope analysis reveals extraordinary dietary flexibility among Sanga cattle of North Central Namibia

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Intraspecies dietary flexibility, such as variable consumption of graze vs. browse in herbivores, has received scant attention on a spatial scale despite growing evidence of substantial variability within and among populations, especially in bovids. Here, we report on extraordinary differences in cattle diet among two communal pasture areas across seasons in northern Namibia: King Nehale (KN, open grassland) and Okongo (OK, dense woodland). Percentage C_3 browse and C_4 grass consumption was determined from $\delta^{13}C$ values of dung samples, using a Bayesian stable-isotope mixing model (SIAR – stable isotope analysis in R). During the wet and early dry season, KN cattle consumed 11 and 19% browse, respectively, and the OK cattle consumed 84% browse. At the end of the dry season, the browse intake of KN cattle increased to 33% while that of OK cattle decreased to 55%. Vegetation structure influenced the graze/browse consumption strongly in both areas. A better understanding of this extraordinary dietary flexibility is imperative as anthropogenically driven habitat change is projected to lead to the extinction of perceived grazing specialists.

Keywords: *Bos taurus africanus*; bovid; browser; carbon-13; diet; grazer; herbivore; isotope ecology; isotope measurements and methods

1. Introduction

Herbivore forage is generally categorised into two distinct classes or dietary types, commonly referred to as browse and graze. Herbaceous and woody plants such as trees, shrubs and herbs make up the browse component, while the graze component consists of grasses [1,2]. In general, herbivores have evolved to exploit one of these two foraging strategies, and evidence for differences in digestive anatomy and morphophysiology, oral and dental morphology, as well as body size has been found between grazers and browsers [3,4].

The exceptional species richness of African ruminants is attributed primarily to the differentiation between two feeding guilds: the grazers (eating C_4 grasses) and browsers (eating C_3 plants) [3,5,6]. Clauss et al. [7] recently advocated that the terms 'grazer' and 'browser' should be reserved for the description of natural diet, while morphophysiological differences should be expressed in relation to the morphophysiology of a typical browser, or 'moose type', and that of a typical grazer, or 'cattle-type'. However, whether this categorisation of species based on diet

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*Corresponding author. Email: alex.bond@usask.ca type is justified, has been questioned in the light of growing evidence of variable diets within and among populations, especially of bovine species [5,6,8,9].

Insight into the factors that govern intraspecies dietary variation among large herbivores, as well as the width of dietary flexibility that species can tolerate might help to better understand the apparent discrepancy between morphophysiological adaptation and actual diet. This is especially important in the face of growing anthropogenically induced habitat changes (e.g. bush encroachment) experienced across the African continent [10]. Codron et al. [11] found evidence that diet type specialisation is a function of long-term exposure to C_4 grasslands, which could limit species' ability to change if grasslands are replaced by other vegetation types. In the face of global change [12], it is, therefore, essential to determine and understand the dietary type flexibility of ruminant species if we hope to take appropriate conservation action.

Cattle are classified conventionally as grazers [13,14], and are even used as the model type for typical grazer (cattle-type) morphophysiology [7]. They have a very distinct rumen content stratification, lack of papillae on the dorsal rumen wall and a distinct difference in particle and fluid passage from the rumen which is expected to hamper their ability to deal with frothy rumen contents associated with a high browse intake [15]. In tropical and subtropical areas, they rely on C_4 grasses for nutrition, but in this study, we investigate claims from North Central Namibia that the indigenous Sanga cattle (*Bos taurus africanus*), known locally as Nguni, browse extensively [16–18]. Our objective was to quantify the Sanga cattle's (hereafter 'cattle') browse/C_3 food consumption throughout an annual cycle by using diet carbon stable isotope analysis.

2. Methods

2.1. *Study area*

North Central Namibia comprises a mosaic of different vegetation types, varying from open grassland in the southwest, to dense woodland in the northeast (Figure 1) [16]. The mean annual precipitation increases from 350 mm in the southwest to 550 mm in the northeast [16]. Livestock herding and small-scale cereal production characterise the communal areas of the region [18].

Within this area, we selected two study sites (Figure 1). The first comprises the grazing area on the open Andoni plains of the King Nehale (KN) communal conservancy (18.4617 S; 16.6986 E) in the Oshikoto region, bordering the Etosha National Park. These grassland plains occur on saline, loamy soils [19]. Cattle are grazed communally here and penned at night in the nearby villages. Cattle within this area acted as our control, as these animals should be able to find enough grass to persist all year round. The second study site was located in the communal grazing areas surrounding the town of Okongo (OK; 17.5796 S; 17.2192 E) in the Ohangwena region, where dense Burkea–Baikiaea woodland dominated the vegetation structure on deep Kalahari sands [19]. This area was evidently converted from an open state to its current densely wooded composition by fire suppression, and continuous high cattle stocking rates [17]. In this area, cattle have been reported to browse extensively [16–18], because of a lack of sufficient grass fodder. The topography in both regions is relatively flat, and does not restrict livestock movements. No coherent grazing management took place at either study site, and fire was not an important ecological factor in the time leading up to the study period.

2.2. *Sample collection and lab analysis*

We used stable carbon isotope analysis of faecal samples collected over a seasonal cycle at both study areas to quantify the proportional use of graze and browse by cattle. Herbivore faeces reflect

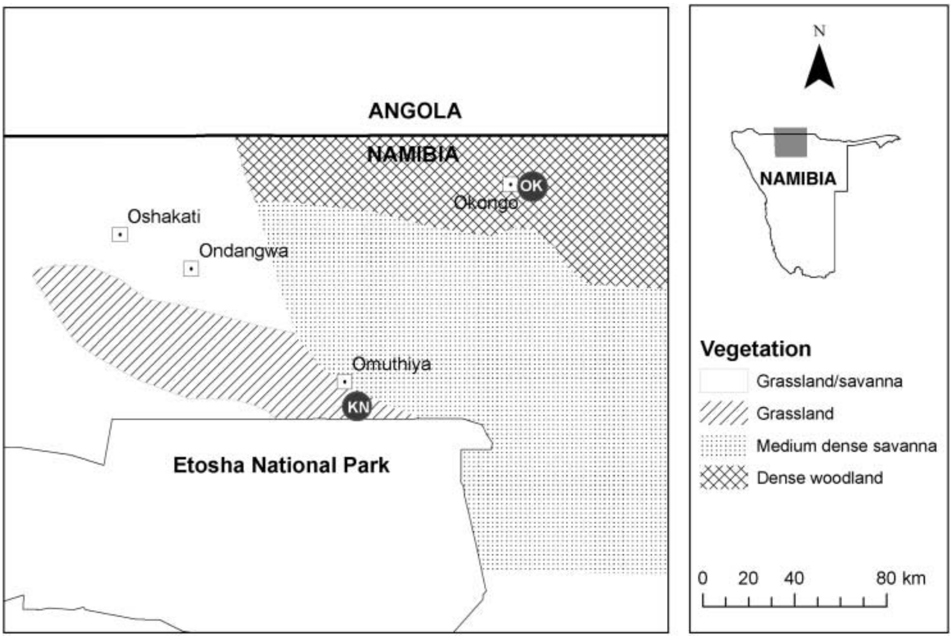

Figure 1. Dung samples from cattle at two sites, OK and KN, in North Central Namibia. Vegetation types were redrawn from Erkillä [16].

the isotopic composition of the diet [20,21]. We determined δ^{13}C values for both C_3 (trees, shrubs and herbs) and C_4 (grasses) plants commonly available to the cattle, to act as end-members in an 1-isotope, 2-source mixing model.

During May 2011, we collected representative leaf samples of the most abundant grasses and browse plant species. In total four grasses, five trees and one herb species were collected from the KN area, while leaf samples from five grasses and five tree/shrub species were collected from the OK area. A number of leaf samples from different individuals of the same species were pooled to obtain an average δ^{13}C value for that particular species. Eight to ten fresh dung samples, assumed to be from different cattle, were collected at each of the study sites during the months of February (wet season), May (early dry season) and August (late dry season). All samples were dried and mill-ground through a 1 mm sieve into a homogenous powder. Powdered samples were combusted individually in an automated elemental analyser (Carlo-Erba), and the resultant CO_2 gas introduced to a mass spectrometer (MAT 252 or DELTA XP) using a continuous flow-through inlet system. $^{13}C/^{12}C$ ratios are expressed in the delta (δ) notation in per mil (‰) relative to Vienna PeeDee Belemnite. Recovery of secondary isotopic reference materials is presented in Table S1 (Supplemental Material). Standard deviations of repeated measurements of laboratory standards were less than 0.25‰.

2.3. *Statistical analysis*

We determined whether the δ^{13}C values of C_3 and C_4 plants differed significantly from each other, and that differences within groups were not significant between sites, using a one-way analysis of variance (ANOVA). We also used ANOVA to test whether cattle δ^{13}C values differed between sites and among seasons.

To determine the proportional contribution of C_3 plants (browsing) in each system and season, we used the Bayesian stable-isotope mixing model SIAR [22] in R 2.15.1 [23]. We determined the

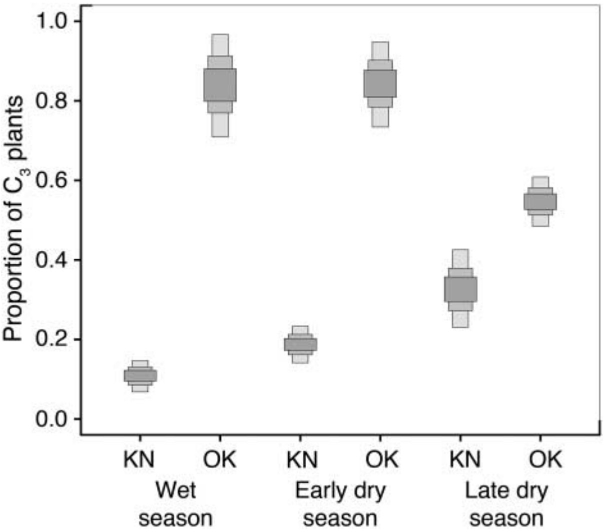

Figure 2. Proportion of C_3 browsed plants consumed by Sanga cattle over three seasons at two different study sites in North Central Namibia as calculated from 8 to 10 dung samples obtained from different individuals at each site during each respective season. The KN communal conservancy is an open grassland area, while the OK area is characterised by dense woodland. Boxes reflect 25, 75 and 95% credibility intervals.

median and 95% credibility intervals (Cr.I.), using 1 million iterations, with an initial discard of 40,000, thinned by 15, resulting in 64,000 posterior draws. We used discrimination factors (Δ^{13}C) from plants to dung of +1.1 ± 0.3‰ for C_4 plants, and +0.7 ± 0.3‰ for C_3 plants [20,21]. All isotope values are presented as mean ± SD.

3. Results

There was no significant difference in δ^{13}C in either C_3 ($F_{1,9} = 0.10, p = 0.76$) or C_4 collected plants ($F_{1,7} = 0.04, p = 0.84$) between the sites. Consequently, we used the pooled average values of the C_3 and C_4 plants of both areas (C_3: −27.5 ± 0.3‰; C_4: −14.1 ± 0.2‰) as the end points in our mixing model.

The δ^{13}C values of the cattle dung samples revealed stark contrasts in diet composition between the two study areas (Figure 2 and Table 1). Cattle δ^{13}C differed between sites ($F_{1,46} = 279.8$, $p < 0.001$), and the site*season interaction was also significant ($F_{2,46} = 27.9, p < 0.001$). During both the wet and early dry season, the cattle of the KN area fed almost exclusively on grass, with the contribution of browse/C_3 consumption estimated at 11% (95% Cr.I.: 8–15%) and 19% (95% Cr.I.: 14–23%), respectively, for the two seasons. During the same time period, 84% of the OK cattle's diet comprising browse in both seasons (wet season: 95% Cr.I.: 70–96% and early dry season: 95% Cr.I.: 73–94%). At the end of the dry season, the browse intake of the cattle at KN increased to an estimated 33% (95% Cr.I.: 23–43%) while that of the cattle at OK decreased to 55% (95% Cr.I.: 48–61%).

4. Discussion

Sprent and McArthur [24] advocated that the diet of animals in the field should be considered as a function of their dietary preferences modified by the availability of different plant types, with a

Table 1. Percentage browse consumption of cattle from two areas in Namibia – King Nehale communal conservancy (KN, open grassland) and Okongo area (OK, dense woodland) as determined from stable carbon isotope analysis of dung samples (*n* = number of samples). Percentage browse consumption was determined using a Bayesian stable-isotope mixing model using C_3 (-27.5 ± 0.3‰) and C_4 (-14.1 ± 0.2‰) plant end-members.

Site, season (*n*)	Cattle δ^{13}C (‰± SD),	Cattle % browse (95% Cr.I.)
KN wet (8)	-13.6 ± 0.1	11 (8–15)
KN early dry (8)	-14.7 ± 0.6	19 (14–23)
KN late dry (10)	-16.6 ± 1.8	33 (23–43)
OK wet (8)	-23.8 ± 2.2	84 (70–96)
OK early dry (9)	-23.8 ± 1.9	84 (73–94)
OK late dry (10)	-19.7 ± 1.2	55 (48–61)

trade-off between the searching cost for preferred plants and the nutritional and energetic gains realised. Our results support this notion, as the dietary intake of the cattle in the two areas clearly reflects the forage conditions to which they are exposed despite their characteristic grazer/'cattle-type' digestive morphophysiology [7]. Our results suggest that the cattle foraging on the open grass plains of KN graze extensively during both the wet and early dry season (>80%), while increasing their browse intake to 33% during the late dry season. This is possibly to compensate for the reduction in grass quality at the end of the dry season, a phenomenon that has been recorded further south in Namibia [25]. In contrast, the fodder intake of the cattle in the woodland-dominated OK area consisted predominantly of browse (84%) in both the wet and early dry season. It was only during the late dry season that the C_4 grass intake increased (from 16 to 45%), probably when the cattle were provided access to C_4 crop residues (pearl millet and maize) on subsistence farming plots [17].

Herbivores are considered to be grazers who can survive under captive conditions on a diet of good quality browse, such as lucerne and alfalfa [4]. In addition, grazing ruminants should have fewer problems eating browsed material than browsers eating grasses based on their dental and forestomach characteristics [7,26]. Cattle have also being recorded browsing up to 47% when green grass was unavailable in the Blue Mountains of Oregon, USA [27]. However, the extent of browsing suggested here for a conventional grazer (≈84%), persisting over multiple seasons in a (semi)natural setting, is certainly unusual. Especially as this is counterintuitive to the predictions of Codron and Clauss [28], which state that grazing ruminants with strongly developed rumen stratification – typical of cattle – should be limited in the amount of browse they can tolerate due to the deleterious effects of the secondary plant compounds associated with it.

Feeding to this extent on a supposed less preferred, but more abundant plant type should have a significant impact on body condition and ultimately long-term survival and reproductive success, which were not quantified in this study. However, no obvious differences in body condition were visibly apparent (C. van der Waal, personal observation). In order to subsist, one would expect the browsing cattle to have higher dietary intake to compensate for the lack of digestible fibre, as well as some or other anatomical/physiological plasticity that enable increased salivary excretion and liver size to deal with the allelochemicals of the browsed material [4,28]. This should be investigated further, not only to better understand the diet of the Sanga cattle of North Central Namibia, but also to improve our understanding of the dietary type flexibility of ruminant species as a whole in the face of global change [12]. If conventional grazers are able to adjust to a diet of substantially more browse, it will be of great benefit to their long-term survival in the light of the increase in bush encroachment and consequent reduction in grass production [10]. However, the exact consequences of such a diet change on reproductive fitness and survival needs to be established not only within a pastoralist setting, but also in a more natural environment with competing browsing species and predators.

Like many ecological concepts, the strict dichotomous classification of groups or individuals as browsers or grazers represents two extremes on a continuum. An individual or population's place on this continuum will be a function of morphology, behaviour and forage availability, and as we have demonstrated, will fluctuate over time with changes in nutritional demands and food availability. This flexibility is important in understanding the evolution of Africa's diverse ruminant herbivore community and suggests that dietary segregation is less apparent than often perceived.

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Supplemental material

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References

[1] Hofmann RR, Stewart DRM. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia. 1972;36:226–240.

[2] Jarman PJ. The social organization of antelope in relation to their ecology. Behaviour. 1974;48:215–267.

[3] Clauss M, Kaiser TM, Hummel J. The morphophysiological adaptations of browsing and grazing mammals. In: Gordon IJ, Prins HHT, editors. The ecology of browsing and grazing. Berlin: Springer; 2008. p. 47–88.

[4] Duncan AJ, Poppi DP. Nutritional ecology of grazing and browsing ruminants. In: Gordon IJ, Prins HHT, editors. The ecology of browsing and grazing. Berlin: Springer; 2008. p. 89–116.

[5] Codron D, Codron J, Lee Thorp JA, Sponheimer M, de Ruiter D, Sealy J, Grant R, Fourie N. Diets of savanna ungulates from stable carbon isotope composition of faeces. J Zool. (London) 2007;273:21–29.

[6] Codron D, Codron J. Reliability of δ^{13}C and δ^{15}N in faeces for reconstructing savanna herbivore diet. Mamm Biol. 2008;74:36–48.

[7] Clauss M, Hume ID, Hummel J. Evolutionary adaptations of ruminants and their potential relevance for modern production systems. Animal. 2010;4:979–992.

[8] Sponheimer M, Lee Thorp JA, de Ruiter D, Smith JM, Van der Merwe NJ, Reed K, Grant CC, Ayliffe LK, Robinson TF, Heidelberger C, Marcus W. Diets of southern African Bovidae: stable isotope evidence. J Mammal. 2003;84:471–479.

[9] Cerling TE, Harris JM, Passey BH. Diets of East African Bovidae based on stable isotope analysis. J Mammal. 2003;84:456–470.

[10] Wigley BJ, Bond WJ, Hoffman MT. Bush encroachment under three contrasting land-use practices in a mesic South African savanna. Afr J Ecol. 2009;47:62–70.

[11] Codron D, Brink JS, Rossouw L, Clauss M. The evolution of ecological specialization in southern African ungulates: competition or physical environmental turnover? Oikos. 2008;117:344–353.

[12] Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Ferreira de Siqueira M, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgeley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE. Extinction risk from climate change. Nature. 2004;427:145–148.

[13] Hofmann RR. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia. 1989;78:443–457.

[14] Forbes JM. Voluntary food intake and diet selection in farm animals. Wallingford: CAB International; 1995.

[15] Clauss M, Hofmann RR, Fickel J, Streich WJ, Hummel J. The intraruminal papillation gradient in wild ruminants of different feeding types: implications for rumen physiology. J Morphol. 2009;270:929–942.

[16] Erkillä A. Living on the land: change in forest cover in north-central Namibia, 1943–1996. Joensuu, Finland: Faculty of Forestry, University of Joensuu; 2001.

[17] Verlinden A, Kruger AS. Changing grazing systems in central north Namibia. Land Degrad Dev. 2007;18:179–197.

[18] Newsham A, Thomas DSG. Knowing, farming and climate change adaptation in north-central Namibia. Glob Environ Change. 2011;21:761–770.

[19] Mendelsohn J, El-Obeid S, Roberts C. A profile of north central Namibia. Windhoek: Gamsberg Macmillan; 2000.

[20] Sponheimer M, Robinson T, Ayliffe L, Passey BH, Roeder BL, Shipley L, Lopez E, Cerling TE, Dearing D, Ehleringer JR. An experimental study of carbon-isotope fractionation between diet, hair, and faeces of mammalian herbivores. Can J Zool. 2003;71:871–876.

[21] Codron D, Codron J, Sponheimer M, Lee Thorp JA, Robinson T, Grant CC, de Ruiter D. Assessing diet in savanna herbivores using stable carbon isotopes ratios of faeces. Koedoe. 2005;48:115–124.

[22] Parnell AC, Inger R, Bearhop S, Jackson AL. Source partitioning using stable isotopes: coping with too much variation. PLoS ONE. 2010;5:e9672.

[23] R Development Core Team. R: a language and environment for statistical computing. Version 2.15.2 [computer program]. Vienna: R Foundation for Statistical Computing; 2012.

[24] Sprent JA, McArthur C. Diet and diet selection of two species in the macropodid browser–grazer continuum: do they eat what they ‘should’? Aust J Zool. 2002;50:183–192.

[25] Rothauge A, Smit GN, Abate AL. The diet selected by free-ranging beef cattle and its effect on the condition of a semi-arid savanna in Namibia. Agricola. 2007;17:16–27.

[26] Clauss M, Lechner-Doll M, Streich WJ. Ruminant diversification as an adaptation to the physicomechanical characteristics of forage: a re-evaluation of an old debate and a new hypothesis. Oikos. 2003;102:253–262.

[27] Holechek JL, Vavra M, Skovlin J, Krueger WC. Cattle diets in the Blue Mountains of Oregon. II. Forests. J Range Manage. 1982;35: 239–242.

[28] Codron D, Clauss M. Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species. Can J Zool. 2010;88:1129–1138.