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ORIGINAL PAPER

Trophic ecology of two savanna grazers, blue wildebeest *Connochaetes taurinus* and black wildebeest *Connochaetes gnou*

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Abstract The feeding niches and trophic ecology of two South African grazers, blue wildebeest *Connochaetes taurinus* and black wildebeest *Connochaetes gnou*, are compared using stable carbon and nitrogen isotope data from feces and tooth dentine collagen. As sympatric, closely related taxa predicted to occupy similar trophic positions, the blue and black wildebeest provide a good model for studying the mechanisms of coexistence and macroevolution in mammals. Data from feces collected from a single reserve in the Free State Province reveal different trophic behaviors between two herds of blue wildebeest and between both compared with a single herd of black wildebeest. These data suggest that sympatric coexistence of blue and black wildebeest is facilitated by differential niche occupation at family group or herd levels, rather than between species. However, such separation does not occur over longer time scales: results from dentine collagen support the hypothesis that the two species are indistinct in terms of trophic behavior, although blue wildebeest show more feeding flexibility, probably because of their wider habitat tolerance range. Similarities in premaxillary width of males and females of both species also suggest that both species are adapted to similar feeding styles. Thus, it is unlikely that changes in trophic behavior provided the trigger for divergence of the black from the blue wildebeest lineage in the Middle Pleistocene. We argue that the case of these two species represents an example of speciation that was not driven by resource competition, as is often assumed for many turnover events in mammalian evolution. We briefly discuss a previous suggestion that links black wildebeest evolution to their more territorial breeding behavior associated with Middle-to-Late Pleistocene landscape changes in southern Africa.

Keywords Carbon isotopes · Dentine · Diet · Feces · Nitrogen isotopes

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Introduction

Wildebeest *Connochaetes* spp. (Bovidae: Alcelaphini) are among the most prominent grazers in the African savanna biome. Two species co-occur in southern Africa, the blue wildebeest *Connochaetes taurinus* and black wildebeest *Connochaetes gnou*. Present-day distribution of blue wildebeest includes two areas, one extending from East Africa southwards into northeastern Mozambique and the second from Zambia southwards through northwestern Namibia, Botswana, Zimbabwe, and the northern and northeastern parts of South Africa (Skinner and Smithers 1990). This distribution is congruent with the virtually Pan-African occurrence of early *C. taurinus*, which is known from several Early to Middle Pleistocene localities in North, East, and southern Africa (Gentry 1978; Geraads 1981; Vrba 1995, 1997). Black wildebeest are endemic to South Africa, restricted today to the open grasslands of the central interior, primarily in the Free State and Northern Cape Provinces (Skead 1980; Skinner and Smithers 1990). South African endemism of black wildebeest appears to have persisted since their divergence from *C. taurinus* in the Middle–Late Pleistocene, the earliest evidence for this evolutionary split

being known from deposits at Cornelia in the northeastern Free State (~0.8 Ma; Brink 1993, 2004a; Vrba 1995).

The distribution patterns of the two species seem to follow disparity in their habitat tolerance ranges. While blue wildebeest occupy a wide variety of savanna habitat types, including woodland, open-grassland, and semi-desert environments, black wildebeest are almost entirely confined to open grassland habitats (Hirst 1975; Skead 1980; Skinner and Smithers 1990). However, these differences in habitat requirements do not appear to reflect differences in trophic behavior. Both species are grazers that prefer short, green grass, and both are known to supplement their diets with browse (trees, shrubs, forbs) when grasses are limiting (Van Zyl 1965; Skinner and Smithers 1990; and see data in Gagnon and Chew 2000). Furthermore, the wide habitat tolerance of blue wildebeest extends the distribution range of this species so that it occasionally overlaps in occurrence with black wildebeest, although this was likely more common in the past than post-1900 (Skead 1980). Indeed, even though in confined areas the two often interbreed and produce viable offspring (Fabricius et al. 1988), there are several provincial and private game farms in the Free State Province in which both species still occur (Vrahimis, personal communication; personal observation). Further back in time, the South African Pleistocene fossil record provides substantial evidence for overlap in distribution ranges of the two species (Brink et al. 1999; Plug and Badenhorst 2001).

Sympatric occurrence of blue and black wildebeest, especially in the past, raises the question of how two closely related species coexist. That they appear to occupy similar trophic positions suggests alternative modes of differentiation, e.g., behavior, facilitated coexistence, and evolutionary divergence (Brink 2004b). However, the concept of trophic redundancy may be misleading because responses of two ecologically similar species to environmental heterogeneity through space and time may be sufficiently different to effect overall shifts in trophic position (e.g., Brown et al. 2001). Indeed, there is some evidence to suggest that black wildebeest have a greater propensity to switch to browse-based foods than do blue wildebeest (Van Zyl 1965; Skinner and Smithers 1990; Estes 1991; Gagnon and Chew 2000).

One method for addressing spatiotemporal variations in diet is stable isotope ecology (see Post 2002). Upscaling ecological processes across individual, population, and community levels can be achieved because isotopic data from different materials provide similar information about diet over different time scales. For example, stable isotope data archived in mammalian bone collagen provides an integrated near-lifetime dietary average (because bone is consistently remodeled throughout an animal's life), tooth dentine records information only for the period of accretion (several months to years), and feces offer short-term insight over several days (Tieszen et al. 1979, 1983; Sponheimer et al. 2003a; Codron et al. 2005a,b). Stable isotope proxies for diet are based mainly on analysis of $^{13}C/^{12}C$ ratios in biological materials, which in African savanna herbivores faithfully reflect proportions of C_3 (trees, shrubs, forbs) to C_4 (grass) biomass intake (Vogel 1978; Tieszen et al. 1979; Lee-Thorp and van der Merwe 1987; Cerling and Harris 1999). $^{15}N/^{14}N$ ratios provide a proxy for trophic position (Sealy et al. 1987; Post 2002). However, recent studies have shown variation in mammalian ^{15}N abundances in response to changes in dietary protein by an order of magnitude exceeding that reported for trophic level shifts (Sponheimer et al. 2003b; Robbins et al. 2005).

The aim of this paper is to test the hypothesis that blue and black wildebeest, even sympatric populations, occupy a single trophic niche (Brink 2004b). Dietary reconstructions are based on $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in feces and tooth dentine collagen of wildebeest inhabiting South African grassland environments. These data are combined with fecal %N as a proxy for diet quality (Holecheck et al. 1982), and premaxillary width as an indicator of feeding selectivity (Bell 1971; Owen-Smith 1982; Solounias and Moelleken 1993), to examine patterns of trophic variation within and between the two wildebeest species.

Materials and methods

The bulk of this study focuses on animals from the open grassland habitats of the Free State (FS) Province of South Africa. The FS is situated on the high plateau in the central interior of South Africa, bordered to the north by the Vaal River and to the south by the Orange River. The entire Province forms part of the Grassland Biome of South Africa (Rutherford and Westfall 1994). Mean annual rainfall varies between ca. 400 and 600 mm, generally decreasing from west to east, and falls mostly during the austral summer (between October and March). Vegetation patterns correspond with the general pattern of grass distribution in southern Africa, i.e., "sourveld," regions of less year-round grass productivity and palatability to ungulates occurring in higher rainfall areas, and "sweet-veld", habitats of higher grass productivity and palatability found in areas of lower rainfall and less soil drainage (Rutherford and Westfall 1994). Some specimens used in this study represent animals from elsewhere in the Grassland Biome, including the more arid Northern Cape Kalahari to the west of the FS (mean annual rainfall 200 to 400 mm), and to the east the Hluhluwe-Umfolozi region of northern Kwazulu-Natal (KZN; 800 to 1,000 mm).

Feces of blue and black wildebeest were collected in May 2006 from the Gariep Nature Reserve (GNR), a small (~7,000 ha) provincial reserve in the southern FS bordering

the Gariep Dam along the Orange River and extending into parts of the Northern Cape. We chose to sample feces during this dry season month to represent limiting periods in which trophic separation among sympatric herbivores can be expected to be more pronounced. We identified two blue wildebeest herds and one black with the assistance of local rangers and collected feces from each herd within a few minutes after deposition. Each dung pile sampled was taken to represent a separate individual from within a herd, including 20 specimens for each species.

For the longer-term component, dentine collagen was sampled from molar teeth of 23 specimens (10 black and 13 blue wildebeest) at the Florisbad Research Station (National Museum, Bloemfontein). Individuals were selected to represent areas across the FS (or in similar grassland habitats, i.e., Northern Cape), which included animals that lived during recent years (1990 to present) and in the earlier part of the twentieth century (1930 to 1934). Blue wildebeest predating 1950 were only available from KZN. Dentine powder was removed using a diamond-tipped microdrill with a 1-mm diameter burr. Samples were only taken from M2 or M3 of selected individuals, i.e., teeth formed at post-weaning ages.

Feces were oven-dried at 60°C for 24 h and mill-ground into a homogenous powder through a 1-mm sieve. Dentine powder was exposed to 0.2 M HCl to isolate the organic protein (collagen) phase of skeletal material. Treated samples were individually combusted in an automated Elemental Analyzer (Carlo Erba Instruments, Milan, Italy), and the resultant CO_2 and N_2 gases were introduced to a Finnigan MAT 252 or DELTA XP Mass Spectrometer (Finnigan, Bremen, Germany) via a continuous flow-through inlet system. $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios are expressed in delta notation (δ) in parts per mil (‰) relative to the Vienna PeeDee Belemnite (VPDB) and atmospheric N_2 standards, respectively. Standard deviations of repeated measurements of laboratory standards were less than 0.1‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$. This procedure also provided the elemental composition (%C, %N) of each sample. Dentine collagen samples showed C/N ratios well within the normal range expected for biological proteins (3.0 to 3.6, Table 1; see De Niro 1985); thus, isotope data from these samples are considered reliable. Two specimens show slightly higher C/N ratios (NMB 56=3.7 and NMB 9358=3.8), but are retained in the data set because these values are only marginally higher than expected, and because $\delta^{13}C$ and $\delta^{15}N$ values do not deviate appreciably from the range of values recorded for other specimens.

The width of the premaxilla in ungulate herbivores provides another indicator of trophic behavior, reflecting the degree of feeding selectivity to which a species is adapted (Bell 1971; Owen-Smith 1982; Gordon and Illius 1988; Janis and Ehrhardt 1988; Solounias and Moelleken 1993). Animals with wider muzzles are normally less selective and rely more on bulk feeding. Premaxillary width also mirrors the width of the incisor arcade, another dimension of oral morphology predicted to vary with the degree of diet selectivity. Premaxillary width of selected male (11 blue and 10 black wildebeest) and female (9 blue and 10 black wildebeest) specimens from the Florisbad collections was measured as the distance between the widest points on either side of the enlarged portion of the muzzle to the nearest millimeter. We consider this approach sufficient for studying differential feeding selectivity from the functional (biting) anterior portion of the mouth between two morphologically similar species.

One-way ANOVA is used to test for significant differences between stable isotope data from the feces of the two species and for differences in fecal %N. Sample sizes for the two blue wildebeest herds from GNR are relatively small (n=9 and 10, respectively); thus, we use the nonparametric Mann–Whitney U test to examine differences between herds. Differences in the isotope composition of blue and black wildebeest feces are also tested visually using 95% confidence ellipse bands around bivariate scatter plots to separate groups of data. Similar procedures are used to explore data from dentine collagen, although in this instance comparisons are made based on both raw data and data adjusted for environmental isotope variability. Specifically, these adjustments include subtracting 1.5‰ from $\delta^{13}C$ of specimens predating 1950 to correct for post-1950 ^{13}C-depletion of atmospheric CO_2 and resultant changes in plant isotope composition (Marino and McElroy 1991), and correcting $\delta^{15}N$ of specimens from KZN to estimate FS equivalents. Available plant data from these two provinces are few, yet one may predict higher $\delta^{15}N$ among FS than KZN plants due to the lower rainfall regime of the former (Heaton 1987; Swap et al. 2004). Indeed, limited data available comparing FS and KZN plants suggests that C_4 vegetation is on average 1.3‰ higher in FS (see data in Swap et al. 2004 for Drakensberg and Piet Retief, KZN, and Vryburg, Vastrap, and Kuiepan, FS). Hence, 1.3‰ was added to $\delta^{15}N$ of KZN blue wildebeest dentine collagen. Plant $\delta^{13}C$ may also vary across space, especially along a steep rainfall gradient (Stewart et al. 1995; Swap et al. 2004), but these differences, especially among C_4 vegetation, are unlikely to be substantial within southern African savannas (Codron et al. 2005c).

Results

Feces

Fecal $\delta^{13}C$ of blue and black wildebeest from GNR reflect the C_4-dominated diets of savanna grazers (mean=−15.3‰±

Table 1 Stable carbon and nitrogen isotope data for dentine collagen of specimens of *C. gnou* and *C. taurinus* from collections at the Florisbad Research Station

Sample ID	Date	Region	$\delta^{13}C_{VPDB}$ (‰)	$\delta^{15}N_{Air}$ (‰)	C/N
C. gnou					
NMB 80	1930	Free State	–8.0	9.3	3.2
NMB 81	1934	Free State	–7.9	11.8	3.2
NMB 92	1934	Free State	–7.7	9.0	3.1
NMB 93	1934	Free State	–11.2	8.2	3.5
NMB 94	1934	Free State	–8.2	10.2	3.1
NMB 96	1934	Free State	–7.7	9.3	3.0
NMB 8742	1993	Free State	–9.0	9.9	3.4
NMB 9358	1998	Free State	–11.7	10.4	3.8
NMB 12392	2004	Free State	–9.8	10.7	3.2
NMB 12406	2004	Free State	–10.0	11.6	3.2
C. taurinus					
NMB 49	1930	Kwazulu-Natal	–9.1	5.4	3.1
NMB 50	1930	Kwazulu-Natal	–7.6	8.8	3.3
NMB 51	1930	Kwazulu-Natal	–5.5	7.3	3.0
NMB 52	1930	Kwazulu-Natal	–7.8	7.6	3.3
NMB 56	1930	Kwazulu-Natal	–11.3	7.2	3.7
NMB 60	1930	Kwazulu-Natal	–6.3	8.1	3.1
NMB 9347	1998	Free State	–10.4	9.0	3.3
NMB 9353	1998	Free State	–8.9	10.6	3.2
NMB 9355	1998	Free State	–8.3	12.5	3.3
NMB 9359	1998	Free State	–8.8	10.1	3.0
NMB 12172	2001	Northern Cape	–8.8	9.9	3.2
NMB 12205	2001	Northern Cape	–11.1	10.9	3.6
NMB 12391	2004	Free State	–10.4	8.2	3.4

1.0 SD, n=19 and −14.8‰±0.2 SD, n=19, respectively; see data in Tieszen et al. 1979; Codron et al. 2005a,b). The difference in mean fecal $\delta^{13}C$ between the two species is significant ($F_{1,\ 36}$=4.704, P<0.05) but too small to be considered a true reflection of dietary differences (<1‰). Carbon isotope differences between the two blue wildebeest herds are, however, large enough to suggest a real dietary difference, in that herd 1 has significantly lower values (−16.2‰±0.5 SD, n=9) than herd 2 (−14.5‰±0.4 SD, n=10; P<0.0001) and black wildebeest (P<0.0001; Fig. 1). It is also notable that dietary variation, as reflected by fecal $\delta^{13}C$, is greater within both blue wildebeest herds than among black wildebeest. Fecal $\delta^{13}C$ within herd 1 varies by 1.6‰ across individuals (−17.0 to −15.4‰, n=9), in herd 2 by 1.3‰ (−15.0 to −13.7‰, n=10), and in black wildebeest by only 0.7‰ (−15.2 to −14.5‰, n=19). Mean fecal $\delta^{15}N$ of blue wildebeest (4.5‰±1.1 SD) is lower than that of black wildebeest (5.3‰±0.4 SD, $F_{1,\ 36}$=9.334, P<0.01; Fig. 1). However, this difference only exists between herd 2 (3.7‰± 0.8) and black wildebeest, whereas herd 1 has similar $\delta^{15}N$ (5.4‰±0.4) compared with the latter species (P=0.64).

Mean fecal %N of blue and black wildebeest is almost identical (1.4%±0.4 SD for blue, 1.3%±0.2 SD for black; $F_{1,\ 36}$=1.229, P=0.28). In addition, no difference exists in fecal %N between the two blue wildebeest herds (P=0.82). Fecal %N is, however, positively correlated with fecal $\delta^{15}N$ in both species (r^2=0.25, P<0.05 in both cases), indicating that herbivore $\delta^{15}N$ increases linearly with increased dietary crude protein levels (Fig. 2). This correlation agrees with recent predictions that higher protein diets, more specifically diets comprising higher quality proteins (i.e., a higher proportion of protein consumed is retained for metabolism), result in higher mammal tissue $\delta^{15}N$ (Sponheimer et al. 2003b; Robbins et al. 2005).

Dentine collagen

Before considering the data from dentine collagen, it is important to note the differences in scale between collagen and fecal $\delta^{13}C$ because of the different isotope discriminations that exist between these two materials, i.e., relative to diet, feces are ~0.9‰ depleted in ^{13}C, while collagen is ~5.0‰ enriched (Ambrose and Norr 1993; Sponheimer et al. 2003b; Codron et al. 2005a). Thus, a diet with a $\delta^{13}C$ of, say, 14.0‰ would yield a $\delta^{13}C$ value close to −9.0‰ for dentine collagen and a fecal $\delta^{13}C$ value of −14.9‰.

As with feces, dentine collagen $\delta^{13}C$ of wildebeest are consistent with C_4-dominated diets (mean=−8.8‰±1.7 SD, n=13 for blue and −9.1‰±1.5 SD, n=10 for black; Table 1; see data in Vogel 1978 and Cerling and Harris 1999). No difference exists between the species (P=0.80), but both show distinct temporal changes. Blue wildebeest $\delta^{13}C$

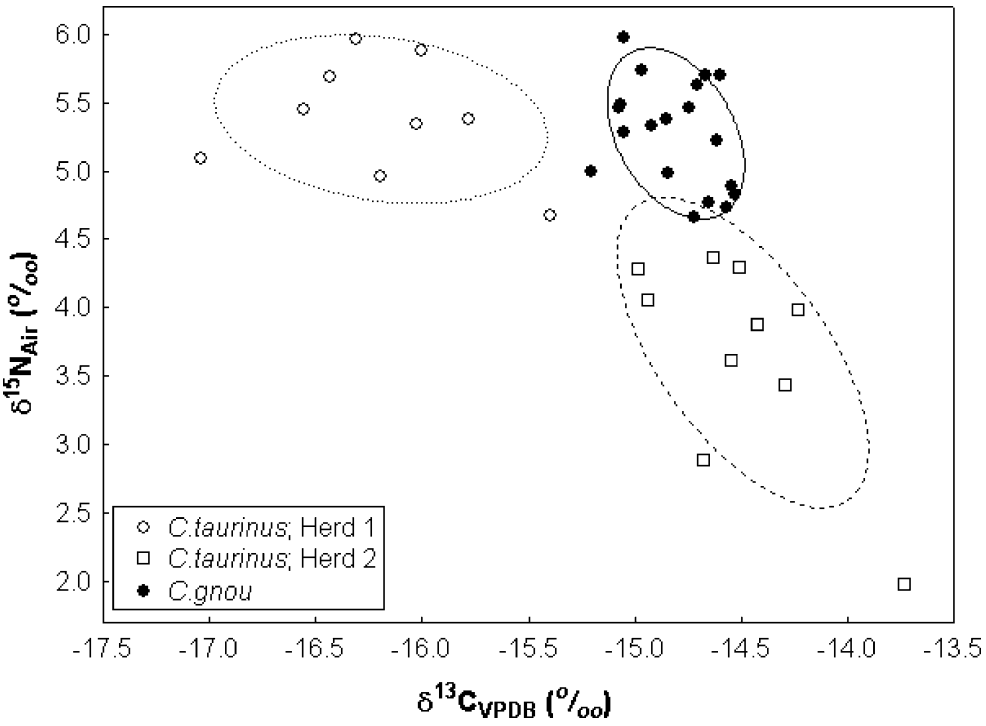

Fig. 1 Stable carbon and nitrogen isotope ratios in feces from two herds of *C. taurinus* and one of *C. gnou* on the Gariep Nature Reserve. The *ellipses* show cluster separation with a coefficient of 0.95

is on average 1.6‰ lower in dentine of modern specimens compared with specimens predating 1950, and a similar difference (1.7‰) exists among black wildebeest (Table 1). These data closely reflect the ~1.5‰ decrease in atmospheric δ^{13}C due to fossil fuel burning in the latter half of the 20th century (Marino and McElroy 1991).

Dentine collagen δ^{15} N of blue is lower than that of black wildebeest (mean=8.9‰±1.9 SD, n=13 and 10.0‰±1.1 SD, n=10, respectively; P<0.05; Table 1). This difference, however, only persists for blue wildebeest specimens from KZN that have substantially lower δ^{15}N (mean=7.4‰± 1.1 SD, n=6) than that of specimens of both species from the FS (P<0.01). The difference in δ^{15}N between pre-1950 blue wildebeest (all from KZN) and post-1950 specimens (FS) is 2.8‰, whereas this difference is much smaller in black wildebeest from both time periods (1.0‰; all specimens from

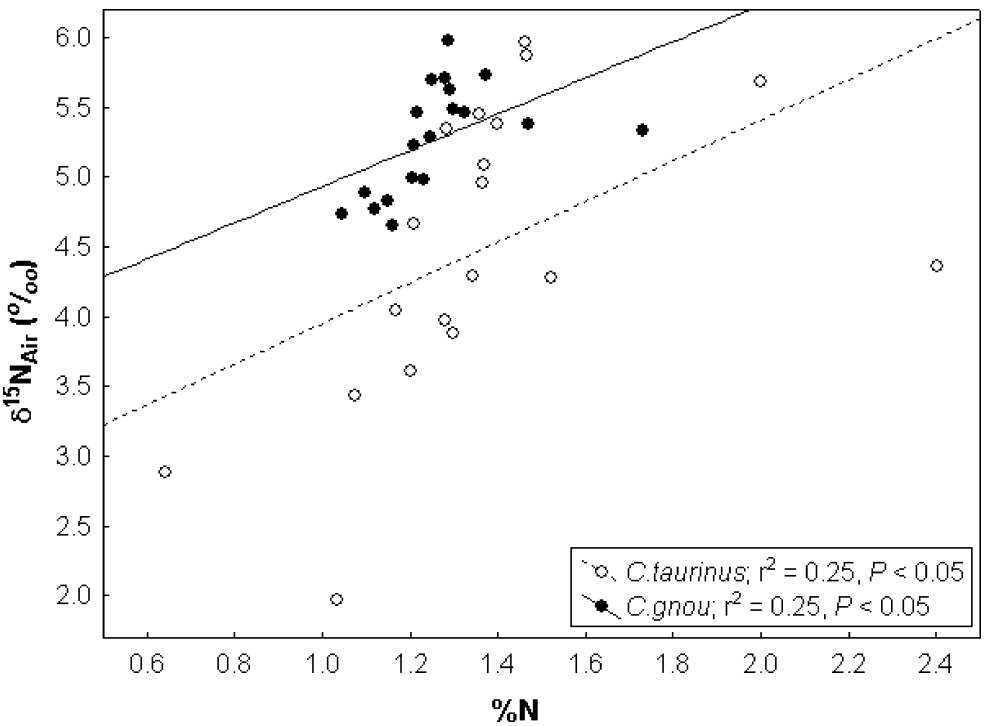

Fig. 2 Linear correlation between δ^{15}N and %N of dry matter in feces of *C. taurinus* and *C. gnou* from the Gariep Nature Reserve

FS). The lower $\delta^{15}N$ of blue wildebeest from KZN, therefore, likely reflects the consumption of relatively ^{15}N-depleted plants from the higher rainfall region of the KZN (see Heaton et al. 1986; Swap et al. 2004).

After adjustments of dentine collagen data to control for expected effects of twentieth century changes in the carbon isotope composition of atmospheric CO_2 and spatial variation in plant $\delta^{15}N$ (see "Material and methods"), no differences could be found in $\delta^{13}C$ (P=0.24) or $\delta^{15}N$ (P=0.32) between blue and black wildebeest (Fig. 3). However, despite considerable interspecific overlap, the data for blue wildebeest extend across a wider range (−12.8 to −7.0‰) than those of black wildebeest (−12.7 to −9.0‰), as is the case for feces.

Premaxillary width

Measurement of the premaxillary width of 20 individuals of blue and black wildebeest, respectively, revealed no differences between the two species (mean=70.8±53 and 69.9± 4.7 mm, respectively; Mann–Whitney P=0.60; Fig. 4). Males and females of both species differed significantly (P<0.01 in both species), but even this did not result in differences between the species (P=0.34 for males, 0.60 for females). Indeed, the ranges observed for males (68.2 to 77.4 mm for *C. taurinus* and 67.5 to 77.5 mm for *C. gnou*) and females (62.5 to 74.0 mm for *C. taurinus* and 63.3 to 73.6 mm for *C. gnou*) were virtually identical. Hence, the two species do not appear to be adapted to different trophic behaviors in terms of degrees of diet selectivity.

Discussion

Results of this study confirm that blue and black wildebeest are predominantly grazers, but both portray an ability to consume some proportion of C_3 foods. Field studies have reported that their diets comprise between ~10 and 20% dicots (or even more in some cases; Van Zyl 1965; Gagnon and Chew 2000), which is more or less congruent with our data. Cerling et al. (2003) reported carbon isotope data for bovids from East Africa, which demonstrate blue wildebeest to be consistent, near-pure grazers. By contrast, carbon isotope data for southern African bovids imply diets of ~10% or more C_3 foods in the diet of blue wildebeest from the subcontinent (Sponheimer et al. 2003c; Codron et al. 2005b). Given the apparent disparity in diet between East and southern African blue wildebeest populations, dietary variation as recorded by carbon isotope data in the current study is not altogether surprising.

Data from field studies suggest higher browse intake by black compared with blue wildebeest (e.g., Van Zyl 1965; Estes 1991; Gagnon and Chew 2000). Evidence from feces demonstrates that there are indeed dietary differences, but that these exist between herds rather than species. For example, animals belonging to the blue wildebeest herd 1 seemed to have supplemented their predominantly C_4-based

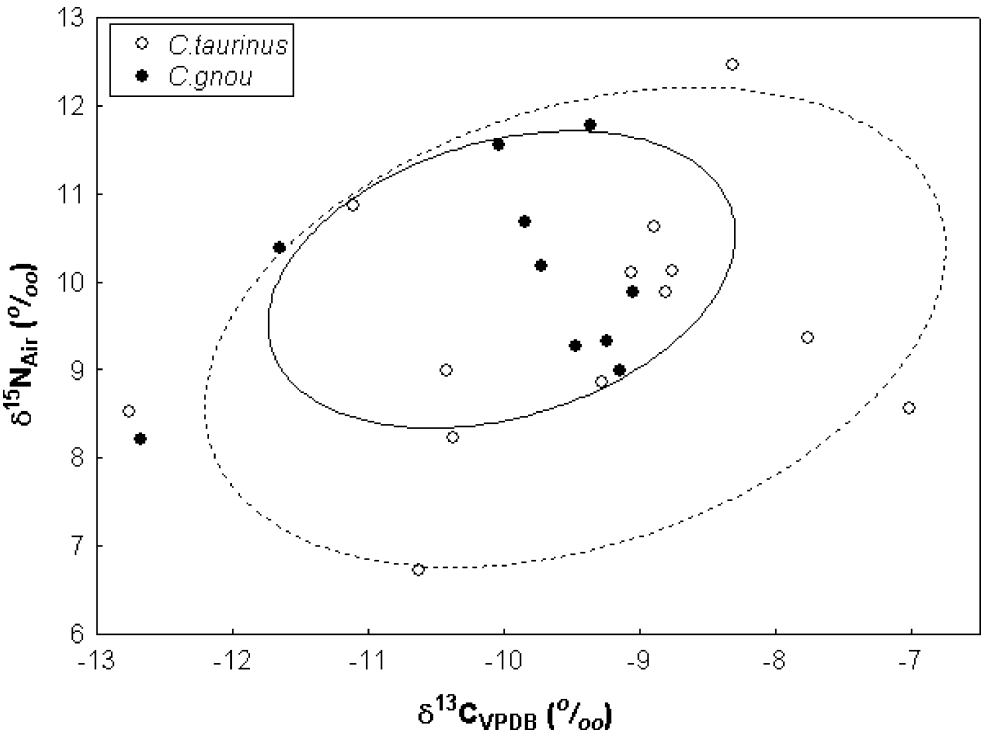

Fig. 3 Stable carbon and nitrogen isotope ratios in dentine collagen of *C. taurinus* and *C. gnou*. The data are adjusted for 20th century changes in $\delta^{13}C$ of atmospheric CO_2 (1.5‰ subtracted from $\delta^{13}C$ of specimens predating 1950) and spatial differences in $\delta^{15}N$ of vegetation (1.3‰ added to $\delta^{15}N$ of specimens from Kwazulu-Natal; see C_4 plant data in Swap et al. 2004). The *ellipses* show clustering with a coefficient of 0.95 (*solid C. taurinus*, *dotted line C. gnou*)

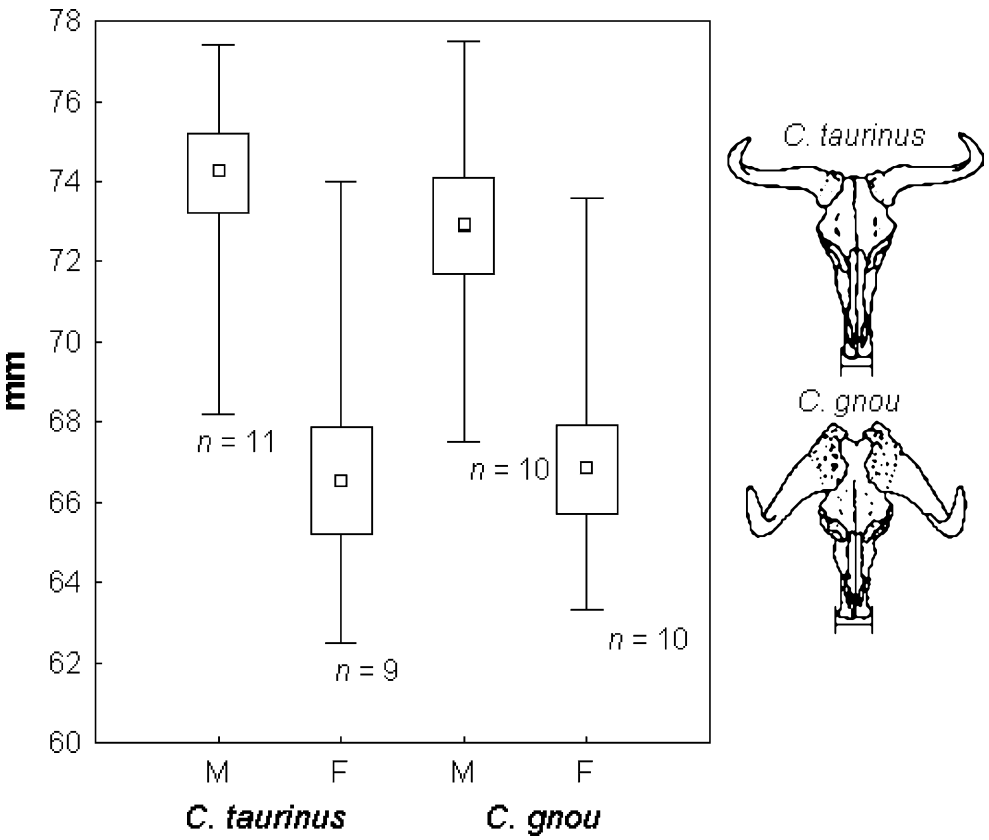

Fig. 4 Width of the premaxilla of male (*M*) and female (*F*) *C. gnou* and *C. taurinus* specimens from collections at the Florisbad Research Station. *Symbols* in the graph depict the means, *boxes* ±1 SE, and *whiskers* minimum–maximum ranges

diet with some C_3 foods, such as tree foliage and/or forbs and other dicots of the shrub layer. Alternatively, the lower fecal $\delta^{13}C$ of herd 1 may indicate that they consumed a relatively greater proportion of C_4 grasses that follow the NAD-ME and/or PCK photosynthetic sub-pathways, which are ^{13}C-depleted relative to NADP-ME grass subtypes (Cerling and Harris 1999). However, while carbon isotope differences between these C_4 subtypes across environments are between ~1.0 and 1.5‰, the difference is much smaller (~0.5‰) within the Kruger National Park in the northeast of South Africa (Codron et al. 2005c). Assuming similar patterns across the South African savanna, i.e., between Kruger Park and the current study areas, differential feeding on NAD/PCK vs NADP grasses, therefore, cannot fully explain differences in fecal $\delta^{13}C$ of herd 1 compared with herd 2 (1.7‰) and black wildebeest (1.4‰). Further data for local Free State vegetation are required to investigate the potential influences of different grass subtypes on wildebeest isotope ecology more fully. It is also possible that data for herd 1 reflect consumption of C_3 monocots such as reeds (*Phragmites* spp.) and sedges (Cyperaceae), which do contribute to wildebeest diets (Owen-Smith, personal communication) and of which roughly 40 to 50% are C_3 in the South African central interior (Stock et al. 2004).

Differences in fecal $\delta^{15}N$ between blue wildebeest herd 2 and black wildebeest might suggest differences in trophic position and/or food choice, but there was no difference between herd 1 and the latter species. It may be that these patterns reflect different dietary compositions of animals from the three herds. The lower fecal $\delta^{15}N$ of herd 2 compared with herd 1 ($P<0.0001$) is congruent with possibilities inferred from $\delta^{13}C$ data, in that NADP-ME grasses have lower $\delta^{15}N$ compared with NAD and PCK grasses, and because reeds and sedges are ^{15}N-enriched relative to other savanna plant types (Codron et al. 2005c). Whatever the case, it is clear that any dietary differences between species were even less pronounced than between the two blue wildebeest herds; thus, one cannot predict trophic separation based on these data.

The lower $\delta^{15}N$ of blue wildebeest dentine collagen might reflect differences in trophic position of the two species, paralleling lower $\delta^{15}N$ in the feces of this species. However, in the case of feces, the difference between species was not consistent for both herds of blue wildebeest. Thus, it is likely that a simple interspecies comparison of $\delta^{15}N$ in dentine collagen may be misleading and that more subtle differences may exist at other scales. In other words, patterns evinced in dentine are likely influenced by spatiotemporal separation between individuals sampled and the effects of environmentally induced variations on animal and plant $\delta^{15}N$, and indeed $\delta^{13}C$ (e.g., Heaton et al. 1986; Tieszen 1991; Codron et al. 2005c). Data for dentine collagen for both species parallel expectations for the effects of twentieth century changes in the carbon isotope

composition of atmospheric CO_2, and for spatial variations in plant $\delta^{15}N$. After controlling for these effects, dentine collagen data for both species could not be separated, suggesting no long-term trophic differences between the two species. Nevertheless, blue wildebeest do appear to have the more variable feeding behavior. Carbon isotope data for blue wildebeest show quite a substantial variation across individuals, herds, and/or subpopulations (4.3‰ in feces, 5.8‰ in dentine collagen), whereas black wildebeest show variations of only 0.7‰ in feces and 3.7‰ in dentine collagen. These data likely reflect the broader habitat tolerance range of the more widely distributed blue wildebeest (Skead 1980; Skinner and Smithers 1990).

The apparent lack of trophic separation has significant implications for understanding the evolution of wildebeest and as a model for understanding processes of speciation among mammals in general (Brink 2004b). Evolutionary biologists continue to debate whether climate-induced habitat change or biotic interactions (primarily competition) act as ultimate drivers of speciation and extinction (Vrba 1992, 1995; Prothero 1999; Day and Young 2004; Barnosky 2005). Trophic differentiation is an important mechanism allowing sympatric species to avoid competition; thus, one might have expected a trophic shift to have accompanied divergence of black from blue wildebeest. While stable isotope evidence from feces do reflect dietary and trophic differences among sympatric populations on GNR, the difference between the two blue wildebeest herds is in fact greater than the difference between either compared with black wildebeest. The implication is that sympatric wildebeest may avoid competition for resources through variable trophic behaviors of different family groups and/or herds. In this light, it can be argued that black wildebeest merely behave as a separate blue wildebeest herd, rather than a trophically distinct species. Further, data from dentine collagen reveal no dietary differences between the two species; thus, the short-term feeding differences inferred from feces, while apparently facilitating coexistence between sympatric populations, do not persist over longer time intervals.

Morphological adaptations to diet are also similar across the two species, not only in terms of premaxillary width reported here, but also in other dental dimensions related to feeding style such as hypsodonty (Janis 1988). Similarities in premaxillary width invoke similar feeding styles in terms of diet selectivity (Owen-Smith 1982; Janis and Ehrhardt 1988; Solounias and Moelleken 1993), with neither species appearing to have the particularly more selective feeding behavior. This compliments the result that fecal %N, and therefore the nutritional value of the diet (crude protein content) of blue and black wildebeest, is similar. The lack of difference in degree of food selection is somewhat surprising given the difference in body size of the two species. Reductions in body size have already been documented as a feature of divergence of black from the blue wildebeest lineage (Brink 1993). One might have expected smaller-bodied black wildebeest to require a more nutritive food base in order to maintain higher metabolic rates (Demment and Van Soest 1985). It seems that, in spite of decreases in body size, black wildebeest have retained blue wildebeest-like adaptations to nutritional ecology and, therefore, continue to function similarly to blue wildebeest in terms of feeding style.

Interspecific competition can therefore be ruled out as a decisive factor underlying divergence of black from the blue wildebeest lineage. One must therefore look to alternate mechanisms, and one possibility that becomes immediately obvious is that habitat changes in the Middle–Late Pleistocene provided the trigger for black wildebeest speciation (Brink 2004b). In particular, progressive bush clearing and increased openness of grasslands in the central interior of South Africa may have facilitated the evolution of early black wildebeest in what is today the only habitat type inhabited by this species (Brink et al. 1999). Indeed, modern and fossil forms of black wildebeest appear to be tied to open grassland habitats because of visibility requirements of their territorial breeding system, rather than because of any trophic or dietary requirements (Brink et al. 1999). More generalist blue wildebeest would have persisted in time through adaptive habitat tolerance and diet flexibility (cf. Vrba 1992; Hernandez Fernandez and Vrba 2005). The two species would have been able to live sympatrically in some areas by switching feeding niches over short time scales.

We have demonstrated that stable isotope data is a suitable tool for comparing trophic behaviors across closely-related, ecologically similar species. In the case of blue and black wildebeest, isotope data do not separate between the two species, but they do conform to the more generalist behavior expected for the former. This technique is also able to detect subtle differences in diet between family groups and/or herds, even within one fairly small reserve (~7,000 ha). However, our fecal data are limited to only three herds and within only one season. Data from dentine collagen suggest that patterns observed in feces do not persist over the long-term; thus, one should expect different trends in feces over multiple time scales. For example, in other months or seasons, black wildebeest may be found to consume more C_3 vegetation than blue wildebeest and different herds within both species may show dietary distinctions. Current findings will benefit from future studies using data for multiple seasons and/or years and from reserves in which several herds of both species occur. Stable isotope ecology can also provide similar information about the diets of fossil fauna (e.g., Lee-Thorp et al. 1989; Cerling et al. 2005). Hence, it will

be interesting to examine stable isotope patterns among fossils of wildebeest to determine whether the two lineages have always occupied the same trophic niche and thereby confirm, refine, or reject the evolutionary hypotheses presented here.

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